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ICHTHYOSAURS OF THE BRITISH MIDDLE AND UPPER JURASSIC

BENJAMIN C. MOON & ANGELA M. KIRTON

PART 1, *OPHTHALMOSAURUS*

Pages 1–XXX; Plates 1–30

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ABSTRACT

The ichthyosaur material of the British Middle and Upper Jurassic referable to *Ophthalmosaurus icenicus* (Ichthyosauria: Ophthalmosauridae) is revisited and re-described; this is the most completely known post-Liassic British ichthyosaur. Much of this material derives from the Callovian Oxford Clay Formation, particularly from the Peterborough Area of Cambridgeshire, UK, deposited in the Leeds Collections. Pre-Callovian ichthyosaur remains are infrequent, incomplete, and non-diagnostic. Material referred to *Ophthalmosaurus icenicus* shows high variability in the extent of ossification. Based on examination of the type and referred material, *Ophthalmosaurus monocharactus,* and *Ophthalmosaurus pleydelli* are rejected as junior subjective synonyms of *Ophthalmosaurus icenicus* due to a lack of diagnostic characters and pathology of specimens. *Ichthyosaurus megalodeirus* is rejected as a *nomen nudum* and the type material is referred to *Ophthalmosaurus icenicus*. *Ophthalmosaurus icenicus* is considered a separate species from *Ophthalmosaurus natans* based on several autapomorphies, but requires re-evaluation of the material.

Les ichtyosaures du jurassique moyen et supérieur britannique. 1ère Partie. *Ophthalmosaurus*

RÉSUMÉ

Le matériel d’ichtyosaure du jurassique moyen et supérieur britannique attribuable à *Ophthalmosaurus icenicus* (Ichthyosauria : Ophthalmosauridae) est révisé et re-décrit ; c’est l’ichtyosaure post-liassique britannique le plus complet connu. La plus grande partie du matériel provient de la formation Oxford Clay (Callovien), et particulièrement de la région de Peterborough dans le Cambridgeshire, Royaume-Uni, et est entreposé dans les collections de Leeds. Les restes d’ichtyosaures pré-calloviens sont peu fréquents, incomplets, et non diagnostiques. Le matériel attribué à *Ophthalmosaurus icenicus* montre que l’extension de l’ossification est très variable. L’examen du matériel type permet de rejeter *Ophthalmosaurus monocharactus*, et *Ophthalmosaurus pleydelli* comme synonymes subjectifs plus récents de *Ophthalmosaurus icenicus*, basé sur un manque de caractères diagnostiques et de pathologie des spécimens. *Ichthyosaurus megalodeirus* est rejeté comme *nomen nudum* et le matériel type est attribué à *Ophthalmosaurus icenicus*. *Ophthalmosaurus icenicus* est considéré une espèce séparée de *Ophthalmosaurus natans* basé sur plusieurs autapomorphies, cependant, une révision du matériel est nécessaire. [Translation by Yves Candela.]

~~TITLE IN GERMAN~~Ichthyosaurier des britischen Mittel- und Oberjura. Erster Teil: *Ophthalmosaurus*

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ZUSAMMENFASSUNG

In dieser Arbeit werden die Funde von Ichthyosauriern des britischen Mittel- und Oberjura, welche *Ophthalmosaurus icenicus* (Ichthyosaurier: Ophthalmosaurus) zuzuordnen sind, überarbeitet und neu beschrieben; hierbei handelt es sich um den vollständigsten bekannten britischen Ichthyosaurier des Postlias. Ein Großteil dieses Materials stammt aus der Callovium Oxford Tonformation, insbesondere aus der Umgebung von Peterborough in Cambridgeshire, Großbritannien, und ist Bestandteil der Leeds-Sammlungen. Vorhandene Funde von Ichthyosauriern des Prächallovium sind selten, unvollständig und nicht diagnostisch. Das Verknöcherungsausmaß der als *Ophthalmosaurus icenicus* bezeichneten Exemplare weist eine hohe Variabilität auf. Basierend auf der Untersuchung des Typus und der zugeordneten Funde werden *Ophthalmosaurus monocharactus* und *Ophthalmosaurus Pleydell* aufgrund des Mangels an diagnostischen Merkmalen, sowie der Pathologie der Exemplare als jüngere subjektive

Synonyme für *Ophthalmosaurus icenicus* abgelehnt. *Ichthyosaurus megalodeirus* wird als Nomen nudum abgelehnt, und die Funde des Typus werden als *Ophthalmosaurus icenicus* bezeichnet. Aufgrund mehrerer Autapomorphien wird *Ophthalmosaurus icenicus* einer anderen Art als *Ophthalmosaurus natans* zugeordnet; allerdings erfordert dies eine erneute Bewertung der Funde. [Translation by David Schlaphorst.]

Ихтиозавры среднего и верхнего британского юрского периода. Часть первая: *Ophthalmosaurus* ~~TITLE IN RUSSIAN~~

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АБСТРАКТ

Ихтиозавровые материалы среднего и верхнего британского юрского периода, относящие *Ophthalmosaurus icenicus* (Ichthyosauria: Ophthalmosauridae) возвращаются к рассмотрению и снова описывается; это – наиболее полно известный британский динозавр с отдела лейас. Большая часть таких материалы, которая находится в Лидских коллекциях, происходит из келловейского оксфордского глинообразования и особенно из района Петерборо в Кембриджшире, в Великобританий. Докелловейские останки ихтиозавров являются редкими, неполными, и недиагностическими. Материалы, относящие *Ophthalmosaurus icenicus* проявляют высокую ступень изменчивости насчёт степени оссификации. На основе изучении типа и относящих материалов, *Ophthalmosaurus monocharactus* и *Ophthalmosaurus pleydelli* отклоняются как младшие субъективные синонимы *Ophthalmosaurus icenicus* из-за недостатка

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диагностических характеров и патологии экземпляров. *Ichthyosaurus megalodeirus* отклоняется в качестве nomen nudum и материалы относятся к *Ophthalmosaurus icenicus*. *Ophthalmosaurus icenicus* считается как отдельный вид от *Ophthalmosaurus natans* на основе несколько аутапоморфий, но дополнительная оценка материалов нужна. [Translation by Anastasia Reynolds.]

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ICHTHYOSAURS OF THE BRITISH MIDDLE AND UPPER JURASSIC. PART 1. *OPHTHALMOSAURUS*

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INTRODUCTION

Ichthyosaur specimens are, relatively speaking, not uncommon in the Middle and Upper Jurassic of the UK. Indeed, in some horizons they may form the majority of large vertebrate remains found. Despite this, these later ichthyosaurs have often been sidelined because of the greater attention paid to the more spectacular Lias Group fossils found so abundantly along the Dorset and Yorkshire coasts. Continued and repeated transgressions through the Middle Jurassic (Aalenian–Bathonian; Hallam 2001) covered much of southern England with shallow but productive seas by the late Middle and early Late Jurassic (Callovian–Kimmeridgian), which supported a complex food web, with ichthyosaurs dominating the upper tiers (Bradshaw *et al*. 1992; Martill *et al*. 1994; Wilkinson *et al*. 2008). These seas are represented by the two great clay formations (Oxford Clay and Kimmeridge Clay formations) that dominate the later part of the Jurassic in Britain, and extend to north-western Europe. The frequency with which ichthyosaur fossils have been, and are still, uncovered, and their occasional completeness, makes these formations important sources of ichthyosaur remains; the relative scarcity of adequate descriptions belies this richness and diversity of specimens. The ages of these ichthyosaur-bearing formations, between the comparatively well-known ichthyosaurs of the Lower Jurassic and the Lower Cretaceous, makes this an important transitional episode between the two groups. During this time, Ophthalmosauridae originated and diversified, leading to the separation of the subclades Ophthalmosaurinae and Platypterygiinae (Fischer *et al*. 2013). The palaeogeographical position of the British Isles, along a seaway that joined the Tethyan and Boreal marine realms, makes this an important junction between those two disparate ichthyosaur faunas (Bradshaw *et al*. 1992).

The amount of material, particularly incomplete specimens, has caused differences in opinions on the taxonomy of these ichthyosaurs (e.g. Lydekker 1888; Huene 1922b; McGowan 1976). Middle and Upper Jurassic ichthyosaurs suffer especially from the number of taxa based upon single and short series of vertebral centra (Owen 1840; Phillips 1871), which essentially do not change form between the Lower Jurassic and Cretaceous. This monograph aims to resolve the taxonomy and affinities of British Middle and Upper Jurassic ichthyosaurs by reappraising and re-describing the available material within a modern, systematic framework. It is based upon the unpublished, although ubiquitous, Ph.D. thesis of Dr Angela Kirton (1983), who has graciously passed on her text and illustrations. However, all the material has been re-examined by BCM and full descriptions written anew, which form the main part of this monograph. With the most available material, *Ophthalmosaurus icenicus* Seeley, 1874b (Text-fig. 1) is described first in detail. *Brachypterygius extremus* (Boulenger, 1904), *Nannopterygius enthekiodon* (Hulke, 1871), and *Macropterygius* sp. are also described more briefly (see Part 2~~see Taxa valida in Systematic Palaeontology below~~), and these four species are compared to other ichthyosaur taxa with a focus on recently identified phylogenetic characters (see ~~see~~ Osteological Comparisons in Part 2~~Osteological Comparisons below~~). Invalid British Middle and Upper Jurassic taxa are listed with discussion (see Taxa invalida in Part 2~~Systematic Palaeontology below~~). Brief discussion is made on the variation and taxonomic relations of *Ophthalmosaurus icenicus*, and the palaeobiogeography of Middle and Upper Jurassic ichthyosaurs.

ABBREVIATIONS

ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; BRSUG, School of Earth Sciences, University of Bristol, Bristol, UK; BUCCM, Buckinghamshire County Museum, Aylesbury, UK; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, UK; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CRYNH, Croydon Natural History & Scientific Society, Croydon, UK; DORCM, Dorset County Museum, Dorchester, UK; GLAHM, Hunterian Museum, University of Glasgow, Glasgow, UK; GPIT, Institut und Museum für Geologie und Paläontologie der Universität, Tübingen, Germany; LEICT, New Walk Museum, Leicester, UK; NEWHM, Great North Museum: Hancock, Newcastle-upon-Tyne, UK; NHMUK, Natural History Museum, London, UK; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland; OUMNH, University Museum of Natural History, Oxford, UK; PETMG, City Museum and Gallery, Peterborough, UK; SESNE, Société d'Étude des Sciences Naturelles d’Elbeuf; SM, Schwegler Museum, Langenaltheim, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SOTUG, University of Southampton Geology Collections, University of Southampton, Southampton, UK; WESTM, Weston-super-Mare Museum, Weston-super-Mare, UK.

HISTORY OF RESEARCH

Although the first ichthyosaur remains to be recognized as belonging to a separate, extinct group were not found until 1811 by Joseph and Mary Anning (Torrens 1995), ichthyosaur fossils had been found and published beforehand. Perhaps the earliest representations were by Lhwyd (1699, pp. 78, 83, pls 17–19 (*pars*)), which show a proximal scapula and humerus, identified as *Solearia*, and several vertebrae, identified as *Ichthyospondyli*. Home's (1814, 1816, 1818, 1819, 1820) descriptions of what is now *Temnodontosaurus platyodon* (Conybeare, 1822) allowed for these isolated and disparate specimens to be correctly identified, but up to then all British ichthyosaurian remains had come from the Lower Jurassic Lias Group of Dorset. Materials from the Middle and Upper Jurassic were noted by De la Beche & Conybeare (1821, p. 580), primarily from the Kimmeridge Clay Formation at Kimmeridge, Dorset, and Shotover, Oxfordshire, but these were too fragmentary to be described (Conybeare 1822). Owen (1840, p. 124) described and named the first Upper Jurassic specimens, erecting *Ichthyosaurus thyreospondylus* Owen, 1840 and *Ichthyosaurus trigonus* Owen, 1840 on the basis of vertebrae from the Kimmeridge Clay Formation (see Taxa invalida in Part 2 ~~below~~).

Seeley (1869) catalogued specimens in the Woodwardian (now Sedgwick) Museum, Cambridge, including several specimens from the Middle and Upper Jurassic. Again, much of this comprised isolated remains, but several specimens were assigned by Seeley to new taxa: *Ichthyosaurus chalarodeirus* Seeley, 1869, *Ichthyosaurus hygrodeirus* Seeley, 1869 and *Ichthyosaurus megalodeirus* Seeley, 1869 (see Taxa invalida in Part 2

~~below~~). Specimens collected by Mr J. C. Mansel-Pleydell from the Kimmeridge Clay of Kimmeridge Bay were described by Hulke (1870, 1871, 1872), and these included the holotype of *Ichthyosaurus enthekiodon* Hulke, 1871. Phillips' (1871) account of the geology of Oxfordshire includes reference to several ichthyosaurian specimens from the Middle Jurassic Stonesfield Slate (= Stonesfield Member, see Stratigraphy below), Middle–Upper Jurassic Oxford Clay (including those collected by Mr Charles Leeds) and Upper Jurassic Kimmeridge Clay formations, and he erected several taxa (see Taxa invalida in Part 2 ~~below~~). Lydekker (1888) reviewed many of these taxa, and found most to be uncertain and based upon incomplete remains. Despite completing several monographs of Mesozoic reptiles (e.g. Owen 1869, 1881), Owen did not cover the ichthyosaurs of the Middle and Upper Jurassic, aside from a brief mention of Middle Jurassic remains (*Ichthyosaurus brachyspondylus* Owen, 1881) from Russia (Owen 1881, p. 127), and figuring vertebrae from the Kimmeridge Clay Formation (NHMUK 46473e, see material of *Nannopterygius enthekiodon* below; Owen 1881, pl. 22, *fide* Lydekker 1889, pp. 33–34). Lydekker (1889) catalogued specimens in the then British Museum (Natural History), including several he referred to *Ophthalmosaurus icenicus* and *Ichthyosaurus enthekiodon*. He later added to this, and further named *Ophthalmosaurus pleydelli* Lydekker, 1890 from the Kimmeridge Clay Formation of Dorset; Mansel-Pleydell (1890) described this specimen more fully.

From 1867, Mr Charles E. Leeds, later joined, and then succeeded, by his brother, Mr Alfred N. Leeds, began collecting from the brick pits in the Oxford Clay Formation around Peterborough. These proved to be prolific in vertebrate remains, ichthyosaurs being particularly common. Examination of the collection by Seeley (1874b) led to the identification of a new genus and species of ichthyosaur, *Ophthalmosaurus icenicus*, distinguished on the form of its pectoral girdle and forelimb. The efforts of the Leeds brothers in collecting material led Woodward & Sherborn (1890, p. xv) to call the collection “unrivalled”. Acquaintance with Dr Henry Woodward, then Keeper of Geology at the then British Museum (Natural History), led to the sale of the ‘first’ Leeds Collection to the museum between 1890 and 1893 (Leeds 1956); several subsequent purchases were made up to 1920. Other parts of the collection have been distributed to GLAHM, GPIT, LEICT, and PETMG, among others. The collection includes around 50 species of vertebrates, as well as arthropods, molluscs, and brachiopods. Andrews (1910, 1913) completed an extended description of the marine reptiles from this collection (ichthyosaurians, crocodilians and plesiosaurians), identifying one ichthyosaur taxon: *Ophthalmosaurus icenicus*. This species later became one of the prize display specimens in the NHMUK (Andrews 1915), and is still found in the main entrance foyer (Text-fig. 1). The Leeds Collection was an important resource in the revision of the stratigraphy of the Oxford Clay Formation (Cox *et al*. 1992). This, along with further excavations, formed the basis of Martill’s (1985, 1986, 1987) stratigraphic and taphonomic study of vertebrates from the Peterborough Member. He identified a particular concentration of vertebrate material in this member, relative to the two above, and that more articulated remains are largely found in two specific beds (see Oxford Clay Formation in Stratigraphy below).

Following the description of *Ophthalmosaurus icenicus*, and the discovery of *Baptanodon* Marsh, 1880b (= *Sauranodon* Marsh, 1879) in the Upper Jurassic of the USA (Marsh 1880a, b), debate over the taxonomic status of these two genera has continued (see Synonymy of *Ophthalmosaurus* and *Baptanodon* in the Discussion of the genus below). Bauer (1898) completed a study of ichthyosaurs in the upper Weißer Jura (approximately Upper Jurassic) and equivalent beds of Europe. Here he provided extensive descriptions of remains referred to *Ichthyosaurus posthumus* Wagner, 1852, but, in taxonomic review, considered most Upper Jurassic ichthyosaur taxa (including *Ophthalmosaurus icenicus*, but excluding *Ichthyosaurus enthekiodon*) to be junior synonyms of *Ichthyosaurus trigonus*. A new specimen, later decided to be from the Kimmeridge Clay Formation, allowed Boulenger (1904) to erect the new species *Ichthyosaurus extremus* Boulenger, 1904, which like *Ophthalmosaurus icenicus* and various species of *Ichthyosaurus* König, 1818, was based upon the structure of the forelimb.

For much of the first half of the Twentieth Century, British ichthyosaur palaeontology was somewhat in the doldrums, particularly as regards work on materials from the Middle and Upper Jurassic. Important contributions were made by Huene (1916, 1922b, *et seq*.), mostly on the taxonomy and relations of Liassic ichthyosaurs, although he did complete a generic revision of *Ichthyosaurus enthekiodon* and *Ichthyosaurus extremus* to *Nannopterygius enthekiodon* and *Brachypterygius extremus* respectively (Huene 1922b, pp. 97–98). *Ophthalmosaurus* Seeley, 1874b was revisited by Appleby (1956, 1958), who re-described portions of the material and catalogued collections derived from the Leeds’ Oxford Clay collection. In particular, Appleby (1956) discussed the variation found in specimens referred to *Ophthalmosaurus*, finding, like Andrews (1910), that there was a continuous range. Appleby did, however, consider the notches on the coracoid to be taxonomically important, and divided *Ophthalmosaurus icenicus* into two species: *Ophthalmosaurus icenicus* and *Ophthalmosaurus monocharactus* Appleby, 1956 (see the Discussion on the taxonomy of *Ophthalmosaurus icenicus* below). Delair (1959) reviewed the ichthyosaurian remains found in Dorset, including the material evidence for each taxon; like those before, he found many taxa were based on insubstantial vertebral remains.

Towards the end of the Twentieth Century, the pace of ichthyosaur research increased. This included the use of new quantitative and phenetic techniques used in both taxonomy and systematics (McGowan 1974a, b, 1976; Johnson 1977, 1979). McGowan (1976) again reprised the taxonomy of Middle and Upper Jurassic ichthyosaurs, finding many to be *nomina dubia* or *nomina nuda*. Kirton (1983) completed a thorough redescription of Oxford Clay and Kimmeridge Clay ichthyosaurs, which has served for many years as the master description, despite remaining unpublished, and she recognized four valid taxa: *Ophthalmosaurus icenicus*, *Nannopterygius enthekiodon*, *Brachypterygius extremus* and *Grendelius mordax* McGowan, 1976. Delair (1985) figured poorly known specimens, including a possible counterpart to the holotype of *Brachypterygius extremus* (WESTM 1978.219) and CRYNH 209, an ophthalmosaurid from the Middle Jurassic Cornbrash Formation.

The most recent work to include Middle and Upper Jurassic ichthyosaurs has focused on placing them in a phylogenetic context. Three whole-group generic-level phylogenies (Motani 1999b; Maisch & Matzke 2000; Sander 2000), following from previous smaller analyses (Mazin 1982; Caldwell 1996), found a monophyletic Ophthalmosauridae within the Parvipelvia that includes all post-Early Jurassic ichthyosaur taxa. As new discoveries have been made, these phylogenies have been extended and re-run, with a special focus on these two clades (e.g. Fernández 2007a; Fischer *et al*. 2014).

Worldwide, ichthyosaur remains from this time are most common from the Upper Jurassic, although diagnostic specimens are known from the Middle Jurassic also. In the Aalenian, this is limited to *Stenopterygius aaleniensis* Maxwell *et al*., 2012b from south-western Germany. Valenciennes (1861a, b) presented two specimens, possibly pertaining to the same individual, from the Kimmeridge Clay Formation of northern France, naming these *Ichthyosaurus cuvieri* Valenciennes, 1861a and *Ichthyosaurus normanniae* Valenciennes, 1861b respectively. Further remains from the Tithonian of northern France were described by Sauvage (1888, 1902a, b, c, d). He recognized five species of ichthyosaur (Sauvage 1902b): *Ichthyosaurus ovalis, Ichthyosaurus thyreospondylus, Ichthyosaurus trigonus, Nannopterygius enthekiodon*, and *Ophthalmosaurus cuvieri* (Valenciennes, 1861a) based mostly on vertebral and limb material, although he also described skull material (Sauvage 1902a). Sauvage (1911) described further material referred to *Nannopterygius enthekiodon, Ophthalmosaurus cuvieri* and *Ichthyosaurus trigonus*, including limb material that Huene (1922b) later used to erect the genus *Macropterygius*. This latter material is similar to that from the Kimmeridge Clay of the UK ~~described below~~ (see ~~the~~ description of *Macropterygius* in Part 2 ~~Systematic palaeontology below~~). More recently, disarticulated remains from the Tithonian of Boulogne, France, were described and referred to *Ophthalmosaurus* sp. (Bardet *et al.* 1997). While referral to species level is not possible based on the material available, this material provides evidence for the presence of *Ophthalmosaurus* in the Tithonian of northern France.

Wagner (1852), Jäger (1856) and Meyer (1864) described remains, including the ichthyosaurian *Ichthyosaurus leptospondylus* Wagner, 1853, from the lithographic limestones (Solnhofen Formation, Kimmeridgian–Tithonian) of Bavaria, southern Germany. Bardet & Fernández (2000) revisited these, re-assigning them to *Aegirosaurus leptospondylus* (Wagner, 1853). Fragmentary ichthyosaur remains were reported from the Upper Jurassic–Lower Cretaceous sequence of west coast USA by Camp (1942) and Camp & Koch (1966). Rusconi (1938, 1940, 1942, 1948) described Middle and Upper Jurassic ichthyosaur remains from Mendoza, Argentina, that are strikingly similar to those from both the UK and the USA. The Neuquén Basin has proven productive for ichthyosaur fossils. Five ichthyosaur taxa are known from this locality: *Chacaicosaurus cayi* Fernández, 1994, *Caypullisaurus bonapartei* Fernández, 1997b, *Mollesaurus periallus* Fernández, 1999, *'Ophthalmosaurus monocharactus'* and *Arthropterygius* sp. (Gasparini 1988; Gasparini *et al*. 2007; Fernández & Maxwell 2012). *Arthropterygius* Maxwell, 2010 has also been found in the Late Jurassic of northern Canada (Russell 1993; Maxwell 2010). Ophthalmosaurids have been found in the Oxfordian of Mexico and Cuba (Fernández & Iturralde-Vinent 2000; Buchy & López-Oliva 2009; Buchy 2010). Fernández (1997a) referred a basioccipital from the Portlandian of Madagascar to *Brachypterygius* sp., which was later assigned to *Brachypterygius extremus* by McGowan & Motani (2003) (see Part 2 ~~below~~), and a partial distal limb to Ichthyosauria *incertae sedis*. The similarity between the above mentioned taxa and worldwide specimens suggest that the connected proto-Atlantic and peri-Tethyan regions experienced strong interchange of ichthyosaur taxa throughout the Middle to Late Jurassic.

Further Upper Jurassic–Lower Cretaceous (Volgian = upper Kimmeridgian–lower Berriasian) ichthyosaurs have been described from Saratov and Volga Oblasts, Russia. Plesiosaur and ichthyosaur remains were mentioned by Zhuravlev (1941, 1943). More complete specimens have since been described briefly, and several taxa erected (Storrs *et al*. 2000), for example, *'Ophthalmosaurus undorensis'* Efimov, 1991, *'Brachypterygius zhuravlevi'* Arkhangelsky, 1998 and *Undorosaurus gorodischensis* Efimov, 1999b. Recent excavations in the Upper Jurassic–Lower Cretaceous of Spitsbergen, Norway, have uncovered several new marine reptile taxa, with ichthyosaurs being the most common representatives (Angst *et al*. 2010; Druckenmiller *et al*. 2012). While these are all Ophthalmosauridae, there is little taxonomic overlap with those from the UK or worldwide. Although a seaway seems to have been present between the Tethys/proto-Atlantic and Boreal oceans at this time, as evidenced by the influx of Boreal ammonite faunas (Hudson & Martill 1994), there is little evidence for interchange between these two ichthyosaur faunas.

STRATIGRAPHY

The Jurassic System in the British Isles is complex and variable, reflecting diverse and rapidly changing palaeoenvironments. A full account is beyond the scope of this monograph, so only those horizons that have produced notable ichthyosaur remains are discussed below (Text-figs 2, 3).

Much of the Middle Jurassic (i.e. Aalenian–Bathonian) has produced few ichthyosaur remains, or marine reptiles more generally. Indeed, worldwide diagnostic ichthyosaur finds from this time are limited to only four taxa: *Mollesaurus periallus*, *Stenopterygius aaleniensis*, *Chacaicosaurus cayi* and *'Stenopterygius grandis'* Cabrera, 1939. Diagnostic specimens are rare; these taxa are represented by few complete fossils (Maxwell *et al*. 2012b; Fernández & Talevi 2014). British ichthyosaur remains from the Aalenian–Bathonian are poorly known. Fragmentary remains referred to *Ichthyosaurus* have been reported from the Inferior Oolite (Aalenian–Bajocian) of Dorset and Gloucestershire, with possible further material from North Yorkshire (Benton & Spencer 1995). Isolated vertebrae have been described from the Stonesfield Member of the Taynton Limestone Formation (= Stonesfield Slate, middle Bathonian: Phillips 1871; Boneham & Wyatt 1993; Benton & Spencer 1995). A partial forelimb (humerus, radius and ulna: CRYNH 209) of an ophthalmosaurid ichthyosaur has been found in the Cornbrash Formation (Bathonian) of Yetminster, Dorset (Delair 1985). It is not until the Callovian, with the exceptional abundance of fossils from the Oxford Clay Formation, that ichthyosaur remains become more abundant and complete.

STONESFIELD MEMBER

The Stonesfield Member (Taynton Limestone Formation, Bathonian, Middle Jurassic: Boneham & Wyatt 1993) of Oxfordshire is one of the few Middle Jurassic horizons that have produced ichthyosaurian remains, but these are limited to a few non-diagnostic vertebral remains. Phillips (1871) mentioned a vertebral centrum (OUMNH J12001) from the Stonesfield Slate and erected *Ichthyosaurus advena* Phillips, 1871 for this (see Taxa invalida in Part 2 ~~below~~). This horizon is a sand-enveloped laminated calcareous grit with oolites and shells (Boneham & Wyatt 1993) interpreted as a result of clastic deposition during a transgressive event. The palaeoenvironment was offshore shallow marine, but with a large terrestrial input, and possible influx and rapid deposition during storm events (Benton & Spencer 1995).

CORNBRASH FORMATION

The Cornbrash Formation straddles the boundary between the Bathonian and Callovian. It is bounded by the Forest Marble, Blisworth Clay or Scalby formations below, and the Kellaways Formation above, extending for up to 10.5 m thick (Cope *et al*. 1980; Page 1989). The limestones of the Cornbrash Formation mark a staged marine transgression, transitioning from nearshore to offshore deposits (Arkell 1933; Bradshaw *et al*. 1992). Vertebrate remains have been recorded, such as dinosaurs and marine crocodilians, but most of these are poorly preserved (Weishampel *et al*. 2005). One ichthyosaur specimen: CRYNH 209, from the Cornbrash of Yetminster is known, representing one of the earliest ophthalmosaurid remains in Europe.

OXFORD CLAY FORMATION

The Oxford Clay Formation spans much of the Callovian (Peterborough and Stewartby members) and the lower part of the Oxfordian (Weymouth Member). It was originally named by Buckland (in Phillips 1818) and redefined as the Oxford Clay Formation by Cox *et al*. (1992). The Oxford Clay Formation outcrops in a north-easterly to south-westerly directed arc across southern and north-eastern England, with well-known localities at Weymouth, Dorset; Oxford, Oxfordshire, and Peterborough, Cambridgeshire, but outcrops extend between Dorset and Yorkshire (Text-fig. 2; Wright

& Cox 2001; Cox & Sumbler 2002). Further outcrop is found in the Inner Hebridean islands of Skye, Eigg and Scalpay (Turner 1966). It is divided into the Peterborough (= Lower Oxford Clay), Stewartby (= Middle Oxford Clay), and Weymouth (= Upper Oxford Clay) members, with a total thickness of up to 185 m (Cox *et al*. 1992).

Peterborough Member. The Peterborough Member is 16.8 m thick at its type section, King's Dyke, near Whittlesey, Cambridgeshire (TL 248967: Hudson & Martill 1994), but may be up to 65 m thick (Cox *et al*. 1992). It is bounded by the sandy Kellaways Formation below, with which it interbeds, also the base of the Oxford Clay Formation, and the Stewartby Member above. The lithology is largely organic-rich (bituminous), fissile shales, interspersed with laterally discontinuous bivalve-dominated shell beds (e.g. *Gryphaea* Lamarck, 1801, *Grammatodon* Meek & Hayden, 1860 and *Meleagrinella* Whitfield, 1885) and sands; Hudson & Martill (1994), after Calloman (1968), separated 55 numbered beds. Its high organic content (over 9%: MacQuaker 1994) allowed more efficient 'self-firing' bricks to be made (Fletton process: Monopolies and Mergers Commission 1976), and led to extensive workings by the London Brick Company in the area around Peterborough, Cambridgeshire. The Peterborough Member spans four ammonite biozones that extend from the uppermost lower Callovian to the lowermost upper Callovian (Text-fig. 3; Martill & Hudson 1991).

Stewartby and Weymouth members. The Stewartby and Weymouth members are lithologically similar and largely distinguished by their faunal compositions (Martill 1986). The base of the Stewartby Member is the top of the highest organic-rich mudstone of the Peterborough Member, and it extends up to 50 m to its upper boundary with the Weymouth Member at the top of the Lamberti Limestone (Cox *et al*. 1992). The type section is located at the London Brick Company's Rookery Pit, Stewartby, Bedfordshire (TL 015409; Cox *et al*. 1992; Berridge *et al*. 1998). This member spans much of the Upper Callovian (Martill & Hudson 1991).

The Weymouth Member is the uppermost member of the Oxford Clay Formation. It is bounded by the top of the Stewartby Member below and it coarsens up into the silty mudstones or siltstones of the West Walton Formation above (Cox *et al*. 1992). This member can be up to 70 m thick. The type sections are located at Ham and Furzy or Jordan cliffs, Weymouth, Dorset (SY 697816). The Weymouth Member spans the Lower Oxfordian (Martill & Hudson 1991).

Both the Stewartby and Weymouth members are more calcareous than the underlying Peterborough Member, comprising blocky and poorly fossiliferous mudstones with a lower organic content and thin calcareous siltstones. The Stewartby Member is more variably silty than the Weymouth Member (Cox *et al*. 1992).

Vertebrate fossils. Vertebrate fossils are most common in the Peterborough Member and are particularly associated with the '*Gryphaea* and Reptile beds' (beds 1–13, 1.2 m), which comprise the lowest part of the Oxford Clay Formation (Martill 1986; Hudson & Martill 1994). This horizon was well exposed by the clay mining in the Peterborough area, and is the source of much of the material in the Leeds Collection (Andrews 1910; Leeds 1956). The nature of the lithology allows the material to be completely removed from the matrix so that specimens can be viewed completely exposed and in three dimensions (Martill 1986). Shallow burial also means that many of the remains have suffered little or no crushing, and so many specimens retain their original, three-dimensional forms (Hudson 1978). Beds 8 and 10 are notable for producing articulated ichthyosaur remains (Martill 1986; Hudson & Martill 1994). More generally, marine reptile remains include the plesiosaurians: *Cryptoclidus* Seeley, 1892, *Liopleurodon* Sauvage, 1873, *Marmornectes* Ketchum & Benson, 2011, *Muraenosaurus* Seeley, 1874a; the thalattosuchians: *Metriorhynchus* Meyer, 1830, *Steneosaurus* Geoffrey, 1825, and *Tyrannoneustes* Young *et al.*, 2013; and the ichthyosaurian *Ophthalmosaurus*, among others (Leeds 1956; Martill 1986; Martill & Hudson 1991). Dinosaurs including the theropod *Eustreptospondylus* Walker, 1964 are also known (Weishampel *et al*. 2005; Sadleir et al. 2008). Partially and fully disarticulated ichthyosaur specimens can be found higher in the Peterborough Member (e.g. BUCCM 1983/1008: Martill 1986, 1987).

Interpretation. The Oxford Clay Formation is interpreted as the result of a transgressive sequence, continuing from the uppermost Bathonian through the Callovian, and forming a shallow epeiric sea in which deep water dysoxic mudstones were deposited across much of Central and East England (Hudson & Martill 1991; Bradshaw *et al*. 1992). Below, the Kellaways Sand Formation interfingers with the Peterborough Member in its lower parts. As the Peterborough Member is comparatively organic-rich, and there is relatively little disturbance of the sediment by benthic organisms, it is likely to have been low in oxygen and with a substrate that was unstable or had a high water content (Hudson & Martill 1991). This ‘soupy substrate’ may have allowed for the prolific and complete preservation seen in this horizon (Martill 1987, 1993). The environment was probably nearshore, based on an apparent influx of terrestrial organic matter and the relative frequency of terrestrial dinosaur remains. Further deepening through the Callovian and into the Oxfordian placed the Stewartby and Weymouth members farther offshore, so reducing the supply of organic material.

CORALLIAN GROUP

The Corallian Group is a complex and highly variable sequence of limestones and sandstones that represent a series of repeated regressions from offshore or nearshore to shore deposits. It is bounded by the Oxford Clay Formation below and the Kimmeridge Clay Formation above, is about 100 m thick, and spans much of the Oxfordian (Cope *et al*. 1980). Important outcrops are in South Dorset, Oxfordshire, and North Yorkshire (Bradshaw *et al*. 1992). Vertebrate remains from the Corallian Group are rare (Benton & Spencer 1995). However, seven specimens have been assigned to ichthyosaurs: OUMNH J50342, J52433–J52435, CAMSM J58841, J10509 and J12051. Most of these isolated or short runs of vertebrae; OUMNH J50342 is a coracoid referred to *Ophthalmosaurus*, but this is not diagnostic. While ichthyosaur remains are certainly present in the Corallian Group, they appear to only have been transient visitors.

KIMMERIDGE CLAY FORMATION

As one of the major source rocks for the North Sea oil industry, the stratigraphy of the Kimmeridge Clay Formation has been intensely studied offshore. Onshore deposits, by virtue of their ease of access and more continuous exposure, have also received a great deal of attention, although with less focus on the vertebrate palaeontology than the

Oxford Clay Formation. The Kimmeridge Clay Formation is closely associated with the Oxford Clay Formation (together they form the major part of the Ancholme Group), and so has a broadly similar outcrop across England, from Dorset to Yorkshire (Text-fig. 2). Further important outcrops that have produced vertebrate remains are found on the Isle of Skye (Arkell 1933). The Kimmeridge Clay Formation is dominated by calcareous and organic-rich mudstones, with frequent oil shales, stone bands and concretion beds (Cope 1967; Cox & Gallois 1981). Its total thickness is over 500 m in parts of South Dorset, the type area (>541 m at Encombe Borehole, SZ 97127831; Barton *et al*. 2011), spanning much of the uppermost Jurassic (see below and Text-fig. 3). It is traditionally divided into two parts after the historic British Lower and Upper Kimmeridgian age (Cope 1967; Cox & Gallois 1981).

The Lower Kimmeridge Clay is bounded by the base of the *Torquirhynchia inconstans* Bed (KC1, after Gallois 2000) below and the base of bed KC36 above (Gallois 2000), spanning the *Pictonia baylei* to *Aulacostephanus autissiodorensis* ammonite biozones. The best exposures of this unit are at Black Head (SY 729818), Kimmeridge Bay (SY 905792), and Ringstead Bay (SY 761814), Dorset. Towards the bottom are several siltstone beds (e.g. Wyke Siltstone, KC5, and Black Head Siltstone, KC8), but the upper portion is mudstone- and oil shale-dominated. The Upper Kimmeridge Clay spans the *Pectinatites elegans* to *Virgatopavlovia fittoni* ammonite biozones, bounded by bed KC35 below and the base of the Massive Bed in the Portland Group above. This portion is completely exposed between Kimmeridge Bay and Chapman’s Pool, Dorset (Gallois 2000; Barton *et al*. 2011). The Upper Kimmeridge Clay is generally more calcareous than the Lower Kimmeridge Clay, forming the distinctive ‘dolomitic ledges’ of Kimmeridge Bay; organic-rich ‘oil shales’ are more common in the middle of the formation (e.g. the ‘Blackstone’, bed KC42).

It is important to note that the International Stage boundary between the Kimmeridgian and Tithonian is near the base of the *Hybonoticeras hybonotum* Ammonite Biozone in the Tethyan domain (Ogg & Hinnov 2012). This is midway through the *Aulacostephanus autissiodorensis* Ammonite Biozone in Britain. Therefore, the uppermost part of the Lower Kimmeridge Clay and the Upper Kimmeridge Clay and Portland Group are Tithonian (Text-fig. 3).

Vertebrate fossils. Vertebrate fossils are found more consistently throughout the Kimmeridge Clay Formation than in the Oxford Clay Formation, but only certain sections have produced abundant remains. The Wyke Siltstone (KC5) has produced some recent striking remains of marine crocodilians and pliosaurs (e.g. Benson *et al*. 2013). Marine reptile finds are also common towards the top of the formation (Taylor & Benton 1986). Notable ichthyosaurian remains include *Nannopterygius enthekiodon*, possibly from one of the *Aulacostephanus* sp. biozones (Lower Kimmeridge Clay; Arkell 1933, p. 451) and *Brachypterygius extremus* from the *Pectinatites wheatleyensis* Ammonite Biozone (Upper Kimmeridge Clay; McGowan 1976). Further remains of terrestrial dinosaurs are not uncommon in the Kimmeridge Clay Formation. The exposures at Westbury, Wiltshire; Ely, Cambridgeshire and Cumnor, Oxfordshire, are also noted for their vertebrate remains (Arkell 1933; Benton & Spencer 1995; Grange *et al*. 1996).

Interpretation. The Kimmeridge Clay Formation is interpreted as a transgressive sequence, overlying the shallower water Corallian Group. The Kimmeridge Clay was deposited in a shallow epeiric sea that covered much of England, Wales and western Scotland (Bradshaw *et al*. 1992). This sea probably did not exceed 50 m depth, as suggested by winnowing and storm beds (Wignall 1994). Dysoxia led to the preservation of organic matter, with palaeoecological studies indicating occasional anoxic conditions (Wignall 1990, 1991); these alternations may indicate climatic control and Milankovitch cyclicity (Barton *et al*. 2011). Higher proportions of epifauna in the top part of the Upper Kimmeridge Clay (*Pectinatites pectinatus* Ammonite Biozone and up) than below suggests a reduction in sedimentation rates and firming of the substrate; below this, the Kimmeridge Clay is more consistently infauna-dominated (Wignall 1990).

PORTLAND AND PURBECK GROUPS

Few ichthyosaurian remains have been found in the Portlandian (≈ upper Tithonian) Portland and Purbeck groups (Delair 1968). Two vertebrae (NHMUK PV R1683 and R1684) from the Portland Oolite and Portlandian of the Isle of Portland, Dorset, and three humeri (OUMNH J1585, J1586 and J1608) from the ‘Portland Rock’ (= Portland Stone Formation) of Swindon, Wiltshire, are known. A partial ichthyosaur skeleton (OUMNH J13795) has been found in the Purbeck Limestone Formation of Swanage, Dorset, but this has since been identified as deriving from the Lower Cretaceous (Delair 1968; Ensom *et al.* 2009). The Portland Group overlies the Kimmeridge Clay Formation on the Isle of Portland, and is itself overlain by the Purbeck Group. Outcrops are extensive in South Dorset (Isle of Portland to Isle of Purbeck) but extend to Wiltshire, Oxfordshire, Buckinghamshire and The Weald (Cope *et al*. 1980). The sequence represents a progressive shallowing and exposure through the Tithonian into the Early Cretaceous. This is shown by the succession of sands and limestones with cherts and oolites that comprise the Portland Sand and Portland Stone formations respectively (Arkell 1933; Barton *et al*. 2011). The lowermost (Jurassic) part of the Purbeck Group (lower Mupe Member) is marginal to emergent, with occasional marine incursions (Barton *et al*. 2011).

MATERIALS AND METHODS

A large number of specimens from several collections were examined in the process of completing the systematic descriptions. These are listed under the relevant headings, and in the Appendix below. Much of this was derived from the Leeds' Collection and other historical collections (see above); more recently available specimens were also included. Dimensions, where given, were taken using plastic callipers to the nearest 0.05 mm (0–140 mm), or tape measure to the nearest millimetre (>140 mm). For each taxon, the material is described; *Brachypterygius extremus* and *Nannopterygius enthekiodon* are compared directly to *Ophthalmosaurus icenicus*, and comparisons of all three taxa to other ichthyosaurs are made separately. Minor preparatory work was carried out on specimen BRSMG Ce 16696 (Text-fig. 38) to expose the left forelimb. This used air pens (sizes 2, 3 and chisel tip) to remove the overburden, and air abrasive (AlO, 45 µm diameter). The preparation exposed the distal portion of the left forelimb in ventral view as well as evidence of remineralized soft tissue preservation. Ichthyosaur occurrence data in the palaeogeographical map (~~Text-fig. 46~~in Part 2) was derived from

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Fossilworks (http://fossilworks.org) and the Palaeobiology Database (http://paleobiodb.org/) in January 2014 (Alroy 2013a, b) with additional subsequent data taken directly from the literature. The palaeogeographical maps (Text-fig. 46 in Part 2) have been simplified from Blakey (2008, 2014).

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SYSTEMATIC PALAEONTOLOGY

TAXA VALIDA

SAUROPSIDA Watson, 1957

DIAPSIDA Osborn, 1903 [Laurin, 1991]

incertae sedis ICHTHYOSAURIA de Blainville, 1835 [Motani, 1999b]

PARVIPELVIA Motani, 1999b

NEOICHTHYOSAURIA Sander, 2000

Remarks. Neoichthyosauria was defined by Sander (2000, p. 22) as the last common ancestor of *Temnodontosaurus platyodon* and *Ichthyosaurus*, and all its descendants, and intended to incorporate all post-Triassic ichthyosaurs. *Dearcmhara shawcrossi* Brusatte *et al.*, 2015 was described from the Bearreraig Sandstone Formation (Toarcian–Bajocian) of the Isle of Skye, United Kingdom, as a neoichthyosaurian. Because of its recent description and uncertain occurrence, it is not included in this systematic palaeontology section, however, comparisons are drawn below (see Osteological comparisons ~~below~~in Part 2).

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THUNNOSAURIA Motani, 1999b

OPHTHALMOSAURIDAE Baur, 1887a [Fischer *et al*., 2011]

Remarks. The clade Ophthalmosauridae (last common ancestor of *Ophthalmosaurus icenicus* and *Arthropterygius chrisorum* (Russell, 1993) and all its descendants, *sensu* Fischer *et al*. 2011) originated in the Middle Jurassic (Fischer *et al*. 2013). The name was originally used by Baur (1887a), but translated as Baptanodontidae in the English version (Baur 1887b). Motani (1999b, p. 484) mistakenly attributed this taxon to Appleby (1956), but renamed it Ophthalmosauria. *Ophthalmosaurus icenicus* and *Brachypterygius extremus* are certainly present within this clade: the definition of Fischer *et al*. (2011, p. 1020) is modified from Motani's (1999b, p. 484) Ophthalmosauria, which these two taxa defined. *Nannopterygius enthekiodon* has not yet been included in a phylogenetic analysis of ichthyosaurs, but was included within Ophthalmosauridae by Motani (1999b, p. 484); this taxon is included in Ophthalmosauridae here also. The assignment of *Nannopterygius enthekiodon* to this clade is discussed below.

Genus OPHTHALMOSAURUS Seeley, 1874b

Type species. Designated by Seeley (1874b, p. 707) as *Ophthalmosaurus icenicus*; described from the Oxford Clay Formation, Peterborough, Cambridgeshire, United Kingdom.

Other species. Currently, *Ophthalmosaurus* (*'Baptanodon'*) *natans* (Marsh, 1879) from the Upper Jurassic of the USA is considered a member of this genus (see synonymy of *Ophthalmosaurus* and *Baptanodon* in the Discussion below); also *Ophthalmosaurus yasykovi* (Efimov, 1999a) from the Upper Jurassic of Russia (see the generic and specific discussions below).

Diagnosis. Moderately large (about 4 m) member of Ophthalmosauridae characterized by: premaxillae and dentaries divergent anteriorly (autapomorphy); small premaxilla-lachrymal contact; maxilla excluded from external naris in lateral view by lachrymal and premaxilla (more extensive exposure in *Athabascasaurus*, *Cryopterygius*, *Platypterygius australis*); narial process on nasal present (absent in *Caypullisaurus*, *Platypterygius*); frontal with small participation in supratemporal fenestra (excluded in *Athabascasaurus*; greater participation in *Platypterygius australis*, *Platypterygius hercynicus*, *Sveltonectes*); squamosal present and triangular (absent in *Platypterygius americanus*, *Platypterygius australis*; square in *Athabascasaurus*); large orbit (>0.2 orbital ratio); paroccipital process slender (shared with *Acamptonectes*); short postorbital region (broader in *Brachypterygius*, *Caypullisaurus*, *Cryopterygius*); basioccipital with broad extracondylar area visible around articular condyle (narrower in *Acamptonectes*, *Athabascasaurus*, *Brachypterygius*, *Platypterygius*); left and right extracondylar areas of the basioccipital separated ventrally by a ridge (continuous in *Acamptonectes*, *Leninia*); stapes contacts supratemporal laterally (shared with *Leninia*); teeth small and strongly ridged (smaller than *Brachypterygius*, *Platypterygius*; weaker ridging in *Maiaspondylus*, *Platypterygius americanus*); ~48 (>44) teeth present in each upper jaw (53 in

Cryopterygius, *Brachypterygius*); anterior teeth located in sockets (autapomorphy); ~42 presacral vertebrae (48–54 in *Platypterygius*; 52 in *Aegirosaurus*, *Caypullisaurus*); ribs with anterior and posterior longitudinal grooves (rounded with single proximal groove in *Acamptonectes*); clavicles expose interclavicle between them at their medial meeting point (autapomorphy); clavicles wrap around and enclose anterior bar of interclavicle (autapomorphy); posterior margin of coracoid rounded (angled transversely in *Nannopterygius*; squared in *Cryopterygius*); humerus with three distal articular facets, anterior facet is the smallest, posterior facet is deflected posteriorly, articulating with pre-axial accessory element, radius and ulna (two distal facets in *Cryopterygius*, *Nannopterygius*; humerus articulates with radius, intermedium and ulna in *Brachypterygius*, *Maiaspondylus*, *Aegirosaurus*; four distal humeral facets in *Platypterygius hercynicus*); forelimb with six digits (more in *Caypullisaurus*, *Platypterygius*); ulna tapers posteriorly with a concave posterior margin in dorsal view (shared with *Acamptonectes*); single pre-axial accessory digit (two in *Platypterygius*, *Caypullisaurus*); forelimb phalanges rounded (polygonal in *Aegirosaurus*, *Brachypterygius*, *Platypterygius*); ischium and pubis fused and plate-like with enclosed obturator foramen (unfused distally in *Cryopterygius*, *Undorosaurus*; obturator foramen lost in *Aegirosaurus*, *Athabascasaurus*, *Platypterygius australis*, *Sveltonectes*); femur with well-developed dorsal and ventral processes (larger in *Platypterygius*); femur with two distal facets (three in *Platypterygius australis*, *Platypterygius hercynicus*); hindlimb phalanges rounded (polygonal in *Platypterygius*).

Etymology. The generic name *Ophthalmosaurus* derives from the Greek *οφθαλμός*: ‘eye’ and *σαύρα*: ‘lizard’, for the relatively and absolutely large orbit.

Discussion. Seeley (1874b) named the new genus *Ophthalmosaurus* from Mr. Charles Leeds’ collection from the Oxford Clay Formation, separating it from *Ichthyosaurus* as the clavicles meet medially in an interdigitating suture and wrap around the anterior of the interclavicle, and naming the type species *Ophthalmosaurus icenicus* (see species discussion below). Marsh (1879) described *Sauranodon natans* Marsh, 1879 for a specimen from the Oxfordian Sundance Formation of the “Rocky-Mountain region” (p. 175) of North America (indicated as Como Bluff, Wyoming, USA, in McGowan & Motani 2003), placing this in the new Order Sauranodonta. Later, Marsh (1880b) realized *Sauranodon* was preoccupied, and suggested the replacement name *Baptanodon*. Marsh (1880a) seemingly misinterpreted the forelimbs that he described as pelvic fins, so that they appeared vastly different from those of other then known ichthyosaurs. There then followed a long-running argument as to whether *Ophthalmosaurus* and *Baptanodon* were generically distinct; this will be discussed further below (see Synonymy of *Ophthalmosaurus* and *Baptanodon* in the Discussion below). Gilmore’s (1902) discovery of teeth in a specimen of *Baptanodon* led him to separate this into the genus *Microdontosaurus* Gilmore, 1902, but this name was withdrawn after teeth were found in the holotype of *Baptanodon* (Gilmore 1903).

Mehl (1927, 1928) erected *Apatodonosaurus* Mehl, 1927 for fragmentary material he described from the Sundance Formation of Wyoming, USA. The forelimb configuration of *Apatodonosaurus* is consistent with *Ophthalmosaurus*, although Mehl

(1928) listed several apparently unique characters; Kirton (1983) attributed this to misinterpretation of the material. Romer (1956), Kirton (1983) and McGowan & Motani (2003) considered *Apatodonosaurus* to be a subjective junior synonym of *Ophthalmosaurus*. Rusconi (1938, 1940) described new materials from the Late Jurassic of Argentina as *Myobradypterygius* Huene, 1927, but later erected the genus *Ancanamunia* Rusconi, 1942 for this material. A more complete description was given by Rusconi (1948), showing features that are consistent with *Ophthalmosaurus*. However, Rusconi (1942) did not figure the material, and inadequate description led Gasparini (1985) to consider *Ancanamunia* a *nomen vanum* (Fernández 2007b). Kirton (1983) suggested that *Ancanamunia* is a subjective junior synonym of *Ophthalmosaurus*, which was corroborated by McGowan & Motani (2003), while Fernández (2007b) only considered material referred to *Ancanamunia mendozana* Rusconi, 1942 to be a junior subjective synonym of *Ophthalmosaurus natans*. Much of the material that Rusconi (1938, 1940, 1942, 1948) described is incomplete and cannot be confidently referred to any taxon, while material referred to *Ichthyosaurus inexpectatus* Rusconi, 1948 has since been suggested to be from the metriorhynchid *Dakosaurus* Quenstedt, 1856 (Vignaud & Gasparini 1996; Fernández 2007b).

More recent discoveries of ichthyosaurs from the Upper Jurassic of Russia provided the basis for several new taxa. Unfortunately, the descriptions and figures of these are often limited, making detailed comparisons difficult, but new efforts are being made to make these fossils available and present revised descriptions. Arkhangelsky (1997) erected *Paraophthalmosaurus* for a new specimen with a semilunate radius and oblique and straight posterior edges on the coracoids. A later reinterpretation of the forelimb material changed this (Arkhangelsky 1998): the semilunate element was formed by fusion of the radiale and an anterior accessory element; what was referred to as the ulna was actually the radius; and the true ulna was not present. Arkhangelsky's (1998) emended diagnosis for *Paraophthalmosaurus* is consistent with *Ophthalmosaurus*; the two were synonymized by Maisch & Matzke (2000, p. 78) and McGowan & Motani (2003, p. 110). However, recent cladistic analysis has found that *Paraophthalmosaurus* forms a clade separate from *Ophthalmosaurus,* although the resolution within Ophthalmosaurinae is low (Arkhangelsky & Zverkov 2014); this incorporates *'Yasykovia' kabanovi* Efimov, 1999a, which is revised to *Paraophthalmosaurus kabanovi*. The pectoral girdle in *Paraophthalmosaurus kabanovi* (Efimov 1999a, figs 4ж, з) has a bipartite scapula-coracoid articulation, divided by a coracoidal fenestra. This we have not seen in examined British material referred to *Ophthalmosaurus*, although Johnson (1979) and Maisch & Matzke (2000, p. 89) state it is found in other well ossified 'stenopterygiid' and ophthalmosaurid taxa, as in *'Stenopterygius megalorhinus'* Huene, 1922b (= *Stenopterygius triscissus* (Quenstedt, 1858); Huene 1949; Maisch 2008) and *'Ophthalmosaurus monocharactus'* (Gasparini 1988). Also, the femur of *Paraophthalmosaurus kabanovi* has three distal facets (if this is correctly identified: Efimov 1999a, fig. 5г), which is different to *Ophthalmosaurus (see Osteological comparisons below)*. Pending revision of the *Paraophthalmosaurus saveljeviensis* type material, we retain *Paraophthalmosaurus* as valid.

Khudiakovia Arkhangelsky, 1999 was erected for a humerus, radius, ulna, radiale, and intermedium, with impressions of surrounding elements. This specimen exhibits the features of *Ophthalmosaurus* and was also synonymized into that genus by Maisch & Matzke (2000, p. 90) and McGowan & Motani (2003, p. 110).

Efimov (1999a) erected four species in the genus *Yasykovia* Efimov, 1999a, which has clear morphological affinities with *Ophthalmosaurus* (e.g. three distal humeral facets for the pre-axial accessory element, radius, and ulna respectively), yet did not compare his new materials with that genus in the original notice. The differences between the species are small, and Maisch & Matzke (2000) attributed these to ontogeny or intraspecific variation, recognizing only one species: *Yasykovia yasykovi* Efimov, 1999a. The figured teeth (Efimov 1999a, fig. 2) have more slender crowns and more bulbous roots than in *Ophthalmosaurus* (see *Dentition* below), but are otherwise similar. Most of the pectoral girdles figured (Efimov 1999a, fig. 4) are like those found in *Ophthalmosaurus*. *Yasykovia* was not found to be sufficiently different from *Ophthalmosaurus* to require its own generic identity by both Maisch & Matzke (2000, pp. 78, 89) and McGowan & Motani (2003, p. 110) and was synonymized. This view will be retained here, excluding the *Paraophthalmosaurus kabanovi* material, although detailed reappraisal of the material is necessary. Further discussion on specific synonymy is included below.

Traditionally, *Ophthalmosaurus* was primarily diagnosed on the configuration of the pectoral girdle and the three distal humeral facets, articulating with a pre-axial accessory element, the radius and ulna respectively (see below and Seeley 1874b). The discovery of *Ophthalmosaurus natans* and more recent taxa, such as *Undorosaurus gorodischensis* and *Arthropterygius chrisorum*, have reduced the latter character’s utility to family level, instead being characteristic of several ophthalmosaurid ichthyosaur genera, but several other diagnostic features may be used in addition (see Diagnosis above). Maisch & Matzke (2000) and Maisch (2010) referred both *Undorosaurus* Efimov, 1999b and *Mollesaurus* Fernández, 1999 to *Ophthalmosaurus*, arguing that the purported differences were insubstantial, arising from poor preservation or individual variation. McGowan & Motani (2003) agreed that all three taxa are very similar, with few distinguishing features, but retained their generic separation until more complete material was available. The specimen described by Gasparini (1988) as *Ophthalmosaurus monocharactus* is unlikely to be *Ophthalmosaurus* based on characters of the forelimb: four distal facets (the posterior facet articulates with a posterior accessory element) and forelimb elements more angular and closely packed. Maisch & Matzke (2000) allied this to similar German material, as suggested by Gasparini (1988), which has since been described as *Aegirosaurus* (Bardet & Fernández 2000). A similar humerus, with four distal facets, from the Kimmeridge Clay Formation of Kimmeridge, UK, can be seen in the private collection of Mr Steve Etches. Efforts are underway to bring this material into availability.

Ophthalmosaurus icenicus Seeley, 1874b   Pls 1–30; Text-figs 1, 4–36

v .	*1869*	*Ichthyosaurus megalodeirus* Seeley; p. 111 [*nom. nud.*] [Oxford Clay Formation (Callovian Stage), Peterborough, UK].
v*	1874b	*Ophthalmosaurus icenicus* Seeley; p. 707, pls 45, 46 [Oxford Clay Formation, Peterborough, UK].
	1888	*Ophthalmosaurus icenicus* Seeley; Lydekker, p. 310 [Oxford Clay and Kimmeridge Clay formations, UK].
v	1889	*Ophthalmosaurus icenicus* Seeley; Lydekker, p. 9, fig. 7.

v	1890	*Ophthalmosaurus icenicus* Seeley; Lydekker, p. 267, fig. 62.
v .	1890	*Ophthalmosaurus pleydelli* Lydekker, p. 268, figs 63, 64 [Kimmeridge Clay Formation (Kimmeridgian Stage), Gillingham, Dorset, UK].
v	1890	*Ophthalmosaurus icenicus* Seeley; Mansell-Pleydell, fig. 2.
v .	1890	*Ophthalmosaurus pleydelli* Lydekker; Mansell-Pleydell, p. 14, figs 3, 4.
?	1898	*Ichthyosaurus trigonus* Owen; Bauer, p. 325 [*nom*. *dub*.] [*pars*.].
	1905	*Ophthalmosaurus icenicus* Seeley; Gilmore, p. 125.
v	1907	*Ophthalmosaurus icenicus* Seeley; Andrews.
v	*1907*	*Ophthalmosaurus icenicus* Seeley; Gilmore, fig. 2 [cop. Seeley 1874b].
	1908	*Ophthalmosaurus icenicus* Seeley; Seeley.
v	1910	*Ophthalmosaurus icenicus* Seeley; Andrews, p. 1, figs 1–42, pls 1, 2.
v	*1915*	*Ophthalmosaurus icenicus* Seeley; Andrews, pl. 5.
	1922b	*Ophthalmosaurus icenicus* Seeley; Huene, p. 89, pl. 19, fig. 10 [cop. Andrews 1910].
	1934	*Ophthalmosaurus icenicus* Seeley; Kuhn, p. 36.
.	*1934*	*Ophthalmosaurus pleydelli* Lydekker; Kuhn, p. 41.
non	*1934*	*Baptanodon* (Marsh); Kuhn, p. 36.
	1946	*Ophtalmosaurus* [*sic*.] *icenicus* Seeley; Kuhn, p. 78 [*lapsus calami*].
v	1956	*Ophthalmosaurus icenicus* Seeley; Appleby, p. 444.
v .	1956	*Ophthalmosaurus monocharactus* Appleby, p. 444.
v	1958	*Ophthalmosaurus icenicus* Seeley; Appleby, pp. 8, 10, pl. 6.
v .	1958	*Ophthalmosaurus monocharactus* Appleby; pp. 9–10, 35, pl. 1.
v	1958	*Ophthalmosaurus* sp.; Appleby, pp. 13, 39, pls 2–5, 7.
v	1976	*Ophthalmosaurus icenicus* Seeley; McGowan, figs 2D, E.
v	1979	*Ophthalmosaurus icenicus* Seeley; Appleby, p. 931, fig. 10D.
	1982	*Ophtalmosaurus* [*sic*.] *icenicus* Sealey [*sic*.]; Mazin, p. 97.
.	*1982*	*Ophtalmosaurus* [*sic*.] *monocharactus* Appleby; Mazin, p. 97 [authority given as Appleby, 1965 (*sic*.)].
[v	1983	*Ophthalmosaurus icenicus* Seeley; Kirton, p. 11, figs 1–36, pls 1–3.]

	1987	*Ophthalmosaurus* sp.; Martill, p. 543, fig. 1 [Lower Oxford Clay Formation, Caldecotte Lake, Milton Keynes].
	1987	*Ophthalmosaurus icenicus* Seeley; Massare, p. 137, fig. 6B.
non	1988	*Ophthalmosaurus monocharactus* Appleby; Gasparini [Vaca Muerta Formation, Cantera El Ministerio, Argentina (38° 49’ S, 70° 12’ E)].
	1991	*Ophtalmosaurus* [*sic*.] *icenicus* Seeley; Bardet *et al*., p. 898.
	1991	*Ophthalmosaurus icenicus* Seeley; Martill, p. 229, fig. 10.5A.
.	*1991*	*Ophthalmosaurus monocharactus* Appleby; Martill, p. 229, fig. 10.5B.
	1991	*Ophthalmosaurus undorensis* Efimov; p. 112, figs 1, 2 [*Aulacostephanus mutabilis* Zone, Volgian Stage, Undory, Russian Federation].
v	1997a	*Ophthalmosaurus* sp.; Maisch, figs 2–5.
v	1998	*Ophthalmosaurus icenicus* Seeley; Maisch, fig. 1.
v	1999	*Khudiakovia calloviensis* Arkhangelsky; p. 89, fig. 1 [Lower Volgian Stage, Saratov Region, Russian Federation].
?	1999a	*Yasykovia yasykovi* Efimov; p. 93, figs 1, 2А, 4А, Б, 5А, Б [*Craspedites subdites* Zone, Volgian Stage, Ulyanovsk Region, Russian Federation].
?	1999a	*Yasykovia mittai* Efimov; p. 97, fig. 4Д, Е [*Kachpurites fulgens* Zone, Volgian Stage, Podmoskaya, Khorlovo, Russian Federation].
?	1999a	*Yasykovia sumini* Efimov; p. 98, fig. 4В, Г, 6А, В [*Kachpurites fulgens* Zone, Volgian Stage, Podmoskaya, Khorlovo, Russian Federation].
non	1999a	*Yasykovia kabanovi* Efimov; p. 98, fig. 2В, Г, 3Ж, З, 4Ж, З, 5В, Г, 6Г, Е [*Epivirgatites nikitini* Zone, Volgian Stage, Gorodishchi, Ulyanovsk Oblast, Russian Federation].
v	1999a	*Ophthalmosaurus icenicus* Seeley; Motani, p. 39, fig. 7A [mod. Kirton 1983].
v	1999b	*Ophthalmosaurus icenicus* Seeley; Motani, p. 485, figs 2G, 3G [mod. Kirton 1983], 5N, 6L.
v	2000	*Ophthalmosaurus icenicus* Seeley; Sander, p. 19, figs 2F, 3D, 4F, 13.
v	2000	*Ophthalmosaurus icenicus* Seeley; Maisch and Matzke, p. 78, figs 8, 12, 13, 19C–F, 23, 28 (all *pars*.).

2000 *Khudiakovia calloviensis* Arkhangelsky; Maisch and Matzke, p. 90.
v 2003 *Ophthalmosaurus icenicus* Seeley; McGowan & Motani, p. 113, fig. 93 [cop. Motani 1999c, fig. 2G], pls 16, 17 [*pars*].
2006 *Ophthalmosaurus icenicus* Seeley; Massare *et al*., figs 3B–5.
v 2008 *Ophthalmosaurus icenicus* Seeley; Araújo *et al*., figs 2, 7, 8.
2010 *Ophthalmosaurus* cf. *icenicus* Seeley; Buchy p. 149, figs 2–4 [La Caja Formation, early Tithonian, Sierra El Jabalí, Mexico].
v 2012 *Ophthalmosaurus icenicus* Seeley; Fischer *et al*., figs 5H, I, 6H.
v 2012c *Ophthalmosaurus icenicus* Seeley; Maxwell *et al*., p. 1209, fig. 1P–T.
2015 *Ophthalmosaurus icenicus* Seeley; Motani *et al.*, fig. 2H.

Type material. Holotype: NHMUK PV R2133, a partial skeleton, designated by Seeley (1874b, p. 699, pls 15, 16, figs 1, 2), from the Oxford Clay Formation of Peterborough, UK. Paratype: NHMUK PV R2134, a left forelimb, figured by Seeley (1874b, pl. 46, fig. 3), from the type locality and horizon. See the specific discussion below for allocation of these type specimens.

Referred material. Diagnostic material includes GLAHM V1070, V1611, V1612, V1885, V1916, V1920; NHMUK PV R2132, R2138, R2149, R2160, R2180, R2181–R2182, R2185, R3013, R3535, R3702, R3893, R4753, R8737, R10031, R10032; PETMG R220, R222, R335. All of these are from the Oxford Clay Formation of Peterborough and the surrounding area. Additional British material referable to *Ophthalmosaurus icenicus* is listed in Table 1.

Diagnosis. Maxilla excluded from external naris by lachrymal and premaxilla (included in *Ophthalmosaurus natans*, *Ophthalmosaurus yasykovi*); prefrontal contacts external naris but this contact is small (does not contact in *Ophthalmosaurus natans*); jugal broad and fan-like anteriorly (tapering in *Ophthalmosaurus natans*, *Ophthalmosaurus yasykovi*); exoccipitals form more of the dorsoventral margin of the *foramen magnum* than the supraoccipital (reversed in *Ophthalmosaurus natans*); teeth strongly ridged (may be smoother in *Ophthalmosaurus natans*); tooth bases slender and sub-quadrangular (autapomorphy; rounder in *Ophthalmosaurus natans*; quadrangular and bulbous in *Brachypterygius, Maiaspondylus, Platypterygius, Undorosaurus*); no fusion between atlas-axis neural spines (sometimes present in *Ophthalmosaurus natans*); clavicles meet medially in unfused interdigitating suture (autapomorphy; fused in *Ophthalmosaurus natans*); coracoids rounded posteriorly (elongate in *Ophthalmosaurus yasykovi*); scapula glenoid contribution larger than coracoid contribution (smaller in *Ophthalmosaurus natans*); deltopectoral crest as high as the dorsal trochanter (smaller in *Ophthalmosaurus natans*, *Ophthalmosaurus yasykovi*).

Etymology. The specific name *icenicus*, from the Latin ‘of the Iceni’, refers to a tribe that occupied the type area before and during the Roman conquest of Britain.

Occurrence. Diagnostic material is known from the Callovian–Tithonian of southern England, France, and Mexico.

Discussion. Seeley (1874b) described material from the Oxford Clay Formation of Peterborough, in the collection of Mr Charles Leeds as *Ophthalmosaurus icenicus*. There, Seeley did not mention his earlier description of Oxford Clay material from the collection of Dr Henry Porter, upon which he erected *Ichthyosaurus megalodeirus*. This latter material was, however, not truly described, diagnosed, or figured, and the available pieces of the specimens were merely listed; this does not fulfil the requirements for an indication by the International Code of Zoological Nomenclature (ICZN) article 12.2 (International Commission on Zoological Nomenclature 1999, amended 2012; see also *Taxa invalida* in Part 2~~below~~). In the original description of *Ophthalmosaurus icenicus*, Seeley (1874b) described two specimens, of which the first (NHMUK PV R2133) was indicated as "the type of a new species" (Seeley 1874b, p. 699) and should be considered the holotype for *Ophthalmosaurus icenicus*. This term was not applied to the second specimen described in that paper (NHMUK PV R2134): Seeley included this specimen to more clearly show the generic differences of *Ophthalmosaurus*. Under ICZN Article 72.4.5 and Recommendation 73D, this specimen (part of the type series) should be labelled as the paratype for *Ophthalmosaurus icenicus*.

Lydekker (1890, p. 268) erected *Ophthalmosaurus pleydelli* for a humerus and presacral vertebral centrum from the Kimmeridge Clay Formation of Gillingham, Dorset, which were later described by Mansell-Pleydell (1890). These specimens were associated with further skull fragments and a vertebra. The humerus was distinguished primarily by being shorter and having shorter and wider distal facets than in *Ophthalmosaurus icenicus*. These characters are within the intraspecific variation found for specimens referred to *Ophthalmosaurus icenicus*, and so *Ophthalmosaurus pleydelli* may be rejected as a subjective junior synonym. Appleby (1956) considered *Ophthalmosaurus pleydelli* to be a junior synonym of either *Ophthalmosaurus icenicus* or *Ophthalmosaurus monocharactus*, and Kirton (1983) considered this a junior synonym of *Ophthalmosaurus icenicus*.

Appleby (1956, p. 444) separated the holotype (NHMUK PV R2133) coracoids of *Ophthalmosaurus icenicus* and another specimen (LEICT 100'1949/20) in the New Walk Museum, Leicester, from other coracoids referred to *Ophthalmosaurus*. These two specimens presented two notches on the coracoid: an anterolateral notch that is common to Jurassic and Cretaceous ichthyosaurs, and a second notch in the posterior margin. Appleby (1956) retained these two specimens in *Ophthalmosaurus icenicus*, and placed the 41 or so specimens with single-notched coracoids in a new species, *Ophthalmosaurus monocharactus* Appleby, 1956. As the number of coracoidal notches was the only diagnostic feature given by Appleby, the vast majority of specimens previously referred to *Ophthalmosaurus icenicus*, but without coracoids, could then only be assigned to *Ophthalmosaurus* sp. However, in the holotype specimen of *Ophthalmosaurus icenicus*, with both coracoids present, the left coracoid that Seeley (1874b) did not describe and figure is incomplete posteriorly, while other left-side elements exhibit gross pathology, especially the scapula, which is strongly disfigured and has become fused to the left clavicle. Seeley also misorientated the coracoid that he figured laterally and anteroposteriorly, initially calling it the right coracoid. This inverted the intercoracoidal and glenoid facets, resulting in narrow anterior and wider posterior notches, both placed more medially than in other ichthyosaurs (see description of the coracoid below). A later correction (Seeley 1893, p. 151, footnote; Kirton 1983) that this should instead be a left coracoid removed the lateral inversion. The interpretation of Kirton (1983) that the bone Seeley (1874b, pl. 45, fig. 1) figured should be a right coracoid in ventral view is followed here as it is consistent with other referred coracoids that are or were known in articulation: the medial facet is broader and angled slightly dorsally, and the anteromedial edge bears a facet for articulation with the interclavicle (Kirton 1983, p. 15; see Coracoid below). Andrews (1910, p. 46) considered the posterior notch in the right coracoid of *Ophthalmosaurus icenicus* to be deformation from the pathology affecting the left side of the pectoral girdle. Appleby (1956, p. 439), in light of the new specimen LEICT 100’1949/20, regarded the number of notches present to be a valid character and of taxonomic importance at the specific level. Kirton’s (1983, pp. 14–17) discussion of this noted that the posterior notch (anterior notch of Seeley 1874b, pl. 45, fig. 1) has a different form and placement to the anterior notch in that bone, and to coracoidal notches present in other ichthyosaur taxa. In particular, the posterior notch in NHMUK PV R2133 is a deep invagination of the posterior margin, whereas the anterior notch (although incomplete) is shallower, wider and more similar to that seen in other specimens of *Ophthalmosaurus icenicus*; the same applies to LEICT 100’1949/20. Kirton (1983, p. 16) likened this form of the posterior notch more to a “fenestration, or an incision in the coracoidal plate, rather than being merely an indentation of the postero-lateral border”. Variation in the coracoidal notching is present both within and between Lower Jurassic ichthyosaur taxa, as in *Ichthyosaurus* and *Stenopterygius* Jaekel, 1904 (McGowan 1974b, 1979). In specimens of *Stenopterygius* with two notches, the posterior notch is a wider embayment, like the anterior notch, rather than the narrower cut into the coracoid seen in NHMUK PV R2133 and LEICT 100’1949/20. As the coracoids of LEICT 100’1949/20 are the only parts known from this individual, and they show no clear deformation, it is uncertain whether the posterior notches here too are effected by pathology. The evidence supports Kirton (1983) and subsequent authors, such as McGowan & Motani (2003), in regarding *Ophthalmosaurus monocharactus* as a subjective junior synonym of *Ophthalmosaurus icenicus*, and this view is followed here.

As mentioned in the generic-name discussion above, the Upper Jurassic material from Russia is in need of further detailed study and taxonomic reappraisal. The specimens upon which these taxa are based are poorly preserved, leading to their uncertain affinities. *Ophthalmosaurus undorensis* Efimov, 1991 was erected on a humerus, atlas-axis and two vertebral centra. The humerus is consistent with material for *Ophthalmosaurus icenicus* and so *Ophthalmosaurus undorensis* is considered a junior subjective synonym of *Ophthalmosaurus icenicus*. The same applies to *Khudiakovia calloviensis* Arkhangelsky, 1999, which is known only from forelimb material (Arkhangelsky 1999). *Paraophthalmosaurus* (= *Ophthalmosaurus sensu* Maisch & Matzke 2000) *saveljeviensis* Arkhangelsky, 1997 and *Paraophthalmosaurus saratoviensis* Arkhangelsky, 1998 were considered synonymous by McGowan & Motani (2003, p. 127), and a *species inquirenda*, possibly referable to *Ophthalmosaurus icenicus*; Maisch (2010) retained *Ophthalmosaurus saveljeviensis* as a separate species. In Arkhangelsky & Zverkov's (2014) cladistic analysis, *Paraophthalmosaurus saveljeviensis* and *Paraophthalmosaurus kabanovi* are recovered as sister taxa within Ophthalmosaurinae, and separate to *Ophthalmosaurus* (see the generic discussion above). The four species in *Yasykovia* were synonymized with *Ophthalmosaurus icenicus* by McGowan & Motani (2003, p. 113), although Maisch & Matzke (2000) and Maisch

(2010) considered them a single separate species: *Ophthalmosaurus yasykovi*. While many features are consistent between the two species, others may be taxonomically important (e.g. humerus longest/widest proximally, coracoid proportions). In this case, *Ophthalmosaurus yasykovi* is provisionally retained as separate from *Ophthalmosaurus icenicus*. However, *'Yasykovia' kabanovi* has been referred to *Paraophthalmosaurus* by Arkhangelsky & Zverkov (2014).

Description. *Premaxilla*. The elongate premaxillae form most of the pre-narial rostrum and of the length of the skull generally (Text-figs 4, 5b; Tbl. 2; Pl. 26, figs 1, 2). They are rather low anteriorly, but increase in height posteriorly towards the contact with the nasals and external naris. In dorsal view, the anterior portions are nearly straight, but are deflected laterally in the posterior half, enclosing the nasals dorsally and vomers ventrally between the two premaxillae. The external surface has a convex curve dorsally that gives the rostrum a trapezoidal outline when the two premaxillae are articulated. Each premaxilla is A-shaped in cross section; this is produced by combination of the lateral wall and a medial flange that extends along the whole length of the bone, bounding the alveolar groove between them. Towards the posterior end of the premaxilla, the lateral wall and medial flange diverge into two long, relatively thin projections (lateral and medial), oriented posteroventrally, holding between them the maxilla, which continues the alveolar groove posteriorly at this point. These are infrequently preserved, but are mostly complete in GLAHM V1921 and NHMUK PV R2160. The lateral wall forms a long process that envelops the maxilla laterally for much of its length, extending towards, and meeting, the external naris. Here the process diverges around the anterior

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margin of the external naris forming a small, rounded supranarial process and much larger subnarial process. This subnarial process extends ventral to the external naris for about one-half of its length, tapering posteriorly and overlying the lateral face of the maxilla. The medial flange extends posteriorly between the maxilla and vomer until contacting the internal naris; the lateral face of this flange forms a small part of the anteromedial border to the internal naris.

The premaxillae are in contact with each other for much of their dorsal length, in a simple butt joint. From about two-thirds of the pre-narial length posteriorly, around half the length of the premaxilla itself, the nasals are exposed dorsally between the premaxillae, separating the lateral projections. At this point, Andrews (1910) noted the presence of an elongate roughened surface that he attributed to ligamentous connection between the premaxillae. The anterior portions of the two premaxillae remain separate when articulated; the space left would likely have been filled with connective tissue. This anterior extension tapers to a point, both laterally and dorsoventrally, which contradicts Andrews' (1910, p. 24) description that they "terminate in a blunt point". This may be because the material he studied was not complete owing to the delicate nature of this area and the portion of unossified material (e.g. NHMUK PV R3702; Andrews 1915). Each nasal runs in a groove along its contact on the medial sides of the premaxillae, which anterior to their dorsal exclusion by the premaxillae, becomes a medial channel between the contacts of the premaxillae dorsally and alveolar grooves ventrally. In this channel, ventral to the nasals, run the thin anterior projections of the vomers, which are applied to the medial side of the lingual wall for almost its entire length. The vomers are exposed between the premaxillae for much of ~~its~~their length. The channel is narrowed anteriorly by the closing dorsal and ventral walls as the premaxilla becomes lower, but it does not close completely, and feeds into a larger anterior vacuity that corresponds to the anterior separation of the premaxillae.

A longitudinal groove runs along much of the lateral surface of the premaxilla from just anterior to the external naris contact anteriorly, just dorsal to the alveolar groove. Numerous foramina open onto the floor of this groove, becoming smaller and more frequent anteriorly. At its anterior extent, the groove becomes discontinuous and is reduced to a series of small pits. These foramina connect to a hollow intraosseous channel that runs along the length of the premaxilla, which also connects to foramina from the internal surface. These foramina likely show the passage of nerves and blood vessels that served the external rostral tissues. The presence of these structures in many ichthyosaurs led Romer (1968) to suggest the presence of a horny bill, albeit of unusual type, although he denied the possibility of fleshy lips (*contra* Kirton 1983). The presence of such structures however seems unlikely.

The alveolar groove extends from the anteriormost point of the premaxilla, and tooth impressions can be seen as shallow, rounded depressions in its floor separated by low, transverse septa on the lingual wall between the tooth positions. There may also be grooves opposite these depressions on the labial wall. These are stronger and smaller anteriorly; the depressions become more socket-like in this region indicating the teeth held here were smaller, which is shown well in NHMUK PV R3893; this feature, alongside the divergence of the premaxillae anteriorly is unique to *Ophthalmosaurus icenicus* among ichthyosaurs. Tooth impression size increases posteriorly, with the largest impressions being around the midpoint of the tooth row. When the two premaxillae are articulated, the lingual wall can be seen ventral to the labial wall in lateral view and both slope obliquely and laterally. The relationship between this orientation of the alveolar groove and the teeth can be seen in NHMUK PV R3893: the tooth bases abut the labial wall, but the sides lie against the lingual wall. This causes the teeth to lie at approximately 45° to the vertical, deflected laterally, but because of their strong lingual curvature (see Dentition below), the crowns are angled at only 20° to the vertical. The anteriormost teeth are oriented more vertically. At the contact with the maxilla, the floor of the alveolar groove slopes posterodorsally to receive the anterior portion of this bone. Although the tooth placements are poorly defined, it is estimated that the premaxillae each bore at least 27 teeth.

Maxilla. The maxilla has a complex triangular shape in lateral view but is largely obscured by the posterior projections of the premaxilla that surround it laterally and medially (Text-figs 4a, 5b; Table 2; Pl. 1, figs 1–3). Dorsally, it is seen as long and narrow as it continues the alveolar groove posterior to the premaxilla. The anterior process slots between the posterior projections of the premaxilla and so has a sloping and tapering anterior process that forms the dorsal floor of the alveolar groove and contacts the premaxilla on the dorsal and lateral sides. An elongate facet on the lateral side of this process, which extends more than one-quarter of the length of the maxilla, shows the extent of contact with the subnarial process of the premaxilla. The lateral face of the maxilla is composed of the external lateral wall of the alveolar groove ventrally, but is extended dorsally into a low triangular flange, which has an undulating anterior slope and straight, roughened posterior slope. At the anterior end of this, a small process is developed, concordant with the dorsal edge of the premaxillary facet ventrally, that forms the anterior extent of the simple nasal facet; its delicate nature means this process is infrequently preserved, so its full extent is uncertain, but this process likely supported the soft tissues. Posterior to the nasal facet, the dorsal margin of the bone is smoothed and rounded following the contours of the external naris, and showing the extent of the participation of the maxilla, although this would have been obscured laterally by the premaxilla and lachrymal in life. The posterior two-thirds of the lateral face of this triangular flange are roughened and ridged showing the great extent of the lachrymal contact. The dorsal edge here develops several posteriorly directed peaks that are largely concealed by the overlapping lachrymal. The posteriormost of these receives the distal tip of the prefrontal laterally. This coverage by the lachrymal differs from Andrews' (1910) description: he limited this to a smaller, posterior portion of the dorsal process and thus allowed the maxilla to contact the external naris in his lateral view reconstruction (fig. 23). The extent of roughening on the lateral surface however supports significant coverage by the lachrymal. The dorsal peak of the maxilla would be located near a similar peak in the lachrymal in life and these may have supported the soft tissues of the nasal capsule. Ventral to the lachrymal facet, the jugal facet is shown by a series of high longitudinal ridges that extend along much of the posterior half of the ventral lateral face. The posterior process of the maxilla tapers posteriorly along this contact.

Internal to the lateral triangular process, a projecting flange forms the floor of the alveolar groove that is deflected upwards medially as it contributes to the palatal surface. The anterior portion of this flange forms the floor of the nasal capsule and shows numerous foramina in this region. Further foramina penetrate through the floor of the alveolar groove, and can be seen in ventral view. These maxillary foramina probably transmitted branches of the inferior orbital artery, the infraorbital nerve and the palatal nerve. Contact with the vomers is made on the anteromedial surface via a shallow longitudinal groove along the ventral deflection of the medial flange. Posterior to this, several posteroventrally-deflected tongues of bone are developed that interlock with the palatine. The posteriormost of these forms the anterior apex of the subtemporal fenestra. The alveolar groove continues along much of the length of the maxilla. At its anterior end, the maxillary contribution is shallow, but the lateral and medial walls rapidly gain in height. The groove gradually narrows posteriorly through much of the length of the maxilla, but begins to taper and shallows rapidly alongside the jugal facet. Andrews (1910) did not consider the maxilla to be tooth-bearing, but various isolated and articulated specimens (e.g. NHMUK PV R3893) show embedded tooth fragments, or depressions indicating their position, along the whole of the alveolar groove. The maxillary alveolar groove held teeth more posteriorly than shown by Kirton (1983, fig. 9): GLAHM V1921 bears impressions to the posteriormost point of the alveolar groove. The teeth became smaller posteriorly as the groove narrowed, shown by the diminishing size of the impressions.

Nasal. The nasals are elongate, triangular bones that form a major part of the posterior rostrum and anterior skull roof (Text-figs 4, 5a; Pl. 1, figs 4, 5, Pl. 26, figs 3–6). The anterior processes extend anteriorly for much of the rostral length, but as they lie in a medial groove of the premaxilla (see above), are obscured from dorsal view by the dorsal wall of this groove. Along their midline, the two nasals meet at a simple, rounded butt joint. From their anteriormost dorsal exposure, the nasals separate the posterolateral processes of the two premaxillae. The dorsolateral wall of the nasal widens and falls ventrally, meeting the maxilla just anterior to the external naris, posterior to half the length of the nasal, in a thickened and roughened facet. Just lateral to the midline, each nasal shows a strong, convex, longitudinal curvature separating the external surface into dorsally and laterally directed faces. This continues the squared cross section of the dorsal rostrum posterior to the premaxillary portion and is particularly strong dorsal to the external naris, where the curvature is raised dorsal to the level of the midline. The elongate depression formed between these ridges was termed the *excavatio internasalis* by Maisch (1997b). There is no evidence for an internasal foramen. The function of this depression is uncertain; Wade (1984) suggested it may be the locus for an organ for echolocation, similar to the melon in cetaceans. Maisch & Matzke (2000) disputed this as the structure of the otic capsule bears little resemblance to that in Cetacea, and the *excavatio internasalis* is much smaller, suggesting an olfactory function instead. The posterior dorsal surface is largely flattened and dorsally deflected, giving the skull roof a distinct curve dorsal to and around the large orbit. As an internasal foramen is not present in *Ophthalmosaurus icenicus*, nor other ichthyosaur taxa that have an *excavatio internasalis*, an olfactory function is also unlikely. The strong dorsal inflection of the skull around the orbit would have been a region that experienced forces from several directions, such as the drag forces from forward swimming and the compressive forces on the snout during biting, requiring strengthening at this point of the snout. Additionally, to increase the streamlining of the skull about the external naris and orbit, the dorsal nasal bone may have been fluted, and the *excavatio internasalis* may have been fat-filled to reduce the angular displacement caused by the orbit. Posteriorly, the nasal overlaps the frontal dorsally and postfrontal laterally respectively in an interdigitating suture, the nasal plate thinning in this region. The ventral margin abuts the prefrontal posterior to its participation in the external narial opening, excluding the nasal from external contact with the lachrymal. Evidence from NHMUK PV R4758 suggests that the lachrymal does not contact the ventral margin of the nasal but is excluded by the narial process of the prefrontal (Kirton 1983). The facet identified as the lachrymal facet by Andrews (1910) may be the posterior portion of the lateral flared edge (see below), which is frequently damaged. Ventrally, the nasal is concave with a low and wide groove along much of the anterior process, extending and tapering until medial to the external naris. The external naris opens into a low, posteriorly oriented channel. Posterior to this, the extensive contact with the frontal covers much of the remaining surface.

The ventral border of the nasal, just posterior to its midpoint, forms much of the dorsal border of the external naris. This border has two parts: the anterior is a short, smooth and thin vertical edge. Behind this is a smooth, straight, horizontal margin that, posteriorly, is projected laterally into a flared edge, which curves ventrally towards the posterior of the external narial opening, forming a funnel, as noted by Andrews (1910). This lateral expansion is rarely completely preserved; it was probably formed from very thin bone in life. A small spur of bone is sometimes developed just internal to the narial opening that is visible in lateral view, between the two portions of the border. Posterior to the lateral expansion, there may also be a small notch, as is developed in GLAHM V1129 and to a lesser extent in NHMUK PV R4753. In specimens where this notch is not seen, the external bone is pierced by one or more foramina (e.g. PETMG R47). These structures likely indicate the passage of vessels for the soft tissues of the nasal capsule. The bony structures of the maxilla, lachrymal and nasal do not permit reconstruction of these tissues, but suggest the presence of muscular structures that may be associated with a valvular mechanism (Parsons 1970; Kirton 1983; Maisch & Matzke 2000).

Lachrymal. This thin plate of bone is positioned lateral to the maxilla, covering much of its lateral surface (Text-fig. 4b; Pl. 1, figs 4, 5, Pl. 26, figs 7, 8). The lachrymal has a triangular shape, extending in three directions: anterior, dorsal, and posteroventral. Its anterior portion forms the ventral and posterior margin of the external naris with its smooth and rounded dorsal border. This is largely horizontal, but a low prominence is developed towards the posterior part of the margin, and just posterior to the dorsal tip of the maxilla, which can be seen interior to the lachrymal in lateral view. The anteriormost tip of the lachrymal has a small contact with the premaxilla on its ventral edge. Laterally, its face is largely smooth, but develops a crescentic ridge that follows the orbital border on its posterior margin. Anteriorly, this is perforated by numerous nutritive foramina. The ridge is continued around the orbit dorsally by the prefrontal, postfrontal and postorbital leading Kirton (1983) to suggest that it supported a thickened dermis that protected the eye. The dorsal process contacts the narial process of the prefrontal at its apex in an interdigitating suture, excluding contact with the nasal (Kirton 1983; *contra* Andrews 1910). The narial process of the prefrontal extends ventrally to cover much of the medial face of the lachrymal. Posteroventrally, the lachrymal is drawn out into a long process that follows the dorsal edge of the maxilla. This process becomes wider posteriorly and develops a ventral groove that contacts the jugal. In this region, the lachrymal, maxilla, and jugal together form the anteroventral margin of the orbit. Medially, longitudinally directed low ridges that form the contact with the maxilla largely cover the face of the lachrymal.

External naris. The external naris is bordered by the maxilla, lachrymal and nasal in *Ophthalmosaurus icenicus* with its form described above (Text-fig. 4). Additionally, it is located laterally on the skull of *Ophthalmosaurus icenicus*, reflecting the square cross section of the jaws and strong dorsolateral curvature of the nasals (see above), so little of the naris is visible in dorsal view.

Prefrontal. The prefrontal has little exposure on the skull roof, which belies its complex form (Text-figs 4, 5a; Pl. 2, figs 1, 2, Pl. 29, figs 1, 2). It is composed of a dorsal sheet and an anteroventrally directed strut that forms the anterodorsal margin of the orbit. The anterior portion of this rounded strut contacts the lachrymal at the posterodorsal margin of the external naris in a strong interlocking facet, underlapping its medial surface on much of the dorsal process and extending to contact the maxilla distally. This extensive contact acted as a strong columnar support between the external naris and orbit, resisting strong compressive forces generated during feeding (Kirton 1983). The strut thickens dorsally and gently curves posterodorsally around the orbit. Towards the main body of the bone, this strut widens, forming lateral and medial flanges that merge into the expanded dorsal sheet. The lateral flange is the smaller and is exposed in dorsal view; this forms part of the supraorbital ridge that can be seen around much of the orbit (see Orbit below), and links those on the lachrymal anteriorly and postfrontal posteriorly. The medial flange is slightly larger and is ridged dorsally. It contacts the nasal and the frontal ventrally. Along the main axis of the dorsal surface of the prefrontal is a parabolic ridge that meets a deep groove in the lateral margin of the overlapping nasal. The posterior part of the prefrontal is covered by the postfrontal dorsally and overlaps a small part of the parietal posteromedially. Here the prefrontal tapers posteriorly beneath the frontal and postfrontal contacting the anteromedial apex of the supratemporal fenestra and the parietal. Ventrally, between the dorsal sheet and the medial side of the central strut, the prefrontal takes part in a rounded depression that is continued by the ventral surfaces of the frontal and parietal. Kirton (1983) suggested that this feature marks the location of the olfactory lobes of the brain.

Frontal. These are small bones of the skull roof, with a correspondingly small exposure dorsally (Text-figs 4b, 5a). The frontals are surrounded by the nasals, postfrontals, and parietals; anteriorly, laterally, and posteriorly, respectively. Contacts superficially appear to be interdigitating sutures, belying the extensive overlap of the bones in this region. This covering, and the delicacy of the bone, makes description problematic as the frontal is often preserved in articulation and so is poorly visible, hence Andrews’ (1910) trifling description. The exposed dorsal surface is largely flat, but is pitted by numerous foramina that Kirton (1983) interpreted as indicating close application of the dermis. Medially, the frontals meet in a straight suture that is broadened dorsoventrally by a ventral deflection of the ventral surface, possibly providing a large surface for bonding by connective tissue (Kirton 1983). The ventral ridge formed by this ventral deflection marks the medial border between two interior depressions on the ventral skull roof, indicating the extent of the telencephalon, which is continued from the prefrontal (see above; Text-fig. 5a). At the posterior end of the medial suture, the frontals enclose almost the entirety of the pineal foramen in dorsal view, the parietals forming only the posteriormost portion of its margin. The pineal foramen is ovoid, pinched at the anterior and posterior, and the frontals are smoothed around the margins. Anteriorly, the nasal overlaps the frontal extensively, so the latter’s surface is ridged and grooved in this region.

Ventrally, the frontal is dominated by the depression accommodating the dorsal structures of the brain (Kirton 1983) that are continuous with those of the nasal anteriorly, prefrontal laterally, and parietal posteriorly. The medial flange of the prefrontal underlaps the frontal laterally; this is obscured from dorsal view by the overlapping nasal and postfrontal. A small contact is made with the postfrontal by interlocking tongues at the posterolateral extent of the frontal. The posterior portion of the ventral surface of the frontal is ridged and contacts the underlapping parietal. The contact between the parietal and postfrontal excludes the frontal from the margin of the supratemporal fenestra dorsally, while the posterior extent of the prefrontal-parietal contact excludes the frontal ventrally.

Parietal. These paired bones form the posteromedial portion of the skull roof and much of the medial border of the supratemporal fenestra (Text-figs 4b, 5a; Pl. 3). The parietal has a generally crescentic shape, with a large anterior main body and a robust posterolateral process. The anterior region of the parietal is overlapped by the frontal giving an interdigitating suture line with ridges and grooves on the dorsal surface. The two parietals meet medially along much of their midline, although their anteriormost sections rapidly diverge around the pineal foramen and under the frontals. The medial suture between the parietals is straight and dorsoventrally thickened, with complex grooves along its medial surface. Lateral to this, much of the dorsal surface of the parietal is largely convex, with the lateral edge curving ventrally to form the smooth medial wall of the supratemporal fenestra. Posteriorly, there is a small rise towards the posterolateral process and there, medial to the processes themselves, the parietal forms a small shelf, under which the supraoccipital fits. The posterolateral process descends laterally along its length to underlie the supratemporal. At its midpoint, the lateral wall of the parietal is drawn ventrally into a pointed descending process, the ventrolateral process, that may have contacted the epipterygoid, as occurs in *Ichthyosaurus* (McGowan 1973a; Kirton 1983). It is likely that the epipterygoid was not ossified in *Ophthalmosaurus icenicus* (see below). Andrews (1910) interpreted a deeply grooved region just anterior to this process as the facet for the epipterygoid (*columella cranii*). Kirton (1983), however, suggested this was instead a point of muscle attachment (*M. levator pterygoidei?*), when compared with *Ichthyosaurus*. This groove is more likely the facet for the epipterygoid, which, although unlikely to be ossified, may have remained in cartilaginous form, as has been argued for *Platypterygius australis* (Kear 2005, p. 599). The groove also corresponds to the epipterygoid facet described by McGowan (1973a, p. 26).

Like the frontal, the ventral surface of the parietal shows evidence of moulding to accommodate the underlying structures of the brain. Laterally, the anterior parietal continues the longitudinal depression found on the frontal and prefrontal that Kirton (1983) interpreted as the impression of the olfactory lobe (see above). Posteriorly, and more medially, a further faint depression may house the cerebral hemisphere (McGowan 1973a; Kirton 1983). These anterior depressions are marked by faint striae. The posterior extent of these depressions is marked by a transverse ridge ("tentorial ridge" of Andrews 1910). Posterior to this is a large rounded depression that is bounded anteriorly by the transverse ridge and the descending process laterally. The surface here is irregular and marked by numerous striae that radiate from the centre of the depression. Kirton (1983, after McGowan 1973a) interpreted this depression as the location of the optic lobe of the mesencephalon. The ventral surface of the posterolateral process is concave, bordered by an anterior ridge, which marks the posteromedial wall of the supratemporal fenestra, and a posterior ridge that marks the parietal shelf. This latter may be grooved to accommodate the dorsal ridge of the underlying supraoccipital (see below), although a significant amount of cartilage may have intervened as the supraoccipital is positioned ventral to the parietal. The ventral surface forms the roof of a narrow opening equivalent to the posttemporal fenestra, between the parietal dorsally, the supraoccipital posteroventrally, and the squamosal laterally (Evans 2008).

The position of the parietal means that numerous bones surround it. Anteriorly, the frontal overlaps by interlocking suture, as seen in dorsal view (Text-figs 4b, 5a). The anterolateral margin of the parietal contacts the prefrontal and postfrontal bones. The prefrontal slots between two laminae of the parietal in its anterolateral corner. The ventral lamina is drawn into a long delicate process that runs along the orbital ridge of the ventral surface of the prefrontal, which is often broken. Contact with the postfrontal is smaller: the parietal has a small facet on its dorsal surface onto which the postfrontal abuts; this is obscured by the overlying frontal. The posterolateral process of the parietal meets and underlaps the supratemporal in a series of well-developed ridges and grooves that strengthen this contact.

Postfrontal. This curved and thickened bone forms the anterolateral border of the supratemporal fenestra, the lateral portion of the skull roof and the dorsal wall of the orbit (Text-figs 4, 5a; Pl. 2, figs 3, 4, Pl. 29, figs 1, 2). The postfrontal is L-shaped in dorsal view, with a wide anterior plate that grades into a more mediolaterally facing posterior strut. A small area of the anterior postfrontal is grooved, marking the extent of interdigitation with the nasal anteriorly and frontal anteromedially. Appleby (1956) noted that the postfrontal overlaps all other bones in its anterior region. Posteriorly the dorsal surface is largely smooth. The medial border is rounded and roughened, with numerous nutritive foramina, which Kirton (1983) suggested might have been the origin of part of the *M. adductor mandibulae externus*. Lateral to this, the postfrontal slopes downwards towards the lateral margin of the skull; the whole bone tapers in this direction. Both Andrews (1910) and Appleby (1956) commented on the thinness of the lateral flange.

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Ventrally, the anterior part of the postfrontal overlies the prefrontal for much of its area via a strongly grooved contact. A small anteromedial facet receives and overlaps the parietal. Posterior to this area, the ventral surface is raised into a longitudinal ridge that marks the dorsal rim of the orbit, continued from the prefrontal anteriorly towards the postorbital posteriorly. This ridge is positioned towards the medial edge of the postfrontal, so that there is a steep slope up towards the supratemporal fenestra medially and a gentler, concave curve that marks the lateral flange of the postfrontal. The lateral flange is the dorsal portion of the supraorbital crest (see Orbit below). The posterior portion of the postfrontal is greatly overlapped by the supratemporal. An elongate groove extends along about one-half the length of the medial margin of the postfrontal, into which a long medial tongue of bone from the supratemporal slots. The posterior edge of the postfrontal itself develops two blunt tongues, dorsally and ventrally. The former overlaps the lateral face of the supratemporal and the latter meets the postorbital in a slot. A groove on the posterolateral edge of the postfrontal receives a tongue of bone from the postorbital.

Supratemporal. The triradiate supratemporal forms the posterolateral margin of both the supratemporal fenestra and the skull roof as a whole (Text-figs 4, 16; Pl. 2, figs 5–8). The main body is located at the posterolateral corner of the cranium and its three rami are directed anteriorly, along the lateral skull roof, medially, along the posterodorsal margin of the skull, and ventrally, medial to the quadrate. The anterior and ventral rami consist of thin sheets of bone that are often broken, but NHMUK PV R2146 preserves much of the supratemporal. Much of the lateral wall of the supratemporal fenestra is formed by the anterior ramus, which has a rounded dorsal margin and narrows anteriorly to contact the postfrontal. The dorsal part of this ramus is a thick and rounded bar. There is a deep groove dorsolaterally with which a ventral groove on the postfrontal interlocks (see above) strengthening this point of the supratemporal fenestra (Kirton 1983). Ventral to the bar, the anterior ramus develops a broad but thin sheet, deepening posteriorly, against which the squamosal superficially lies laterally, marked dorsally by a shallow groove. The squamosal also meets a facet at the posteroventral margin, and the supratemporal is thickened and roughened for this contact. On its medial face, the anterior ramus of the supratemporal is roughened dorsally for muscle attachment; Kirton (1983) suggested that the *M. adductor mandibulae externus* would have attached along most of the lateral supratemporal fenestra. The ventral margin of the supratemporal is underlapped by the postorbital anterior to its contact with the squamosal and is also roughened.

The medial ramus is triangular in shape and consists of a thickened bar that rises anteromedially. A large concave triangular or “somewhat diamond-shaped” (Andrews 1910, p. 16) facet at its medial end is the main contact with the parietal, and is strongly grooved. On the ventral surface of this ramus, there are two deep grooves that receive particularly prominent ridges from the parietal. The supratemporal overlaps the lateral process of the parietal anterodorsally, tapering anteriorly along this process. This anterior orientation creates a noticeably acute angle at the posterolateral corner of the supratemporal fenestra between the anterior and medial rami. Externally, the surfaces of the anterior and medial rami have striations that meet at the posterolateral corner of the bone in a roughened area. On the dorsal part of the posterior surface of the supratemporal, there is a small horizontal, triangular shelf that becomes deeper medially and may be grooved dorsally (e.g. NHMUK PV R2146). Ventrally to this, there is a small depression that marks the facet for the paroccipital process of the opisthotic. Appleby (1956, p. 413), however, suggested this process articulated more medially at the apex between the medial and ventral rami. This paroccipital process of the opisthotic is received between the ventral surface of the horizontal shelf and the main bone, but is poorly developed except in the most well-ossified specimens (e.g. NHMUK PV R2133, R4753). In these cases, it can be seen to comprise two separate facets: one on the ventral surface of the shelf and a smaller facet on the main body of the supratemporal. There is a prominent tubercle in the middle of the posterior face that Kirton (1983) suggested is flanked by a smaller tubercle; the material available does not permit confirmation of this. The bone here is marked by radiating striae that likely are an attachment point for the *M. depressor mandibulae*.

The ventral ramus of the supratemporal is formed by two laminae, laterally and medially, that wrap around and flank the dorsal and medial borders of the quadrate. Dorsally, the quadrate is covered by the short, lateral lamina in a deep ventral groove between this and the medial ramus that was largely filled by the cartilage capping the dorsal edge of the quadrate. A small notch on the lateral edge of the ventral ramus exposed the dorsal edge of the quadrate. The medial lamina is the larger of the two laminae and descends for almost half of the dorsoventral height of the quadrate, along its pterygoid lamella, and envelops its anterior edge and the dorsal edge of the pterygoid. NHMUK PV R2133 shows a split for passage of a blood vessel to the quadrate ventrally (Kirton 1983). At its ventral extent the ventral ramus of the supratemporal intervenes between the pterygoid and stapes, overlapping the dorsal edge of the former and developing a small facet for the latter. Tubercles on the anterior face may mark the origin of the *M. adductor mandibulae externus* (Kirton 1983).

Reconstruction of the occipital region of *Ophthalmosaurus icenicus* has varied between those of Andrews (1910, fig. 4), Appleby (1956, fig. 21), and Kirton (1983, fig. 6). In particular, the amount of interosseous cartilage present between elements. The heavily pitted articular surfaces of basisphenoid, basioccipital, and those elements that contact these suggest that cartilage was present between these elements (see below, Text-fig. 16). In more complete specimens (e.g. GLAHM V1901, V1921; NHMUK PV

R2133, 2161), it is possible to re-articulate the posterior cranial elements. The elements surrounding the otic capsule do not fit closely by virtue of the need to encompass the osseous labyrinth, and the angular displacement between the supraoccipital, exoccipital, and opisthotic that permits this. Further, the articulation between the parietal and supratemporal laterally broadens the occipital region in *Ophthalmosaurus icenicus* beyond that reconstructed by Andrews (1910, fig. 4) and Appleby (1956, fig. 21). This separates the supratemporal and quadrate further, which increases the lateral space around the opisthotic and stapes (Text-fig. 16a). The variability in the ossification of posterior skull elements (e.g. quadrate, basisphenoid, and basioccipital; see below) suggests that these elements may have formed closer contact later in ontogeny. It is possible that this delayed ossification in *Ophthalmosaurus icenicus* is retained as a paedomorphic character. No specimens show direct contact between these elements.

Squamosal. The triangular squamosal has been a problematic element due to its delicacy and its superficial placement on the dorsolateral portion of the skull (Text-fig. 4; Pl. 4, figs 1, 2). The squamosal is occasionally not preserved in ichthyosaur specimens, but has since been demonstrated to be present in most taxa (Maisch & Hungerbühler 2001; McGowan & Motani 2003). Moreover, descriptions are few and incomplete (e.g. Andrews 1910, p. 18). The squamosal is oriented with a horizontal dorsal margin and the longest edge situated anteroventrally, and has a noticeable externally convex curvature that fits around the underlying cheek bones. The anterodorsal portion is strongly grooved where it is overlapped anteriorly by the postfrontal. Ventrally, the curved facet for the overlapping postorbital is developed; this bone covers about half of the anteroventral surface of the lateral squamosal. This area is roughened for this contact and features low ridges and grooves. At the ventral corner, there is a strongly developed facet for the quadratojugal, which overlaps about one-third of the dorsoventral height of the squamosal. This is marked by a curved ridge surrounding the facet and a vertical ridge within the area of contact that corresponds to a groove on the quadratojugal. A narrow posteroventral tongue descends and intervenes between the postorbital and quadratojugal, extending along the posterior edge of the former. Medially, the squamosal contacts the supratemporal dorsally and postorbital ventrally and is smoothed for this contact. The dorsal margin is slightly thickened and complexly shaped to fit into the dorsal groove on the underlying supratemporal. At the posterodorsal corner, a posteromedially-directed, triangular facet, which extends along the dorsal quarter of the posterior margin of the squamosal, articulates with the quadrate. The external surface of the squamosal is confluent with this facet, but internally, its surface is deflected medially to accommodate the quadrate facet. The posterior margin ventral to the facet is raised into a ridge that becomes more pronounced ventrally.

Postorbital. The postorbital is a narrow, crescentic element that forms much of the posterior margin of the orbit and the external surface of the cheek (Text-fig. 4; Pl. 4, figs 3, 4). The anterodorsal portion is developed into a wide transverse flange that continues the supraorbital crest from the postfrontal anteriorly. Anteriorly, the distal tip forms a tongue-and-groove contact between the postorbital and postfrontal. This flange is smoothed externally on the rim of the orbit, narrowing posteroventrally, until the orbital rim is continued by the main body of the bone. Posterior to this flange is a broad, medially positioned lamella that extends the dorsal half of the postorbital and gives it a squared outline. This lamella is slightly roughened on its lateral surface extending onto a small portion of the supraorbital crest, and has a slightly irregular margin. The squamosal twists medially and posteriorly to overlap most of the posterodorsal lamella. Dorsally the postorbital contacts the supratemporal. Ventrally, the postorbital is flatter, although still laterally convex. The anterior margin has a strong, but obtusely angled curvature ventrally to the reduction of the supraorbital crest that corresponds to a heel on the posterior margin. This heel is very irregular, with low ridges on the external surface. Andrews' (1910, fig. 8C) description of this element is brief and he neither describes nor figures this notable change in orientation of the postorbital, or the heel formed. The ventral portion of the postorbital tapers slightly distally, but ends in an irregular ventral margin overlying the jugal.

Medially, the postorbital is largely flattened and slightly roughened on the posterodorsal lamella where it contacts the lateral face of the anterior ramus of the supratemporal. The anterior surface of the supraorbital rim is concave, with the rim itself located medially. The posterior margin of the posterodorsal lamella develops a low ridge, directed anteroventrally, that crosses much of the ventral portion of the postorbital. This marks the anterior extent of the contact with the underlying quadratojugal. The contact has low ridges and grooves that extend to the heel of the postorbital and form the marginal irregularities described above. Anteroventrally, the ridge heightens and a ventral groove accepts the jugal ventral to the roof formed by the concave postorbital. Where this is broken (e.g. NHMUK PV R3893), the concave facet can be seen that corresponds to the convex dorsal process of the jugal. The medial surface of the postorbital is also roughened and low-ridged, and has an irregular ventral margin as the jugal is not completely overlapped.

Quadratojugal. The small and thin quadratojugal is a triangular element that forms the posteroventral corner of the lateral skull and cheek region, but is not well-exposed in either view; it is the most medial element in this region (Text-figs 4a, 6). Kirton (1983) noted that the quadratojugal figured by Andrews (1910, fig. 10) was more triangular than those she figured (Kirton 1983, fig. 4). Kirton interpreted this as a proportional elongation of the quadratojugal through ontogeny (compare NHMUK PV R2180, R4522 and R4753). Larger specimens of quadratojugals in *Ophthalmosaurus icenicus* are more dorsoventrally elongate than in smaller specimens. Kirton's explanation is likely as there would have been extensive growth and remodelling around the quadrate and articular region during ontogeny, which would have affected the growth of the cheek. Much of the anterior lateral surface is roughened where this contacts the medial surfaces of the overlying postorbital dorsally and jugal ventrally. The posterior and ventral margins of the quadratojugal are ridged and mark the boundary of these contacts. The descending tongue of the squamosal runs along most of the posterior part of the lateral surface in a prominent groove, which then ends in a roughened facet for the heel of the postorbital. On the ventral margin, the ridge is slightly undercut dorsally where the dorsal process of the jugal slots into it. The medial surface of the quadratojugal is mostly smooth anteriorly. Its posterior margin is distinctly ridged and, at half of the height of the quadratojugal, the bone projects medially to form a small cup-like facet that is flush with the posteroventral margin and oriented slightly medially. This is where the quadrate articulates, and just dorsal to the facet there is a small triangular depression that Kirton (1983) interpreted as the attachment point for the ligaments that bind these two bones.

Jugal. The jugal has an overall bowed J-shape formed by a long suborbital bar and a posteriorly ascending process (Text-figs 4a, 5b; Pl. 4, figs 5, 6). Anteriorly, the jugal bar overlaps the lateral face of the maxilla, lateral to the external wall of the alveolar groove, with low ridges to accommodate this contact. The anteriormost portion is splayed wide over the maxilla and bounded dorsally by the posteroventral process of the lachrymal, which accommodates the dorsal surface of the jugal in its ventral groove (see above). In this region, the jugal is flattened laterally, but widens posteriorly to a sub-circular cross section by the midpoint of the orbit. The ventral portion of the jugal has a longitudinal groove that tapers posteriorly, erroneously labelled “facet for maxilla” by Andrews (1910, fig. 10), giving the area posterior to this groove the appearance of a strut that is directed and broadens posteroventrally, meeting the ventral margin of the postorbital just anterior to the heel. The jugal bar is bowed both laterally and ventrally to create space for the jaw muscles that pass medially through the subtemporal fenestra, and to house the sclerotic ring. The posterior part of the jugal ascends dorsally as a flattened process that forms the posterior part of the orbit and part of the cheek region. This process is enclosed on its anterolateral surface by the postorbital, the contact for which is marked by dorsoventrally-oriented ridges on the external surface of the jugal. The dorsal tip of this process is rounded. Posteroventrally, the jugal broadens slightly to form a ventral heel that is often roughened, and was interpreted by Kirton (1983) as the attachment site of a ligament. This is most likely point of attachment for the jugomandibular ligament that

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extends from the posteroventral jugal heel to the lateral part of the articular region of the mandible (Herrel *et al.* 1998, Evans 2008).

The medial surface of the jugal bar is more flattened than the lateral surface. The anterior portion is ridged longitudinally, matching the contact on the maxilla. The dorsal surface also has undulating ridges in some specimens (e.g. GLAHM V1921). Medially, the surface of the dorsal process contacts the quadratojugal, showing a slight ridge around the area of contact along the dorsal portion. Running dorsoventrally along the contact, the jugal has a low ridge that slots into a small groove on the lateral surface of the quadratojugal. The posterior margins of the jugal and quadratojugal here form a continuous straight line along the posterior of the cheek. The dorsal process gently narrows dorsally, with the anterior and posterior borders forming low undulations, especially where they are covered laterally and medially.

Orbit. The orbit and sclerotic ring of *Ophthalmosaurus icenicus* are, relatively and absolutely, one of the largest in nature (Text-fig. 4a; Pl. 4, figs 7–10; Motani *et al.* 1999). McGowan (1976, p. 676) defined the orbital ratio as the ratio of orbital diameter to jaw length. For NHMUK PV R3013 this is approximately 280 mm/1000 mm = 0.28 (Table 2). Indeed, a large orbit is found often in Ichthyosauria, particularly Mixosauridae and Thunnosauria. Unlike the supratemporal fenestra, the configuration of the bones that make up the orbit remain consistent in ichthyosaurs. In *Ophthalmosaurus icenicus*, the prefrontal, postfrontal, and jugal – forming the dorsal and ventral margins of the orbit – are angled obliquely anteriorly to the anteroposterior axis of the skull so that the orbit faces slightly anteriorly (Text-fig. 4b). The sclerotic ring aligns with this, implying that the eyes were directed slightly anteriorly also, increasing the binocular visual region.

Sclerotic plates. Despite their delicacy, several sclerotic plates of *Ophthalmosaurus icenicus* have been preserved (Text-fig. 4a; Pl. 4, figs 7–10). Complete, articulated sclerotic rings are rare, however, NHMUK PV R4753 (complete) and GLAHM V1921 (partially complete) possess 15 plates, although Andrews' (1910, fig. 23) reconstruction shows only 14. Andrews also notes (p. 31) the increased ossification of the sclerotic plates through ontogeny. The sclerotic plates are bipartite, separated into orbital and corneal portions. The orbital part is squared, with a crenate orbital margin, and curved to surround the eye within. The corneal portion is flattened and angled at ~130° internally to the orbital portion, tapering to about one-half the width of the orbital part at its corneal margin. This inclination of the sclerotic plates causes a marked doming of the articulated sclerotic ring; about one-half as high as its diameter. The corneal margin of the sclerotic plates may be rounded where it meets the plates on either side. This margin is also straight and does not have the inclination seen in many other reptiles, allowing Kirton (1983) to infer that *Ophthalmosaurus icenicus* did not possess a scleral sulcus. The articulation between the sclerotic plates is formed by interlocking laminae developed on the margins. This is seen as a complex interdigitation in cross section, although at the surface, the suture appears straight, becoming wavy towards the corneal edge. Striae on the surface of the sclerotic plates are mostly parallel to the radial margins. On the internal and external surfaces, at the junction between the orbital and corneal portions, the surfaces have irregular tuberosities from which striae radiate. Interpreted as the attachment point of the muscles important in accommodation (Cramptori's and Brückes' muscles: Kirton 1983), the ratio of apertural to external sclerotic ring diameter of NHMUK PV R4753 is estimated at 0.4.

Vomer. The narrow and elongate vomers suffer from poor preservation and description, like the palatines (see below; Text-figs 4b, 7; Pl. 5, figs 1–4). Andrews (1910) tentatively figured and described a vomer (NHMUK PV R3533) as left, whereas Kirton (1983, p. 43) interpreted this as the right vomer; the latter view is followed here. As discussed above (see Premaxilla above), the anteriormost portion is enclosed within the medial canal of the premaxilla, held ventral to the nasals, and posterior to this, the vomers form the anteromedial portion of the palate. The delicacy of the bone means that no single specimen is known in its entirety, but two examples (NHMUK PV R4753 and GLAHM V1129) allow a largely complete restoration to be made (Text-fig. 7). Overall, the vomers feature a narrow and flattened basal plate from which rises a dorsal sheet that is higher posteriorly. The anterior extensions of the vomer taper anteriorly and make up about one-half of the total length of the vomer. They are angled dorsolaterally, to accept the ventromedial border of the premaxilla ventrolaterally in a slightly concave facet that continues for much of the length of the vomer. Posteriorly, the basal plate broadens and the premaxillary facet becomes less pronounced and is deflected laterally. Although smooth anteriorly, the surface of this facet becomes rugose posteriorly. Medially, along the anterior process, the left and right vomers contact in a simple, roughened butt joint that begins slightly anterior to the premaxillary facet. This contact between the vomers excludes the pterygoids from palatal view for about two-thirds of the length of the vomer, although the pterygoids continue anteriorly for a short distance dorsal to the vomers.

In the posterior portion of the vomer, the dorsal sheet rises in the sagittal plane. Anteriorly, this sheet rises gently from the anterior extension and, dorsally, develops a slight medial flange and laterally positioned concavity. The ventral border of this concavity is formed by a dorsally concave ridge that extends posteriorly to the dorsalmost extent of the dorsal sheet. At this point, the vomer is drawn out into three prominent projections that are directed anterodorsally. No specimen shows these projections in their entirety; in NHMUK PV R4753 these are 5 mm wide, with buttress-like bases on the vomer. The extent of the projections is unknown, but likely supported the structures of the nasal capsule, like similar projections found on the maxilla and nasal (see above). The ridge separates the anterodorsal concavity from a more posterior concavity on the lateral face of the dorsal sheet. Posterior to these concavities, the dorsal sheet falls sharply towards the horizontal posterior extension of the vomer. The ventral margin of the vomer in this region forms the anterior border of the internal naris, where the bone is thickened and rounded. By analogy with modern reptiles, Kirton (1983, p. 44) interpreted this region as the internal nasal chamber. The anterodorsal concavity forms the floor and medial wall of the *vestibulum nasi* with the ventral ridge dividing this from the postvestibular region. Posteriorly lies the choanal tube (part of the *cavum nasi proprium*, the posterior concavity) that forms a direct connection between the *vestibulum nasi* and the choana.

The medial surface of the dorsal sheet features an anteriorly narrowing facet that contacted the anterior process of the pterygoid. Ventral to this, the vomer is expanded medially to enclose the pterygoids and this contact is strengthened by a posterior groove. The posterior process of the vomer fits between the palatine laterally and pterygoid medially. Here the vomer has a narrow overlap onto these bones, but this increases and becomes more rugose anteriorly towards the vertical expansion of the vomer. The posterior extension is flattened and horizontal, narrowing posteriorly.

Palatine. The thin palatine bones form the posterolateral portion of the palate (Text-figs 5b, 8; Pl. 5, figs 5, 6). Like the vomers (see above), their delicate nature has caused uncertainty in previous identifications. Andrews (1910, p. 29, fig. 18; NHMUK PV R4693–5) and Appleby (1956, p. 423, figs 10 & 11, PETMG R220) described what they considered right palatines. Kirton (1983, p. 38, fig. 10), based on the study of additional specimens, interpreted Andrews' specimen as a left palatine and Appleby's as a left vomer, figured in dorsal view. These latter interpretations are followed here.

The palatine comprises a quadrangular posterior plate that divides anteriorly into a narrow lateral process and broader medial process. Between these, the palatine forms the posterior margin of the internal naris. The elongate lateral process is triangular in cross section and tapers distally. On its dorsal surface, it is overlapped by the maxilla laterally, with a longitudinal ridge that marks the extent of contact. This overlap continues posteriorly along the lateral margin of the palatine and is marked by a small, but complex, tongue-and-groove structure that holds the dorsomedial margin of the maxilla. The dorsal surface of the broader medial tongue bears an ascending projection at the posterior end of the internal naris. Kirton (1983) suggested this might have supported the wall tissues of the nasopharyngeal duct. Andrews (1910) showed this process smaller than it is in NHMUK PV R4753 due to breakage. Posteriorly, the palatine is poorly known, but its extent can be deduced from comparisons with specimens NHMUK PV R4753, R4693–5 and GLAHM V1129, and other taxa, for example, *Ichthyosaurus* (McGowan 1973a). The posterior contact with the pterygoid is a transverse interdigitating suture. At its posterolateral portion, the palatine forms a small part of the margin of the subtemporal fenestra.

Ventrally, the palatine overlaps the vomer along its medial border. The border of this contact is marked on the palatine by a small shelf that develops from the point of division of the anterior processes to hold the ventrolateral margin of the vomer. Dorsal to this, the medial edge of the palatine extends dorsomedially as the medial anterior projection (Kirton 1983), and lies flat against the lateral surface of the vertical expansion of the vomer. The contact surface is rugose and finely ridged ventromedially. Both the dorsal and ventral surfaces of the palatine have branching grooves showing the passage of surrounding vessels. Foramina pierce the palatine and can be seen on the dorsal surface of NHMUK PV R4753 around the border of the internal naris. Further grooves show the paths of blood vessels and nerves. Kirton (1983) proposed that these structures marked the paths of the palatine nerve and blood vessels that supplied the nasal tissues, possibly including the nasal artery.

Epipterygoid. No example of this bone has been recognized amongst the material referred to *Ophthalmosaurus icenicus*. It is ossified in the genus *Ichthyosaurus* (McGowan 1973a), but it is not certain whether its absence in *Ophthalmosaurus icenicus* indicates its failure to ossify or loss during collection. The complete lack of known epipterygoids for *Ophthalmosaurus icenicus* suggests that it did not ossify. While facets for articulation with the epipterygoid are present on the parietal dorsally and the pterygoid ventrally, these are reduced compared to *Ichthyosaurus* (McGowan 1973a), for example, supporting the lack of ossification of the epipterygoid. Ossification of the epipterygoid is apparently variable: it was not present in an otherwise complete skull of *Platypterygius australis* described by Kear (2005, p. 599), however, large examples are known from old specimens referred to *'Platypterygius'* (V. Fischer, pers. comm., 2015). This indicates that ossification during ontogeny may occur, although this doesn't seem to be the case in *Ophthalmosaurus icenicus*.

Pterygoid. The pterygoids are the largest elements of the palate, comprising most of the posterior portion (Text-fig. 4b; Pl. 6, figs 1, 2). Each pterygoid is composed of a sheet-like, anterior palatal ramus and a more complex, posterior quadrate ramus; the latter of these is more robust and so this portion is often better preserved.

The anterior ramus consists of a rod of bone that extends from the quadrate ramus of the pterygoid anteriorly, anterior to the level of the internal naris. The anterior portion of the anterior ramus is narrow and dorsally raised to fit between the two vomers, which exclude it from palatal view. In their anterior portions (approximately one-half the length of the pterygoid), the rami from the two pterygoids curve medially and meet ventrally just posterior to the internal naris (Text-fig. 5b), forming the anterior apex of the interpterygoid vacuity. Posterior to the internal naris, the pterygoid expands laterally into a horizontal shelf, which is constricted posteriorly. The pterygoids are raised into medially concave dorsal flanges that accept and hold the anterior parasphenoidal rostrum (cultriform process, see Parabasisphenoid below) between them. Laterally, the walls of this flange fit into the facet on the medial wall of the vomer (see above), and the vomer itself lies upon a small ventrolateral shelf of the pterygoid. Posterior to this region, the dorsal flange becomes shallower, and the medial border of the pterygoid is thicker and rounded, marking the lateral border of the interpterygoid vacuity. Lateral to the main rod of the anterior ramus, the pterygoid is expanded laterally into a broad sheet that accepts the palatine anteriorly in an interdigitating transverse suture, and anteromedially overlaps the posterior process of the vomer on its medial edge. The lateral border of the pterygoid bears fine striations for this union. A low ridge extends anterolaterally along the dorsal side of the lateral sheet, meeting the medial margin of a small lateral flange (GLAHM V1921: Pl. 6, figs 1, 2) that overlaps the palatine. Ventrally, the lateral sheet of the pterygoid is concave posteriorly, interpreted by Kirton (1983) as the origination point for the *M. adductor mandibulae internus pterygoideus*. Posterior to this concavity, the sheet narrows and is variably angled laterally (compare GLAHM V1921 with NHMUK PV R2180 and R3893).

The quadrate ramus is separated from the palatal ramus by a constriction formed by emarginations for the subtemporal fenestra laterally and the interpterygoid vacuity medially. Posteriorly, it is drawn out laterally, medially and dorsally into three wing-like flanges that hold the basisphenoid and quadrate. Laterally, the dorsal and lateral processes together form a continuous, slightly concave surface for contact with the medial face of the pterygoid lamella of the quadrate. The ventral flange of the supratemporal overlaps the medial surface of the dorsal wing of the pterygoid (as noted by Andrews 1910, p. 28; Kirton 1983, p. 40). The medial wing extends ventral to the lateral bar of the stapes and forms a shelf, dorsally holding the basisphenoid; the anterior portion of the medial wing forms a socket to accommodate the basipterygoid process. Ventral to the stapes, the pterygoid forms a floor to the cranioquadrate passage and possibly the inner ear cavity (Kirton 1983). The posterior edge of the medial and lateral wings bear irregular striations and pitting that extends ventrally and may mark the location of muscle insertion for the hypaxial series. This inference comes from the lack of enlarged basal tubers on the basioccipital in *Ophthalmosaurus icenicus* onto which the muscles are attached in other reptile groups.

Quadrate. The large and robust quadrate consists of two lamellae: the medial pterygoid lamella, facing posteromedially, and the lateral occipital lamella, facing posterolaterally; the latter is visible in occipital view and bears the articular condyle ventrally (Text-figs 4a, 5b, 9; Table 2; Pl. 6, figs 3–5, Pl. 29, fig. 3). In occipital view, the quadrate has a broad C-shape – convexly curved medially and emarginated laterally to form the posteromedial border of the quadrate foramen. The dorsal portion of the external face of the occipital lamella is smooth, slightly convex laterally and, in some specimens, a small facet is developed dorsally (e.g. GLAHM V1920), associated with a change in surface texture, which indicates overlap by the lateral lamina of the supratemporal. Ventral to this, the external surface is raised in some specimens along the dorsal margin of the quadrate foramen dorsolaterally from the stapedial facet (e.g. LEICT 100’1949/197). The ventral portion of the occipital face is markedly concave dorsoventrally, broadening towards the margin of the articular condyle on the ventral surface of the quadrate. A small rugose area marks the facet for the quadratojugal, just

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dorsal to the condyle, along the emarginated lateral margin. The quadratojugal also contacts the emargination dorsally, forming the lateral border to the quadrate foramen. Externally, the pterygoid lamella is largely planar. The border with the occipital lamella is marked by a ridge that becomes less well defined ventrally. Medial to this border, and at, or ventral to, one-half of the height of the quadrate, is the elliptical stapedial facet. This facet varies in its excavation and position between specimens; it appears as a shallow rugose depression. When the facet is more deeply excavated, it is surrounded by a raised and sharp ridge, particularly defined posteriorly, with a prominent tuberosity ventral to the facet, seen in well ossified individuals (as in GLAHM V1878). The tuberosity may be extended into a ridge, and features minute foramina leading Kirton (1983) to interpret this tuberosity as the attachment point for the ligament that bound the quadrate and pterygoid. On the floor of the stapedial facet, there is an irregular growth that Kirton (1983, p. 37) suggested to be the point of connection for the intercalary cartilage, between the stapes and quadrate. The dorsal one-third of the pterygoid lamella is roughened and was overlapped by the ventral ramus of the supratemporal, which wrapped around onto the occipital lamella. The ventral two-thirds of the quadrate, excepting the stapedial facet, were closely applied to the quadrate flange of the pterygoid.

Laterally, the margin of the lateral emargination of the quadrate is rounded and smooth, made up of finished bone. The dorsal and medial edges of the quadrate are roughened and grooved for the application of the cartilage that surrounded this bone. Dorsally, the margin of the quadrate slots into a ventral groove on the lateral ramus of the supratemporal (see above). The anterior cartilage may have met the epipterygoid, or extended to this region, even if it remained unossified, as suggested by Kirton (1983, pp

36–37) in *Ophthalmosaurus icenicus* and McGowan (1973a, pp 23–25) in *Ichthyosaurus* (see above). Andrews (1910, p. 19) noted that NHMUK PV R2133 has a well-developed angular protrusion on the ventromedial portion of the quadrate margin. The internal (anterior) face of the quadrate is concave and forms much of the smooth posterior wall of the adductor chamber. The central portion of this face likely provided attachment for the *M. adductor mandibulae posterior*, which may have originated from a depression in this area. A second, more dorsal depression may be seen (as in GLAHM V1899) from which the *M. adductor mandibulae externus* complex may have originated (Kirton 1983). The ventral surface of the quadrate forming the robust and broad articular condyle is irregularly pitted for the application of the articular cartilage. This face is convex both dorsoventrally and laterally, allowing smooth motion of the jaw articulation. The condyle is formed of two bosses, positioned more anterior and posterior and facing anterolaterally and posterolaterally respectively, separated by a groove, approximately transversely oriented. Medially, the condyle is horizontal, but laterally is dorsally deflected, and the groove between the bosses curves anteriorly. The more anterior boss is smaller than the posterior, and articulates with the anterolateral portion of the glenoid fossa on the surangular. The more posterior boss articulates with the concave anterior face of the articular.

The quadrate is highly variable between specimens and individuals of *Ophthalmosaurus icenicus*. This may reflect the degree of ossification exhibited, an effect of the cartilage that surrounds many of the occipital elements, potentially caused by functional-usage or ontogenetic variation. Clear differences can be seen in the ossification of the dorsal and medial margins and the shape of the occipital portion of the lateral emargination. This can cause the outline of the quadrate to vary between wide and rounded to narrower and squared (compare GLAHM V1878 and NHMUK PV R2133), as noted by Andrews (1910) and Appleby (1956). The development of the stapedial facet, its position and surrounding features also varies: NHMUK PV R2133 shows the stapedial facet as on the ventral portion of the bone and with a low ridge outline (possibly reduced by poor preservation), whereas in GLAHM V1920 it is slightly more dorsally positioned.

Parabasisphenoid. The parabasisphenoid (parasphenoid-basisphenoid) is a bone formed by the fusion of the parasphenoid to the ventral surface of the basisphenoid, and therefore these are considered together in the present study (Text-figs 5b, 10; Pl. 7). The cultriform process of the parasphenoid is frequently broken and poorly known in *Ophthalmosaurus icenicus*. This forms the base of the braincase, extending forwards to be held between the anterior rami of the pterygoids (see above). Here the parabasisphenoid is pinched in ventrally and so has a diamond cross section in anterior and posterior views, narrowing anteriorly. Posterior to the parasphenoidal pterygoid facets, the dorsal surface of the cultriform process becomes concave and roughened, and was overlain by the fused trabecular cartilages. For much of the length of this process the bone is deep and narrow, with a medial ventral ridge, but becomes wider and more elliptical posteriorly. The parasphenoid rostrum becomes thinner dorsoventrally as it meets the basisphenoid. Although often difficult to discern, the parasphenoid widens and extends around anterior and lateral margins of the internal carotid foramen (see below) on the ventral surface of the basisphenoid. The parasphenoid also forms a small shelf on the anterior margin of the elliptical external carotid foramen (see NHMUK PV R2180 and GLAHM V1886).

The posterior portion of the parabasisphenoid (basisphenoid) forms a large, complexly shaped ossification anterior to the basioccipital, with lateral wings anteriorly to hold the palatal ramus of the pterygoid. The trapezoidal anterior face of the basisphenoid is mostly smooth periosteal bone and extends laterally from the main body by the basipterygoid processes. This surface extends posteriorly as a concavity on the lateral surface of the basisphenoid and lines an extracranial space, an anterior part of the cranioquadrate passage (Goodrich 1930). Kirton (1983) proposed that the muscle slips from the extrinsic eye muscle group might insert here, as in extant crocodilians (Underwood 1970), although there is no evidence of scarring. A small pit, lateral to the pituitary fossa (see below) may mark the attachment point of an eye muscle. Some specimens preserve small nutritive foramina piercing the anterior surface of the basisphenoid. Medially, the *dorsum sellae* rises vertically, posterior to the pituitary fossa, interrupting the smooth anterior surface. The *dorsum sellae* is developed dorsally into two processes separated by a notch that continues posteriorly on the posterodorsal surface. Kirton (1983) interpreted these processes as ossifications at the base of the *pilae antoticae*. Ventral to the *dorsum sellae*, the paired internal carotid arteries passed through an undivided foramen that is angled posteroventrally, entering the basisphenoid on its ventral surface and narrowing along their course. The hollow on the anterior surface of the basisphenoid between the internal carotid foramen and the *dorsum sellae* is the pituitary fossa marking the area where the pituitary body would have been located. Ventral to the pituitary fossa, lateral to the midline are a pair of slightly raised ovoid depressions that mark the posterior limit of the trabecular cartilages (Kirton 1983), termed the lower cylindrical processes by Siebenrock (1893, translated in Siebenrock 1894; Andrews 1910).

Laterally, the basisphenoid is drawn into the short and robust basipterygoid processes, each with a rugose distal surface and low marginal ridge indicating that this would have been covered in life by cartilage. These processes fit into corresponding sockets between the palatal and quadrate rami of the pterygoids, and the inferred thickness of cartilage led Kirton (1983) to suggest that some movement was possible between the palate and braincase. However, the elongate anterior facets of the pterygoid with the vomer and palatine, and the interlocking contacts on these bones, suggest that movement of the pterygoid would have been minimal. The basipterygoid processes have a groove on their posteroventral edges marking the passage of nerves or blood vessels, possibly the palatine ramus of the facial (VII) nerve (Kirton 1983, p. 22). The lateral surface posterior to the basipterygoid processes is heavily pitted and angled dorsolaterally and slightly posteriorly forming the stapedial facet, which contacts the ventral part of the medial surface of the stapes. This surrounding cartilage may have led to variation in the ossification of the basipterygoid processes: NHMUK PV R2164 shows well defined, squared processes, whereas in R2161 they are more spread and rounded in ventral view (Andrews 1910, fig. 6). The ventral surface of the basisphenoid is finished in periosteal bone and is rounded posteriorly. This surface is pierced centrally by the unpaired internal carotid foramen. The entirety of the posterior surface is deeply pitted for contact with the basioccipital. This is split into two portions, a vertical region ventrally and a posterodorsally angled region dorsally, separated by a horizontal ridge. Vertical ridges separate the basioccipital facet from the lateral stapedial facets. A median groove runs dorsoventrally across the whole of the posterior surface, meeting the dorsal notch between the two processes of the *dorsum sellae*. This groove may indicate that the basisphenoid originally ossified from two lateral centres (Andrews 1910; Kirton 1983) and some examples show cracks or are broken along this line. Andrews (1910) and McGowan (1973a) concluded that the dorsal notch marked the point of an upturned vestige of the notochord.

Prootic. The small, subrectangular prootics are surrounded by the cartilage of the otic capsule, lacking direct bony contact with the rest of the braincase (Text-figs 11, 16; Pl. 8, figs 1, 2). This, and the disassociated nature of the material, makes their orientation and placement problematic. Kirton (1983) resolved this problem by comparing the prootic of *Ophthalmosaurus icenicus* with an acid-prepared Liassic skull (NEWHM G.44.19) indicating that the figured prootic (Text-fig. 11, NHMUK PV R4522) must be a right prootic. This bone takes the shape of a widened D in posterior view: the lateral edge is straight whilst the medial edge is gently curved. Along with the semicircular canals on the internal face (see below), this feature can aid in orienting the bone. This orientation agrees with McGowan (1973a), but disagrees with Appleby (1956, p. 412, fig. 4) who had reversed the two canals and sidedness of the bone.

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The external (anterior) face is roughened and irregularly pierced by nutritive foramina for the origin of muscle slips. Kirton (1983, after Haas 1973) suggested that either part of the *M. adductor mandibulae externus* or the *M. protractor pterygoidei* attached there as in living reptiles. Ventrally and medially, a ridge is developed for this attachment towards, and parallel to, the margins of the prootic. The edges of the prootic were continuous with the cartilage of the otic capsule and so are irregularly pitted. The thickness of the prootic represents cross sections of the walls of the otic capsule, and these are thickest at the ventralmost corner of the bone. The internal (posterior) face of the prootic, like the opisthotic and supraoccipital (see below), shows the impressions of the membranous labyrinth. These each take the form of a V-shaped, smooth-floored excavation. The position of the prootic in the anterolateral region of the otic capsule means that the limbs of the impression should accommodate the anterior vertical and the horizontal semicircular canals respectively (Baird 1970; Kirton 1983). Kirton's (1983, pp. 27–28) comparison with modern reptiles led her to conclude that the wider medial channel must have accommodated the horizontal canal, whereas the narrower lateral impression housed the anterior vertical canal. This was based upon the assumption that the horizontal canal passed externally from its source to a terminal ampulla (Hamilton 1964; Baird 1970), whereas in Appleby's (1956) interpretation, the horizontal canal would pass internally; Kirton's view is followed here (Evans 2008). The horizontal canal swells ventrally and this space is occupied by the terminal ampulla for the anterior vertical canal ("anterior ampulla" of Baird 1970, fig. 7). Medial to the depression for the anterior ampulla, where the two arms of the V converge, the impression is widened further, possibly representing the position of the sacculus. Appleby (1956) indicated this was divided into two parts: the ventral part is a continuation of the horizontal canal impression that Kirton (1983) interpreted as part of the utriculus and may be offset slightly (Andrews 1910, fig. 3A, NHMUK PV R2162).

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Opisthotic. The opisthotics consist of a massive occipital portion, which takes part in the walls of the otic capsule, and a slender paroccipital process that reaches dorsolaterally towards, and articulates with, the skull roof (Text-figs 12, 16; Pl. 8, figs 3–8, Pl. 29, fig 3). Appleby (1956, p. 414) disagreed with Andrews' (1910, p. 9) orientation of the opisthotic; Appleby's interpretation is followed here. The anterior face is concave and the surface is roughened, with small nutrient foramina, for the attachment of muscle slips, possibly of the *M. adductor mandibulae externus* group (Kirton 1983). A ridge extends dorsolaterally across this face and along the paroccipital process. This surface extends dorsally, where it is also roughened and pierced by foramina, indicating further muscle attachment. Ventrally, the opisthotic is roughened for the application of cartilage, and divided into two facets for articulation with the basioccipital anteromedially and the stapes laterally. The basioccipital facet is smaller and consists of a dorsal deflection of the posteromedial corner of the ventral surface of the opisthotic. A larger area of the ventral surface comprises a facet for the stapes, which is divided into two parts by a groove that runs mediolaterally. The anteromedial face of the opisthotic faces the otic capsule. This face shows a wide V-shaped impression formed by two smooth-floored channels that join anteroventrally, impressions of the posterior components of the membranous labyrinth of the inner ear. The posterior channel likely housed the posterior vertical semicircular canal (Baird 1970; Kirton 1983). The anterior channel curves slightly towards the horizontal and is interpreted as the impression for the horizontal semicircular canal (Baird 1970; Kirton 1983). A large concavity in which the posterior ampulla was likely held is developed where the two channels join (Baird 1970; Kirton 1983), and the posterior channel widens towards this junction. The bone that surrounds

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the labyrinth impression is pitted irregularly for the cartilaginous component of the otic capsule. The impressions of the labyrinth are continued by similar impressions seen on the anterolateral face of the supraoccipital and the posterior face of the prootic (see above). Slightly anterior to the ventral ampulla impression, the groove on the ventral surface notches the ventral margin. The medial articulating surface is narrower posteriorly and also notched by the vagus foramen on the posterior face ("jugular foramen" of Andrews 1910), which may curve forward around the anteromedial face (see NHMUK PV R2133).

The posterior face of the opisthotic dorsally shows a continuation of the pitting for muscle attachment from the dorsal surface. Ventral to this, the lateral wall of the channel of the vagus foramen continues horizontally. This is held medially between the dorsal portion of the opisthotic dorsally, which continues as a ridge from the paroccipital process, and the dorsal margin of the basioccipital facet ventrally, which is here raised. The opisthotic possibly contacts the exoccipital around this foramen, but an articular facet can only be seen in well-ossified specimens (NHMUK PV R2161 and LEICT 100'1949/64; Appleby 1956) indicating that the contact was not close, except in these specimens (Kirton 1983). The dorsal exoccipital facet, when ossified, is developed on a bony projection from the dorsomedial corner of the bone, whereas the ventral facet is developed only rarely (Appleby 1956; Kirton 1983). The opisthotic is drawn out dorsolaterally into the paroccipital process, narrowing slightly distally. Kirton (1983) described this as slender, however it can appear variably developed depending on the length of the paroccipital process; the holotype of *Ophthalmosaurus icenicus* (NHMUK PV R2133) has rather a thick, short paroccipital process that is slightly compressed dorsolaterally. Dorsally, this process forms the floor of the posttemporal fossa, and ventrally contributed to the roof of the cranioquadrate passage. At its distal end, the paroccipital process is flattened and roughened for the application of cartilage where it meets the ventral ramus of the supratemporal (see above). The tip is often poorly ossified, and it ends in a blunt ellipse with little evidence for a developed facet on the supratemporal. In well-ossified individuals (e.g. the holotype of *Ophthalmosaurus icenicus*, NHMUK PV R2133, and LEICT 100'1949/64) the distal end forms a two-part supratemporal facet, although still some cartilage would have intervened. Kirton (1983) further suggested the possibility of some movement between these elements, but the two-part opisthotic facet on the supratemporal would likely have mitigated this.

Supraoccipital. The supraoccipital forms an arch around the dorsal part of the *foramen magnum* and takes part laterally in the otic capsule (Text-figs 4b, 16; Pl. 9, figs 1–5). This arch sits atop the exoccipitals (see below) and underlaps the parietals medially (see above). Anteriorly, the dorsal portion of the surface of the supraoccipital is smooth with two anterior-directed ridges that form an anteriorly-open C-shape in dorsal and ventral views. Ventrally, the anterior surface is slightly roughened, especially anteriorly. Two laterally directed foramina pierce the lateral walls on the medial surface; intraosseous canals pass through to the posterior face. The dorsal margin of the supraoccipital has a shallow, transverse groove that is roughened, indicating the presence of the cartilaginous portion of the supraoccipital dorsally, ventral to the parietal. This margin and groove are variably developed depending on the level of ossification of the individuals. The dorsal groove widens laterally and anteriorly towards the edges of the

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supraoccipital and is separated from the internal face by a sharp ridge. The ventral exoccipital facets show the effect of the strong anterior extension of the supratemporal in their apex-anterior, triangular shape. These facets are concave to accept the dorsal surface of the exoccipitals, which fits closely with only a thin layer of connective tissue intervening (Kirton 1983). On the anterolateral face of the supraoccipital, further impressions of the structures from the otic capsule can be seen, which face ventrolaterally. The impressions are T-shaped, the stem directed anteroventrally. Kirton (1983) interpreted these as impressions of the posterior vertical (dorsal) and anterior vertical (ventral) semicircular canals at their point of origin from the common crus.

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The posterior face of the supratemporal is roughened dorsally where it is overlapped by the parietal, smoother ventrally, and is slightly convex following the dorsoventral curvature. Dorsally, it may be squared or more rounded, like a semicircular arch (compare NHMUK PV R2162 and LEICT 100'1949/43). Lateral to the *foramen magnum*, the surface is pierced by foramina (from the internal surface) that lie in shallow depressions and face posterolaterally. Lateral to these foramina, the bone is notched immediately dorsal to the capsular region. Above the *foramen magnum*, the internal arch of the supraoccipital is variable. This may be a simple arch, but frequently a blunt median process projects from the dorsal surface of the *foramen magnum*. The ventral opening of the arch on the supraoccipital is constricted by the medial expansion of the bone in most specimens ("lateral processes" of Andrews 1910; Appleby 1956). Where present, the surfaces of these projections are roughened for the attachment of cartilage or ligaments that may have separated the supratemporal arch from the *foramen magnum* ventrally (Andrews 1910; Kirton 1983). Andrews (1910) suggested that the spinal cord occupied only the ventral portion (i.e. between the exoccipitals) rather than the entire, considerable, vertical extent of the *foramen magnum* (Kirton 1983). The dorsal (supraoccipital) portion of the *foramen magnum* may have carried other structures, including perhaps the paired cerebral veins, as suggested by Kirton (1983), in the two concavities either side of the median process in the roof of the *foramen magnum*. Alternatively, the lateral foramina may have allowed passage of the lateral branches of the *vena capitis dorsalis* into the cranial cavity (Kirton 1983). In some reptile groups, these enter the braincase anterior to the supraoccipital, but may have moved posteriorly, becoming "trapped" (Kirton 1983, p. 31) in the lateral edge of the supraoccipital in *Ophthalmosaurus* and *Ichthyosaurus*. Furthermore, McGowan (1973a), following Andrews (1910), suggested that the foramina carried extensions of the endolymphatic sac, as in extant lizards, for example, Iguanidae and Gekkonidae. Although the purpose of the endolymphatic sac is uncertain (Kluge 1967, 1987; Bauer 1989), it seems to play an important role in adult calcium metabolism or skeletal ossification (Mangione & Montero 2001; Daza *et al*. 2008).

Exoccipital. The two exoccipitals form the sides of the *foramen magnum* as short columns between the supraoccipital dorsally and the basioccipital ventrally (Text-figs 13, 16; Table 2; Pl. 9, figs 6–11). Dorsally, the contact surface is smooth and slopes ventrally and anterolaterally, following the ventral surface on the supraoccipital. Lateral to the supraoccipital facet, each exoccipital has a small contact with the opisthotic. This facet is divided into two parts, and the dorsal part forms a small lip over the contribution of the exoccipital to the vagus foramen. The ventral contact with the opisthotic occurs along the ventral edges of the exoccipital ("posteroventral protuberance" of Appleby 1956). As mentioned above (see Opisthotic) the contact is close only in well-ossified individuals, otherwise cartilage intervened. The ventral surface of the exoccipital is roughened where cartilage was applied for contact with the basioccipital. This facet is elliptical and convex to fit into the exoccipital facets on the basioccipital, although this contact was not as close as the contact between exoccipital and supraoccipital. Anteriorly, the exoccipital is drawn out into tongue-like projections making it more triangular ventrally and extending the contact with the basioccipital (Andrews 1910). Dorsal to this, the dorsal surface protrudes slightly anteriorly to form a groove that extends around the bone laterally as the vagus foramen. Medially, the exoccipital is pierced by two foramina anteriorly (the posterior is larger), on this tongue, interpreted by Kirton (1983, after Andrews 1910) as exits for branches of the hypoglossal (XII) nerve. These foramina pass through the exoccipital before emerging on its lateral and posterior faces. The anterior lateral exit is the smaller foramen and opens into the vagus foramen. Maisch (1997a) described a pair of exoccipitals (SMNS 10170), one of which had three foramina (five between the two exoccipitals) that may have carried the fourth branch of the XII nerve. Specimen GPIT 1795/2 shows a splitting of the anterior foramina. When joined, this would carry two branches (first and second) of the XII nerve. A ridge on the posterior face, extending obliquely down from the dorsomedial edge, is roughened, possibly for the attachment of the occipital muscles (Kirton 1983).

Basioccipital. The massive basioccipital comprises the lowest portion of the occiput and forms the whole, large sub-hemispherical boss of the occipital condyle (Text-figs 4, 5, 14, 16; Pl. 10, Pl. 29, fig. 3). The anterior and lateral faces are flattened and heavily pitted for a relatively thick covering of cartilage (Kirton 1983). The ventral one-half of the anterior face is developed into two oval bosses, separated by a central vertical groove, that mark the contact with the basisphenoid. These bosses form a notch in the ventral surface of the basioccipital that is particularly evident in specimens where the groove is well developed (e.g. NHMUK PV R4522; Text-fig. 14). A diamond-shaped area that bears a small central pit is developed dorsal to the basisphenoid facet. This area may be drawn out into an anterior process (shown in GLAHM V1070) that Kirton (1983) proposed as the homologue of the basioccipital peg more clearly seen in *Ichthyosaurus* (McGowan 1973a). Kirton (1983) further proposed that this structure was a vestige of the notochord extending into the *cavum cranii*. This feature is highly variable between taxa and its presence is homoplastic across ichthyosaur phylogeny (Motani 1999b; Maisch & Matzke 2000). As the diamond-shaped area in *Ophthalmosaurus icenicus* matches the relative position to the notochordal pit in *Ichthyosaurus*, it is likely that this does represent a vestige of the basioccipital peg. The development of the basioccipital peg may represent the extent of ossification of braincase elements in different taxa. Dorsally, the basioccipital features two lateral facets for the exoccipitals. These are concave, rounded depressions with a heavily rugose surface into which the ventral face of the exoccipital fits, likely with much cartilage intervening. The exoccipital facets are almost continuous with the anterior and lateral faces of the basioccipital, but the posterior and medial margins are raised into a high wall. Between the two exoccipital facets is a medial sagittal ridge with a central, longitudinal channel, surfaced with finished bone. This marks the ventral surface of the *foramen magnum*, which is surrounded laterally by the two exoccipitals and the supraoccipital dorsally. Variation is seen in the surface of this channel: the holotype of *Ophthalmosaurus icenicus* (NHMUK PV R2133) has an hourglass-shaped area of smooth bone, while in NHMUK PV 47430 there is only a small triangular section of smooth bone posteriorly, surrounded by roughened bone. The posterior articular surface of the parasphenoid faces posterodorsally, while the anterior face of the basioccipital is flat. Therefore, in articulation, the basioccipital is angled with the anterior surface facing anteroventrally and the basioccipital condyle directed posterodorsally (Text-fig. 16b).

The lateral faces of the basioccipital are divided into two facets that mark the contact with the stapes ventrally and opisthotic dorsally. Like the anterior face, this region is rugose for cartilage attachment. The opisthotic facet is smaller than the stapedial facet and divided into two parts: a posterodorsal, deeply pitted, triangular portion, and ventral and anterior to this, a circular raised area of smooth bone. Based on her reconstruction of the occipital region, Kirton (1983) posited that the cartilage between the opisthotic and basioccipital thinned anteroventrally, suggesting a thinning of the walls of the otic capsule. This is coupled with a small depression just anterior to the contact surface with the opisthotic, interpreted as part of the cochlear recess. The ventral portion of the lateral face is continuous with the basisphenoid facet on the anterior face of the basioccipital and contacts the basioccipital facet on the medial head of the stapes.

The articular condyle occupies much of the central portion of the posterior face of the basioccipital. This surface is irregular for application of the articular cartilage, but not as rugose as the anterior face. The convex condyle is centrally placed and has a near-central notochordal pit that is elongated dorsoventrally and variably developed. Appleby (1956, p. 407) further described discontinuous concentric striations that surround the notochordal pit in well-preserved specimens. Andrews (1910, p. 6) noted that the dorsal part of the condyle might be pinched, as in the type specimen (NHMUK PV R2133). The wide extracondylar area, which extends from the sides of the basioccipital ventrally as an elongate, concave strip is developed around the condyle (Table 3). This includes two convex areas of smooth periosteal bone that are separated from the condyle by posteromedial ridges. The smooth areas of the extracondylar area are variable in extent, and may reach a point dorsal to the notochordal pit on the condyle in some specimens, but not so far dorsally in others, with great variation between these extremes (Appleby 1956). Although not always clear, these areas are separated ventrally by a narrow, roughened area around the ventral notch that may be raised dorsal to the flanking smooth surfaces.

Stapes. Articulating between the braincase and the quadrate, the stapes is integral to the posterior skull, despite being a hyoid derivative (Romer 1956; Text-figs 15, 16; Table 2; Pl. 11, Pl. 29, fig. 3). The stapes has a massive medial head that contacts the basioccipital and basisphenoid and a more slender shaft that extends ventrolaterally to contact the quadrate. Medially, the head of the stapes abuts against broad surfaces on the sides of the basioccipital and basisphenoid (see above) rather than fitting into a *fenestra ovalis* (Romer 1956; Kirton 1983). This head of the stapes is broad, convex and rugose for the application of cartilage. Kirton (1983) noted that only a small area of the stapes contacts the periotic (perilymphatic) cistern, which is unlike the more extensive contacts that are seen in many modern reptiles (Baird 1970). Appleby (1961) reported an anterodorsally directed groove on the posterior side of the head. Dorsally, the stapes articulates with the ventral side of the opisthotic in a bipartite facet, each portion separated by an anteromedially directed groove that corresponds to a similar groove in the stapedial facet of the opisthotic (see above). When in articulation, this groove forms a channel, probably accommodating nerves. The opisthotic facet on the stapes is roughened and cartilage may have intervened in the contact, leading to variable development of this facet. Clear separation can be seen in the articulated braincase of specimen PETMG R220 (Text-fig. 16). The restoration of this specimen is however imperfect, for example, the right stapes does not contact the quadrate laterally (see below).

Lateral to the opisthotic facet, the dorsal surface of the stapes is smooth and continuous anteriorly with the lateral surface of the basisphenoid. This surface falls from the high medial head as the stapes narrows laterally into its shaft. In this portion, the stapes forms part of the posteroventral floor of the cranioquadrate passage dorsally. The stapes contacts the pterygoid in two facets, medially and laterally. The medial contact is ventral on the medial head, which rests on the dorsal surface of the medial flange of the pterygoid (see above), although there is no clear facet on the stapes. Laterally, the stapes contacts the posterior edge of the quadrate flange of the pterygoid where the pterygoid is overlapped by the supratemporal. This facet is more clearly seen as a rugosity on the anterior surface of the distal stapedial shaft that extends for most of the length of the shaft. Kirton (1983) described NHMUK PV R2133 as showing an articulated stapes, quadrate, supratemporal (her squamosal) and pterygoid in articulation. While these elements are no longer articulated, it can still be seen that the stapes had extensive contact with the supratemporal along the anteriormost surface of the stapedial shaft. Dorsal to the rugosity of the pterygoid-supratemporal facet is a ridge that twists ventrally along the shaft as it nears the medial head of the stapes. The ventral margin of the stapedial shaft is notably excavated lateral to the medial head of the stapes, between the two pterygoid facets, creating a space between these two bones; there is no stapedial facet. The distal face of the shaft is a pinched elliptical facet that contacts the medial face of the quadrate. Cartilage would have been applied to the pitted surface and the level of individual ossification would cause the variable development in the stapedial facet on the quadrate (see above).

The relationship of the stapes to its surrounding tissues has caused some of the many features described above. The channel between the opisthotic-stapes contact was assigned to the glossopharyngeal (IX) nerve by Andrews (1910), Appleby (1956, 1961) and Kirton (1983). Their proposed route for the glossopharyngeal (IX) nerve in *Ophthalmosaurus icenicus* is unusual among reptiles. In most living reptiles, the nerve exits through the vagus foramen (see Opisthotic and Exoccipital above), although some taxa have an additional foramen through which this nerve exits the skull (e.g. some turtles: Bellairs & Kamal 1981). Reconstruction of the otic capsule (Text-fig. 16) suggests that the channel emerges from the most ventral region of the otic capsule, near the cochlear recess of the osseous labyrinth (Kirton 1983). Kirton alternatively proposed that it could carry the hyomandibular branch of the facial (VII) nerve. The facial (VII) nerve originates from the anterior edge of the otic capsule, normally passing posterodorsally over the head of the stapes, medial to the dorsal process (Hopson 1979; Stark 1979). In this interpretation, the anterior half of the opisthotic facet on the stapes may be equivalent to the dorsal process. McGowan (1973a) suggested a similar channel in *Ichthyosaurus* may have accommodated the stapedial artery. However, Kirton (1983) thought this unlikely as a similar route is absent in other reptiles: the stapedial artery passes extracranially along the lateral wall of the braincase, dorsal to the stapedial shaft and alongside the *vena capitis lateralis* (Bellairs & Kamal 1981). The glossopharyngeal (IX) nerve typically passes medial to the stapedial artery, ventral to the otic capsule, supporting its passage between the opisthotic and stapes. The space created between the stapes and pterygoid may have allowed passage of the stapedial artery. A notch that may mark the upwards passage of this artery dorsal to the basipterygoidal processes is present on the anterior portion of the medial head of the stapes (Kirton 1983). Appleby's (1961) reconstruction does not show a space between the stapes and pterygoid. He thus concluded that the stapedial artery passed through the groove on the posterior side of the stapedial head. This groove may instead mark the continued path of the structures that passed through the channel in the opisthotic-stapes contact; the absence of a continuation for this groove and its ultimate origin makes its true nature uncertain.

Dentary. The dentary forms much of the anterior and lateral portions of the mandible, extending for much of its length, and holds the entirety of the lower tooth row (Text-figs 4a, 17; Table 2; Pl. 27, figs 1, 2). Its form corresponds to that of the premaxilla in many respects. The anterior extremity tapers towards the anterior of the mandible and medially the two dentaries meet in the anterior part of the mandibular symphysis, which is continued posteriorly by the splenials (Andrews 1910). Externally, the dentary is convex, and wide dorsally to accommodate the tooth row. Towards the dorsal part of the external face, a longitudinal groove with associated foramina passes into an intraosseous passage, akin to that seen in the premaxillae, and extends for approximately two-thirds of the dentary. Anteriorly, this groove becomes discontinuous and the pitting for the foramina that pierce the groove is clearer. From the anterior tip, the dentary deepens posteriorly, reaching its maximum depth at about one-half of its length. The medial face of each dentary is grooved and when articulated they form the anterior portion of the channel which holds the Meckelian cartilage. Like the premaxillae, the anteriormost tips of the dentaries are separated and this space would likely have been filled by connective tissue. Posterior to their anterior separation, the dentary is largely in contact with the splenial medially and the internal face is longitudinally grooved and roughened. It is often difficult to see the anterior extent of contact with the anterior fork of the splenial, but this contact may be marked by changes in the surface texture of the dentary towards the dorsal and ventral margins of the medial surface. At the posterior of the mandibular symphysis, there is a low ridge towards the ventral of the medial face of the dentary that runs ventrally and around its ventral margin. This marks the extent of contact with the angular, which intervenes between the dentary and splenial and briefly runs along the ventral margin of the dentary.

Dorsally, the dentary forms the alveolar groove between the raised lateral and medial walls. The anteriormost portion, along part of the symphysis has no medial wall and the teeth are small. Strong depressions on the lateral wall of the alveolar groove indicate close placement of the teeth. Posteriorly, the groove widens to accommodate larger teeth and the medial wall is raised dorsal to the lateral wall so that the curved teeth (see below) are angled dorsolaterally like in the premaxilla. The groove extends and is dentigerous for about two-thirds of the length of the mandible, almost the entire length of the dentary. Towards the posterior of the dentary, the alveolar groove narrows, and the posteriormost tooth is positioned slightly posterior to the external naris. The groove shallows, narrows, and is pinched out posterior to the posteriormost tooth by the lateral and medial walls. Posteriorly, the dentary tapers dorsoventrally and mediolaterally, becoming more superficial on the lateral face of the mandible. Here, the dentary is excluded from medial view by the surangular and splenial.

Splenial. The splenial covers much of the internal (medial) surface of the lower jaw (Text-fig. 17; Pl. 12, figs 1, 2, Pl. 27, figs 3, 4). Its anterior region is forked, with the rami applied to the dorsal and ventral margins of the dentary, and allowing the confluence of the Meckelian canals between the two dentaries. The rami of the fork are also rugose on their exposed medial faces marking their participation in the mandibular symphysis (Andrews 1910), which extends posterior to the main body of the splenial. The opening for the Meckelian canal may be the foramen described by Gilmore (1905, 1906). For much of its length the splenial takes the form of a thin, vertical sheet of bone. Dorsally placed on the internal (lateral) face, a ridge with a wide, longitudinal groove ventrally is developed where the splenial forms the medial and dorsal walls to the Meckelian canal. The ridge becomes lower and less distinct posteriorly, gradually moving towards the gently undulating dorsal margin of the bone as the prearticular intervenes. Andrews (1910) thought that the surangular formed a portion of the internal wall of the alveolar groove; this is in addition to the dentary so that the surangular does not have any indentation from the tooth placement. A small part of the splenial is in contact with the surangular, but posteriorly, this is usurped by the prearticular. The ventral margin is simpler as the sheet of the splenial simply curves around the angular, a sliver of which can be seen in lateral view. Posteriorly, the splenial narrows dorsoventrally into a point lying against the angular, with its ventral margin fitting into a small groove. Dorsally on this taper, there is a small anteroventrally-aligned notch directed towards a small foramen, possibly for passage of the *chorda tympani* branch of the VII nerve (Kirton 1983).

Surangular. The surangular forms much of the posterior part of the mandible, between the angular, prearticular and articular (see below), as well as sharing the jaw articulation with the articular (e.g. NHMUK PV R2180, Pl. 14, figs 1, 2, 5, 6) and forming a major attachment for muscle groups (Text-fig. 17; Pl. 12, figs 3, 4, Pl. 27, figs 5. 6). Much of its anterior section is a vertical sheet, placed medial (internal) to the dentary, which forms the lateral wall of the Meckelian canal. This is marked by a ridge dorsal to a channel in the medial surface of the surangular that is placed dorsally at its anterior, but becomes more centrally placed as the surangular dorsoventrally widens posteriorly. Both the dorsal and ventral margins are rounded, especially posteriorly, as the dentary and angular respectively surround the surangular. The anterior extremity of the surangular is unknown. Another groove (the *fossa surangularis*) runs along the lateral face of the surangular ventral to the dentary and is pitted by foramina that pass through the bone and into the Meckelian canal, allowing passage of nerves and blood vessels. These nerves and vessels emerge medially through an elongate, ventrally placed foramen. Posteriorly, this groove becomes discontinuous and is reduced to several pits of the foramina.

The surangular is held between the dentary (laterally) and the splenial (medially) for much of its length; although some evidence of the extent of contact can be seen, there are no well-developed facets. Posterior to the termination of the alveolar groove, the surangular becomes more robust. The dorsal margin is drawn up dorsally into a low, rounded paracoronoid process, to which the *M. adductor mandibulae internus pseudotemporalis* division was attached (Kirton 1983). Posterior to the paracoronoid process, the dorsal margin of the surangular is raised into a sharper, dorsomedially directed preglenoid process. Striations cover this process on its medial surface and over a rounded ridge situated posteroventrally, likely indicating attachment area of the *M. adductor mandibulae externus* group (hence is termed the "M.A.M.E. process" by Fischer *et al.* 2012, p. 14; Kirton 1983). Andrews (1910) considered these two processes together to be the functional equivalent of the coronoid process, the coronoid being non-ossified or lost (see below). The dorsal margin is excavated posterior to these processes, marking the location of the jaw glenoid. Posterior to the paracoronoid and preglenoid processes, the dorsal margin of the surangular is deflected laterally and the medial face excavated slightly to form the glenoid fossa. The surface of this area is roughened for the application of the articular cartilage that would have rotated against the anterior boss of the quadrate condyle; the cartilage extended posteromedially onto the articular. Here, there may be a tubercle developed (Andrews 1910). As the angular broadens dorsoventrally towards its posterior end, it covers much of the lateral face of the surangular. The surangular is roughened for this contact, and a low ridge may mark the dorsal line of contact. At its posteriormost part, the surangular is roughened and the posterior margin is crenate where the cartilage of the retroarticular process would have covered it and the angular (see below).

Angular. The angular is an elongate bone that forms the ventral margin of much of the mandible and the floor of the Meckelian canal (Text-figs 4a, 17; Pl. 13, figs 1, 2, Pl. 14). Anteriorly, it is thin and narrow and excluded from view by the dentary and splenial, which envelop the bone and meet ventrally. Along most of the lower jaw, the angular is visible ventrally, and a narrow portion can be seen mediolaterally. Ventrally, the margin is rounded and widens posteriorly, whereas the dorsal margin is moulded into two deep grooves. The more laterally placed groove holds the ventral margin of the surangular and the medial groove forms the floor of the Meckelian canal, which would be filled in life by the Meckelian cartilage. These two grooves are bounded by high walls that ascend medially and laterally on the angular, becoming higher towards the posterior end of the bone. A third groove is placed ventrally on the medial face and holds the ventral margin of the splenial; all three grooves continue along most of the angular. The posterior of the angular curves slightly dorsally and the lateral side ascends to cover much of the surangular (see above). Along its posterior margin, the angular is finely crenate, like the surangular, where it was covered by cartilage of the retroarticular process. Internally, the angular meets the articular, the latter of which has two distinct facets for this contact, and borders the prearticular also (see below; Andrews 1910).

Coronoid. The coronoid in *Ophthalmosaurus icenicus* is lost entirely. Because of this, the muscle attachments of the coronoid process have shifted in *Ophthalmosaurus* *icenicus* to the paracoronoid process of the surangular (see above). Andrews (1910, p. 34, fig. 20) identified the prearticular as the coronoid, however, its true identity was not recognized until later (e.g. Romer 1956, p. 212; Kirton 1983). Martill (1987) also indicated the presence of a right coronoid in BUCCM 1983/1008, but again this likely represents the prearticular. It seems that this element is notably reduced or absent in all ichthyosaur taxa and so makes identification and comparison of this element problematic. The position of the coronoid in the medial lower jaw also makes it likely that any disturbance that would expose this bone may conspire to remove it entirely.

Prearticular. The prearticular in *Ophthalmosaurus icenicus* was identified as the coronoid by Andrews (1910, see above), but this was corrected by Romer (1956, p. 212) and Kirton (1983) (Text-fig. 17; Pl. 13, figs 3, 4). It is an elongate, thin bone, which, coupled with its position in the middle of the mandible, means that it is infrequently preserved and identified. The prearticular forms a very thin medial wall of the Meckelian canal along much of its length, tapering both dorsoventrally and laterally at its anterior end. Its relationship with the angular is unclear, but it may insert into the more medial groove alongside the Meckel’s cartilage, or run along the medial dorsal edge. Arching of the dorsal margin allows the prearticular to contact the surangular for some distance dorsal to the Meckelian canal. The prearticular is obscured from medial view by the splenial. Posteriorly, the prearticular rises towards a peak that lies just ventral to the paracoronoid process of the surangular in articulation (see NHMUK PV R2180); this equates to the coronoid process, although it does not function as such (Andrews 1910). Posterior to region, the prearticular narrows dorsoventrally to form a bar that lies just against the internal face of the medial flange of the angular, forming part of the medial wall of the adductor fossa that separates the prearticular from the surangular. The medial face is rugose and this spreads ventrally onto the angular, possibly marking the insertion of a medial portion of the *M. adductor mandibulae internus pterygoideus* division (Haas 1973; Kirton 1983); similar relations are seen in extant lizards and *Sphenodon*. At its most posterior part, the prearticular covers the ventral edge of the articular.

Articular. This compact and posteriorly rounded bone is found at the posterior of the mandible and forms the posterior surface of the jaw articulation with the quadrate condyle (Text-fig. 17; Pl. 14). It is held by the surangular laterally and the angular and prearticular ventrally so that the ovoid anterior surface is angled slightly dorsally and medially (Text-fig. 17b). This surface meets the articular facet of the quadrate and is slightly concave and pitted for the articular cartilage that would spread between it and the glenoid on the surangular just anterior to the articular. The long axis of this ovoid face aligns with the long axis of the posterior boss of the quadrate, to which it articulates. Ventrally, the articular would have been continued anteriorly by the mandibular cartilage and is pitted for its application. The lateral face is flattened where it meets the surangular laterally, and has a horizontal groove in its middle section that follows the contours of the underlying bone. Andrews (1910) noted that two facets are present ventrally for contact with the medial face of the angular. The medial face is slightly roughened and saddle-shaped; convex dorsoventrally and anteroposteriorly concave. Ventrally this face is roughened for overlap by the prearticular whereas the dorsal margin is much thinner and closely applied to the surangular laterally. The posterior of the articular is round and roughened and continued in cartilage that extended into a short and rounded retroarticular process (Kirton 1983).

Dentition. The dentition of *Ophthalmosaurus icenicus* has long been problematic: the size of the teeth and their poor attachment has meant that few specimens have been recovered with teeth in position, or even with teeth present at all (Text-fig. 18). Early descriptions noted the small size of the teeth and that they might have been restricted to the anterior of the rostrum despite there being well-developed alveolar grooves along the whole of each jaw ramus (see above; Lydekker 1889; Andrews 1907, 1910). Gasparini (1988) described *'Ophthalmosaurus monocharactus'* with several teeth present in the maxilla (figs 2a & 3a), however, this taxon is not consistent with *Ophthalmosaurus* (Maisch & Matzke 2000, p. 89). Kirton (1983) considered *Ophthalmosaurus icenicus* to have approximately 40 teeth in each jaw ramus based on tooth counts on NHMUK PV R3893 and from the impressions in NHMUK PV R4753 and GLAHM V1129. ~~My own (BCM)~~The first author's examination of these specimens shows these to be minimum estimates: in each, teeth may be missing or impressions indistinct, but all can be confidently referred to *Ophthalmosaurus icenicus* based upon associated diagnostic material. NHMUK PV R3893 has at least 27 premaxillary teeth or impressions in each ramus, with the anteriormost tip of the premaxilla missing; it is unlikely that the true count would have been much higher. In GLAHM V1921, the tooth impressions are more distinct along the whole of the maxilla and dentary; this specimen had 23 teeth in the maxilla and probably 48 (more than 44) dentary teeth. The maxilla in NHMUK PV

R3893 is incomplete posteriorly, but held at least 12 teeth in its anterior portion. This brings the total number of teeth in each jaw ramus to around 50.

In *Ophthalmosaurus icenicus*, the teeth are small, especially compared to other ichthyosaurs, with the largest held towards the middle of each alveolar groove. Tooth size rapidly decreases approaching each end of the groove as it narrows; this is clearest anteriorly where the small teeth were held in defined sockets (see above). Kirton (1983) estimated the largest tooth (an incomplete tooth from GLAHM V1129) to be 37.3 mm high apicobasally and 11.4 mm maximum diameter across the root, no larger teeth were found. Few specimens allow the calculation of McGowan's (1976, p. 677) tooth index (10 × crown length of highest tooth/jaw length); Kirton's (1983, p. 70) values were found to be correct for NHMUK PV R2180, R2181 and GLAHM V1129: 0.140, 0.216 and 0.183 respectively. Higher values are found for smaller individuals: NHMUK PV R2181 has relatively large teeth that lie in contact with those alongside; that these teeth point slightly distally (Andrews 1910) might be due to post-mortem displacement.

The teeth are slightly curved, making the lingual side shorter than the labial side. The bulbous base forms about two-thirds of the total height and is compressed transversely (Fischer *et al*. 2011, character 3). This differs from *Brachypterygius, Platypterygius,* and *Undorosaurus* (see below; McGowan 1972c; Efimov 1999b), in which the tooth bases are bulbous and quadrangular, suggesting that the condition is not homologous between these taxa. There was no bony attachment between the tooth base and the alveolar groove; the placement of the teeth in the alveolar groove refers *Ophthalmosaurus icenicus* to the aulacodont dentition of Mazin (1983) and Motani (1997). The root is covered by cementum that is thinly striated longitudinally by the underlying plication of the tooth. In this region, the infolding dentine disturbs and breaks up the pulp cavity and the tooth base assumes bulbous appearance (Schultz 1969, 1970; Kirton 1983). In NHMUK PV R3893, some replacement teeth are present and there is resorption of the tooth roots. The replacement teeth develop lingually and lie in an elongate resorption pit on this side of the mature tooth root. Apically from the base, the tooth is smoother, thinly coated by acellular cementum (Andrews 1910; Kirton 1983; Maxwell *et al*. 2011, 2012a), and the cementum is only faintly marked by striations that are continuous with the crown. This acellular region is visually separated from the crown by the well-defined base of the enamel (Fischer *et al*. 2011, character 2), which forms a clear line around the tooth. The enamelled crown is a straight cone, circular in cross section, Massare's (1987) 'pierce' guild, with a pointed tip and has further longitudinal striations on the enamel that are less distinct and finer than on the tooth base. Wear facets in NHMUK PV R2181 and GLAHM V1129 are found on the distal and mesial side, likely from abrasion as the interlocking teeth of the upper and lower jaws were brought together (Kirton 1983). Further isolated teeth have been assigned to *Ophthalmosaurus icenicus*, but their generic nature means that it is impossible to be certain that they derive from this species.

Hyoid apparatus. Few examples of the hyoid apparatus are known from *Ophthalmosaurus icenicus*, or from ichthyosaurs generally. The hyoid apparatus consists of a pair of curved and transversely compressed, rod-like bones that would be medial to the jaw rami (McGowan 1973a), but whose exact placement is uncertain. Each end of the hyoid bone is flattened to form an elongate, elliptical surface that is pitted for the application of cartilage. Kirton (1983) discussed the homology of these bones, which had been designated the *cornu hyale* by Sollas (1916) and McGowan (1973a). As this bone is not ossified in reptiles (Romer 1956), Kirton (1983) instead homologized the paired hyoid bones with the cornu branchiale I (= ceratobranchial I), which are ossified and have a similar form (curved rods) to the bones in *Ophthalmosaurus icenicus*. Sollas (1916) recreated a complex hyoid apparatus, most likely due to disarticulation in the posterior part of the specimen that he sectioned.

Atlas–axis complex. The atlas and axis centra are fused to each other even in the youngest individuals known; a low vertical ridge marks the remnant of their separation along the side of the centra (Text-fig. 19; Pl. 15). Together the complex has a triangular shape in anteroposterior view, tapering ventrally. The anterior face of the atlas is concave for articulation with the hemispherical boss of the basioccipital, with a central pit in many specimens, although the anterior face becomes more convex marginally. Unlike the posterior face of the axis, the anterior surface of the atlas is slightly irregular, likely indicating where cartilage would have intervened between the atlas and the basioccipital. This extends around the anterior face, giving the lateral faces a small anterior rim of unfinished bone, and further dorsolaterally onto the articulation surfaces with the neural arches and ribs. Anteroventrally, the atlas is bevelled (seen well in lateral view), and this might have accommodated a separate atlantal intercentrum (Kirton 1983). The irregular surface here continues onto a ventral cartilage-covered ridge that might have extended along the first three or four centra (indicated by similarly rounded and roughened ventral portions). The neural canal is formed by a shallow channel dorsally on the centrum that is finished in smooth bone and slightly raised dorsal to the surrounding pitted bone. Lateral to this, paired pedicels mark the articulation with the atlantal and axial neural arches; the interior of these facets are slightly excavated to form a clear rim. The lateral faces of the atlas and axis are slightly concave between the anterior and posterior rims and the ridge marking the suture between the atlas-axis. In lateral view, the axis appears slightly shorter than the atlas. Placed dorsally, the rib facets are poorly defined and vary both between individuals and between the right and left sides of a single specimen (e.g. GLAHM V1916; Text-fig. 19). The diapophyses are broad, pitted areas, subtriangular in shape, placed dorsally and anteriorly on both the atlas and axis and are often confluent with the neural arch facets. The parapophyses form lower, rounded plinths that are situated towards the posterior margins of the atlas and axis. Kirton (1983) noted that the diapophysis and parapophysis may amalgamate into a poorly defined, raised surface of pitted bone (GLAHM V1061 and V1611). These features arise from the low degree of ossification, particularly around the anterior articular surfaces. The posterior face of the axis is more deeply concave than the anterior face of the atlas, and also smoother and more sharply defined. The posterior articular face of the axis is smaller than the anterior face of the atlas, and tapers greatly ventrally. This occurs gradually through the whole complex so that the axis forms a narrow ventromedial keel, giving the bone a heart shape in posterior view, and this is continued caudally by the next centrum. An axial intercentrum ossification does not seem to have been present. Together, the atlas-axis complex has a slight posterodorsal inclination, so that the more posterior centra are more dorsally positioned and continue the rise towards the trunk.

The atlas and axis neural arches and spines are about one-half and two-thirds the height of their centra respectively, lower than the more posterior cervical and dorsal neural spines; both are unfused to the centra. Unlike all more posterior neural arches, the atlantal neural arch is ossified in two halves that are in contact medially; all other arches are fused along the midline (Text-fig. 19; *contra* Andrews 1910; Kirton 1983). Each half of the atlantal neural arch is composed of a robust ventral pedicel that is rounded ventrally for articulation with the centrum. This pedicel is deflected medially and narrows into the blade-like neural spine, which meets its counterpart medially. Between the two sides, the articular surface is a broad flattened area, separated from the ventral column by an oblique ridge. This is separated from the more posterior portion of the surface that forms the overlap with the axial neural spine by a faint, subvertical ridge. The columnar part of the arch forks around the neural spine providing surfaces anteriorly and posteriorly for the zygapophyses. A small anterior tubercle might have articulated with a proatlas (Kirton 1983). Posteriorly, the two halves of the neural spine remain deeply separated and the postzygapophyses are elongate and slightly curved. In articulation, the atlas and axis neural arches overlap distinctly, but do not fuse, unlike in *Ophthalmosaurus natans* (Druckenmiller & Maxwell 2010, character 26). The axial neural spine is fused medially, but retains a pronounced medial ridge and deeply split posterior edge that allows great overlap of the third cervical vertebral neural arch. Its form is similar to the atlas neural arch, but is taller, particularly in the spine, and has more highly developed zygapophyses. These begin to take the form found through much of the rest of the vertebral column: large elliptical surfaces raised dorsal to the neural spine, although each side remains clearly separate from the other. At its distal tip, the axial neural spine is grooved where cartilage would have capped it. The atlantal and axial neural spines are noticeably posteriorly deflected, more so than in more posterior neural arches.

Vertebral column. The vertebral column of *Ophthalmosaurus icenicus* shows weak regionalization in the size and shape of the centra (Text-fig. 20). No specimen shows the entirety of the vertebral column: the small, posterior fluke centra are frequently lost, and many other specimens have been crushed to some extent or disarticulated so that the true positions are lost. Kirton (1983) identified CAMSM J63920–64037 as the most complete exemplar, while Buchholtz (2001) described PETMG R340 as complete from anterior to the mid fluke region; it is likely that *Ophthalmosaurus icenicus* had a total of around 130 vertebrae. Regional division of the column is hampered by the continuous and variable positions of the neural arch and rib facets, but is generally split into two portions: presacral and caudal, based upon the position of the ilium (McGowan & Motani 2003). The caudal region may be further subdivided with the position of the tailbend – the apical region – separating the anterior preflexural portion of the tail from the posterior postflexural portion. As the pelvic girdle is not sutured to the vertebral column, the position of the sacral region can be difficult to determine. Andrews (1910) used the point at which the diapophysis and parapophysis join to mark the first ‘caudal’ vertebra as a reference. This might not be the true position of the sacrum, although Kirton (1983) proposed it lay around the 42nd vertebra as there is a sudden increase in central height in this region in adult specimens. Buchholtz (2001) suggested a count of around 39 presacral vertebrae, using neural canal width; a method derived from measurements on other ichthyosaurs. Appleby (1956) further separated the ‘cervical’ vertebrae, those up to where the neural arch facet and diapophysis lose contact, some 20–25 vertebrae, which extend posterior to the pectoral girdle. McGowan & Motani’s (2003) terminology is employed in the description of the vertebral column. Additionally, the presacral vertebrae are divided based upon contact between the neural arch facet and diapophysis into anterior (contact is present) and posterior (contact is absent) portions, Kirton’s (1983) anterior and posterior trunk vertebrae respectively. Thunnosaurian ichthyosaurs mostly have around 40–45 presacral vertebrae, but this is greater in mixosaurids, which have 45–50, and up to 60 in *Cymbospondylus petrinus* (Merriam 1908). The length of the vertebral column, and the distinctiveness of the vertebrae, particularly centra, means that these are the most commonly occurring ichthyosaur elements. In some places, vertebrae are the only incidence of ichthyosaur material (Huene 1931, 1936; Kuhn-Schnyder 1980). Early research frequently used slight differences in vertebral morphology, often attributable to intraspecific or intracolumnar variation, to define taxa (e.g. Owen 1840; Phillips 1871); many of these are now considered invalid (see Taxa invalida in Part 2~~below~~).

Presacral vertebrae. Around 40 presacral vertebrae are present in *Ophthalmosaurus icenicus*, based upon estimates of the pelvic girdle position (39–42; Kirton 1983; Buchholtz 2001), which occurs just anterior to where the diapophysis and parapophysis join (approximately at vertebra 45: Andrews 1910) (Text-figs 21–24; Pls 16–18). The centra immediately posterior to the atlas-axis rapidly decrease in height, but posterior to the axis there is a gradual increase in centrum height throughout the presacral column (Text-fig. 20; Buchholtz 2001). The centra become slightly longer towards the middle of the presacral region, around vertebra 25. The centra of the few vertebrae directly posterior to the atlas-axis complex are similarly heart-shaped: keeled ventrally and more square dorsally. This keel rapidly becomes less well developed on more caudal vertebrae, so that by vertebrae six to eight the centrum is almost circular; this keel may have formed the attachment point for sub-vertebral muscles (Kirton 1983).

Posterior to the reduction of the ventral keel, the presacral vertebrae are discoidal throughout the rest of the series; the anterior and posterior faces are straight-sided in lateral view. Each centrum is strongly amphicoelous, with small pits placed centrally, but the face of the anterior and posterior face concavities is convex, so that vertebral centrum has an hourglass-shape in sagittal cross-section. This form is typical of post-Triassic ichthyosaurs, and similar vertebrae have been described by Kiprijanoff (1881, pl. 11) and Fraas (1891, pl. 14, figs 5b, 6b). Ventral to the neural canal, the centrum is slightly thickened to form a triangular convexity that is separate from the more continuously convex-concave face that forms the rest of the centrum depression. This convexity is indistinct, extending from the centre of the centrum face, and is bounded by two slight grooves that are directed towards each of the neural arch facets dorsolaterally. ~~That this~~This is present across several vertebrae and specimens, and therefore suggests that this is not a form of pathology (Stepanov *et al.* 2004). The thickening of the centrum would have resisted the compressive forces applied to the vertebral column (Kirton 1983). Dorsally, the centrum has a wide longitudinal canal that forms the floor of the neural canal. The surface of the floor of the neural canal is roughened, with longitudinal striations. The neural canal is bordered laterally by the two neural arch facets, which are raised dorsal to the neural canal to form pedestals. These facets are narrow but anteroposteriorly elongate, extending from the anterior to posterior margin on the dorsal surface, with a deep concavity centrally into which the neural spine was located. The surface of the neural arch facet is pitted as cartilage would have intervened in the articulation. Laterally from the convexities, the neural arch facets in the anterior *c.* 25 vertebral centra are confluent with the diapophysis of the bicipital rib facet (see Ribs below). The diapophysis is positioned towards the anterior of the centrum and takes the form of a large, raised and rounded articulation. The surface of the diapophysis is pitted for application of cartilage, continued from the neural arch facet medially. The size of the diapophysis in these anterior centra, where it is confluent with the neural arch facet, gives the dorsal portion of the centrum a slightly square shape in anterior or posterior view; this is particularly evident in the centra immediately following the atlas-axis complex. Around vertebra 25, the diapophysis begins to separate from the neural arch facet. The parapophysis, the ventral articulation of the bicipital rib facet, is a smaller tubercle that is positioned about halfway down the lateral centrum, against the anterior margin in the anterior vertebrae; its surface is also pitted for the application of cartilage. This tubercle migrates posteriorly on the lateral face of the centrum up to vertebra 25, but maintains connection with the anterior margin by a low, roughened ridge. The lateral and ventral faces of the centrum are continuous and anteroposteriorly concave throughout. This concavity is accentuated by the anterior and posterior margins forming raised lips that border the lateral and ventral surfaces. The lateral and ventral surfaces are smooth and pitted by numerous nutritive foramina. Between approximately vertebrae 25 and 38, the diapophysis, separate from the neural arch facet, and parapophysis rapidly migrate ventrally on the side of the centrum to the ventrolateral corner, and become slightly closer to each other. In the last few of these vertebrae, the rib facets maintain their separation.

Posterior to vertebra 39, the diapophysis shrinks and migrates ventrally towards the parapophysis, joining with it to form an anterodorsally–posteroventrally elongate synapophysis around vertebrae 42–43; Kirton's (1983) definition of the presacral/caudal boundary. At this point, the ribs become unicipital (see below). In the posterior presacral to anterior caudal regions, with the rib articulations placed ventrolaterally, the ventral margin of the centrum is much straighter than in the more anterior and posterior centra. In the aforementioned region, the ventral edges of the centra begin to develop a low, keel-like ridge along the midline. This keel becomes more strongly developed in posterior vertebrae, particularly into the caudal series (see below), but between about vertebrae 29–36, the keel is divided by a median groove (Kirton 1983). Some specimens preserve lithified intercentral discs along with the bony vertebrae; these would have likely been poorly ossified or cartilaginous in life. The intercentral discs are thin and biconvex, moulding the amphicoelous nature of the centra. They would have filled the space between the vertebrae, but would not have created any large separation between vertebrae: the margin of the centrum faces would likely have been nearly in contact. This would have allowed little movement over much of the vertebral column, which would have prevented the majority of the skeleton from participating in axial propulsion. Similar intercentral discs have been reported in *Ophthalmosaurus natans*, which increase in length posteriorly – separating the vertebral centra – to the middle caudal region, decreasing further posteriorly (Massare *et al.* 2006). It is uncertain whether this was the case in *Ophthalmosaurus icenicus*, however, *Acamptonectes densus* shows ‘locking’ of the S-shaped vertebral facets in the cervical and dorsal regions (Fischer *et al.* 2012).

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The neural arches too retain a similar form through much of the presacral region, taking the form of tall, squared projections that are deflected slightly posteriorly (Text-figs 25, 26; Pl. 18). Caudal to the atlas-axis complex, they rapidly increase in height until vertebra six. These first few neural arches resemble the arches of the atlas-axis complex, with rather narrow bases and slightly posteriorly deflected neural spines. In lateral view, the arches are formed by the anteroposteriorly elongate columns, more widely separated than in the atlas-axis complex, that have slightly convex and roughened bases for articulation with the neural arch facets on the centra. Dorsal to this articulation, the arches rapidly converge towards the midline, enclosing the neural canal ventrally and meeting at less than one-quarter of the height of the neural spine. The prezygapophyses and postzygapophyses are positioned largely dorsal to the neural arch and canal, but the ventralmost portion does diverge around the dorsal of the neural arch. Longitudinally, along its posterior margin, the neural spine is grooved, possibly marking the point of fusion of separate ossification centres (Kirton 1983), into which the sharp ridge of the anterior margin of the following neural spine slots. This creates a sharp midline peak longitudinally in the roof of the neural canal that divides the pre- and postzygapophyses into two elongate articular areas just lateral to the midline of the neural spine. The prezygapophyseal articulations face anterodorsally, whereas the postzygapophyses face posteroventrally to contact the prezygapophyses from the vertebra posteriorly. Kirton (1983, p. 80) suggested that the overlapping of these neural arches would have restricted movement of the cervical region. The neural arch is thin and elongate, with a square dorsal margin in lateral view. Dorsally, along the entirety of the presacral portion of the axial column, the neural spine is grooved longitudinally and would have been continued in cartilage. Posterior to vertebra six, the margins of the neural arches become more rounded, particularly towards the dorsal part of the neural canal; there is little evidence of separate ossification of the lateral halves. The lateral pedicels of the arches converge more rapidly dorsal to the neural canal and the neural spine dorsally in this region is narrower. Both the pre- and postzygapophyses are situated entirely dorsal to the neural canal and meet at the midline. The ridges and grooves found in the most anterior neural spines are reduced here. The prezygapophyses are bilobate, retaining a median ridge and sightly concave; the postzygapophyses are more completely joined, with a less obvious median groove, and form a large elongate articular surface. In the presacral vertebrae, the neural spines are deflected slightly posteriorly relative to the vertical axis through the centrum; this reflects the curved nature of the axis in creating the fusiform body shape (Kirton 1983). As the centrum length increases towards vertebra 25, so the length of the neural arches increases in lateral view, but the neural spines decrease in height in more posterior vertebrae towards the caudal region.

Caudal vertebrae. From the point where the diapophysis and parapophysis join, the tail vertebrae gradually change shape posteriorly towards the apical region and caudal fluke (Text-figs 27, 28; Pl. 18). The centra in the anterior portion of the caudal series remain large, with a similar form to the most posterior presacral centra, but become shorter anteroposteriorly, so that they have a more discoidal form. Kirton (1983, pp. 81–82) interpreted this as allowing more flexibility and as an important region in generating thrust during axial propulsion. As the centra become shorter, the synapophysis takes up relatively more of the anteroposterior length of the centrum. It eventually becomes confluent with both the anterior and posterior margins of the centrum, and is here somewhat thickened, so taking on an externally square shape, although the articulation remains rounded. The ventrolateral keels on the centra (see Presacral vertebrae above) become higher and narrower, appearing sharper, in the more posterior vertebrae, with two foramina piercing the surface between the keels by vertebra 50, each slightly lateral to the midline. The anterior and posterior margins of the centrum between these keels are narrow, but widen either side into what Kirton (1983, p. 82) interpreted as facets for the haemal arches. These facets become more pronounced by vertebra 60, whereas the keel becomes reduced. From approximately vertebra 55, centrum height starts to decrease, this decrease becoming much more rapid from vertebra 66 towards the caudal fluke. These centra, however, become proportionally wider and the rib articulation migrates slightly dorsally up each side of the centrum, towards the middle.

The apical region tail bend is created by a series of five modified, procoelous vertebrae, around vertebrae 71–75, termed apical centra (McGowan & Motani 2003). This procoely is partially created by a strong rounding of the centrum margins on both the anterior and posterior faces, but each face retains a central pit. The irregular surface of the apical vertebrae suggests a large covering of these centra in cartilage. In more strongly ossified individuals, the procoely becomes more pronounced so that the anterior face of the centrum becomes strongly convex and articulates with the posterior face of the preceding centrum in a ball-and-socket joint that allows a great range of motion in the apical region (Kirton 1983). The first centrum in this series is sub-circular, like the centra immediately anterior to it, but posteriorly, the centra rapidly become narrower and U-shaped in anterior and posterior views. Dorsally, the neural arch facets become more prominent, and the neural canal between these facets narrows and deepens slightly into a deep median channel, accentuating the overall U-shape. Rib facets are present on the anterior three apical centra only, halfway down the lateral faces and positioned posteriorly, but with raised ridges connecting to both the anterior and posterior margins of the centrum; all centra posterior to this lack rib facets. In addition, these apical centra are slightly wedge-shaped, with ventral margins shorter than the dorsal margins, creating a distinct ventral flexion, over several vertebrae, that separates the caudal fluke vertebrae. McGowan (1989, p. 430) used trigonometry to measure the angle subtended by each apical centrum in *Eurhinosaurus longirostris* and *Leptonectes tenuirostris*, calculating values of 2–5° per centrum. Similar calculations for *Ophthalmosaurus icenicus* yield a more constant value of about 1.5° in PETMG R340 (Text-fig. 28). However, as the centra are more rounded in *Ophthalmosaurus icenicus*, compared to wedges in the above taxa, this might mean that the tail bend had a stronger deflection, and greater overall mobility. Disarticulation of the available material means that the true amount of deflection of the tail fin is unknown. Posterior to the apical vertebrae, the centra of the caudal fluke retain a U-shape, but become more flat-faced, the anterior and posterior faces are neither as concave as in the anterior vertebrae, nor as convex as the apical centra. The caudal fluke is supported ventrally by 50–60 vertebrae that decrease in size posteriorly into tiny discs; the terminal elements become so small that they are either not preserved or cannot be collected. Unlike the more anterior centra, these are more completely ossified and sharply defined. Many of these are aligned straight, with parallel anterior and posterior margins

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in lateral view, but Kirton (1983, p. 85) identified distal elements in CAMSM J63920–64037 that show a slight wedge shape, opposite to that of the tail bend, indicating a distal recurve. There are no rib facets present on these centra, but neural arch facets are present as dorsal pedestals, with the neural canal running in between. The ventrally raised areas, interpreted as haemal arch facets, persist throughout the caudal region.

Unlike the centra, the neural arches and spines rapidly decrease in height in the anterior caudal region (Text-figs 26, 29). The arches become lower and the spines shorter so that the posterior elements have a regular triradiate form. The pre- and postzygapophyses decrease in size more anteriorly than the neural spine, and are reduced to small, sub-circular areas positioned directly dorsal to the neural canal. Most noticeably, the neural spines steadily become deflected more posteriorly in the posterior caudal vertebrae as they are reduced, so that both sets of zygapophyses are nearly horizontal by about vertebra 66 and the neural spine overlaps the spine of the more posterior vertebra. Throughout the caudal region, the neural spines retain a groove in the dorsal margin. In the apical region, the neural spines are wider and strongly bulbous dorsally, with strongly roughened and pitted surfaces, suggesting a large amount of ligamentous connective tissue (Kirton 1983, p. 84). There is no development of the zygapophyses, and these neural arches were unlikely to have been in contact, allowing motion in the apical region. Few neural arches are preserved from vertebrae posterior to the apical region, but these caudal fluke neural spines show a similar, albeit diminishing, form. Neural arch facets are present on the vertebral centra in much of the fluke region, but the respective arches were likely very small and may have been lost, or possibly not ossified. The lateral ventral keels, and associated thickening of the centrum margins in the caudal region, interpreted as facets for the haemal arches (see above), ~~continues~~ continues along much of the tail bend too. No elements can be certainly identified as haemal arches, and these were likely poorly ossified also, as supported by the poorly defined facets.

Ribs. The ribs follow the same poor regionalization as the vertebrae, with little difference between regions (Text-fig. 30). Rib facets on the vertebral centra show that ribs were present on all vertebrae up to the apical region, at about the 73rd vertebra. In the anterior region of the vertebral column, the ribs possess two proximal heads: the tuberculum and capitulum, articulating with the diapophysis and parapophysis on the vertebral centra respectively. The tuberculum and capitulum are flattened and pitted for application of cartilage. The larger capitulum is aligned with the proximal part of the rib shaft, whereas the tuberculum is smaller and deflected dorsally, creating a Y-shaped proximal dichotomy. In articulation, this means that the proximal portion of the rib is angled dorsolaterally, before curving ventrally in its distal portion. This gives *Ophthalmosaurus icenicus* a broad body in anteroposterior view, which McGowan & Motani (2003, p. 19) described as "barrel-chested". The dorsal and ventral margins of the rib are roughened and would have provided attachment for muscles. Proximally, the anterior rib shafts are strongly curved, but this becomes less marked distally. The ribs are flattened anteroposteriorly for much of their length, but become rounded distally. Longitudinal grooves run for between one-half and two-thirds of the proximal length of the rib on both the anterior and posterior faces, beginning at the midline and moving towards the internal margin distally. In the posterior presacral ribs, the tubercula are

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reduced and the two proximal heads of the rib become closer. Between the tuberculum and capitulum, a thin sheet of bone develops, similar in form to webbing between digits. The ribs in this region also become shorter and less strongly curved; distally, the ribs taper. On the anterior face, at the apex where the capitulum and tuberculum separate, a small muscle tubercle is developed. The tuberculum and capitulum finally join to form a single-headed rib, with an elongate articulation, in the sacral region: around vertebra 43, where the diapophysis and synapophysis join (see Presacral vertebrae above). There is no evidence for connection with the pelvic girdle or specialisation of the ribs in this region. The ribs of the caudal region are shorter and taper distally. The proximal head of the rib is aligned slightly posterodorsally–anteroventrally, and the rib is directed ventrolaterally and slightly posteriorly. These ribs have a weakly developed anterior groove and very poorly developed groove posteriorly; the distal end is tipped by cartilage. At the posterior end of the vertebral column, the ribs are shorter and develop as horizontally flattened nubbins of bone, distally roughened and presumably finished in cartilage (Text-fig. 30).

Gastralia. Gastralia are uncommon in the material of the Leeds Collection, but several examples from *Ophthalmosaurus icenicus* are known. Fragments are preserved in GLAHM V1916 and more complete examples are present in NHMUK PV R8737. The gastralia are thin, gently curved rods of bone, with diameters varying from 3.85–7.50 mm in the latter specimen. The lengths of individual gastralia vary~~varies~~ from around 150 mm to 290 mm, the longer ones probably coming from the middle part of the torso. Each gastralium is sub-circular in cross-section through its midpoint, but at each end becomes flattened for articulation. The articulations between the gastralia are ridged longitudinally and the elements here overlap. The curve of the rod largely occurs in the middle third of its length, each more distal portion being noticeably straighter. The larger gastralia show a curve of 140–150° over their length, although the shorter elements display smaller angles. Some elements show a reversing of the curve distally. Although NHMUK PV R8737 preserves many gastralia, a complete set cannot be reconstructed, and as the gastralia are disarticulated, it is difficult to restore their true relationship to the dorsal rib cage.

Pectoral girdle. The pectoral girdle in *Ophthalmosaurus icenicus* is large, robust, and provided a large area for the attachment of musculature associated with the large forelimbs (see below; Text-fig. 31). In spite of this, the bones of the pectoral girdle would have been surrounded by a thick layer of cartilage in life, and variable degrees of ossification has caused differences in the morphology of these pectoral elements, particularly the coracoids and scapulae (see Maxwell & Druckenmiller 2011, fig. 3). This variation has reduced the taxonomic utility of the pectoral elements, but as robust elements, they are often found, and detailed description is warranted. Maxwell & Druckenmiller (2011) have discussed the taxonomic utility of the pectoral girdle in other Jurassic ichthyosaur taxa, concluding that the generic form of the pectoral girdle found in ophthalmosaurids shows no phylogenetically informative characters to this clade, and only four are applicable to Parvipelvia (Fernández 2007a; Fischer *et al*. 2013).

Clavicle. The clavicles are elongate and curved, strap-like bones that meet medially in a complex, interdigitating suture, but do not overlap (Text-fig. 31; Pl. 19, Pl. 28, figs 1, 2). Seeley (1874b) did not think that the clavicles met, but were separated, because the clavicles in the holotype (NHMUK PV R2133) are incomplete medially. This contact between the two clavicles is not complete, as the two clavicles diverge to expose a tuberosity on the interclavicle (see below). There is no fusion between the two clavicles at their midline, or with the underlying interclavicle, except in the largest individuals (e.g. NHMUK PV R3535). Where this does occur, the closeness of the fusion makes it difficult to follow the suture (Kirton 1983). The anterior face of the clavicle is convex and smooth along most of its surface, except anteromedially. It is likely that there would have been many muscles connected here (Johnson 1979; Kirton 1983), although there is no strong indication of scarring on the surface. Medially, the clavicle is broad and straight, but curves dorsally in its lateral portion. The distal portion narrows greatly to form a tapering horn-like extension that curves dorsally to meet the proximal scapula.

The posterior surface of the clavicle is deeply grooved medially and would have been applied to the anterior face of the horizontal bar of the interclavicle in life. The surface of the clavicle is roughened and striated for this contact. Ventrally, the clavicle has a strongly raised ridge that holds the ventral part of the horizontal bar of the interclavicle. The posterior groove shallows laterally, particularly as the clavicle is deflected dorsally into an irregular channel, into which the acromion process of the scapula fits. Towards the lateral, horn-like extension, the ventral edge is sharply angled laterally in some specimens (e.g. PETMG R220), but may be straighter in others (e.g. NHMUK PV R2149). A depression fits onto the anterior edge of the scapula, separated from the acromion facet anteriorly (Appleby 1956), and the surface is roughened for contact with the scapula.

Interclavicle. In *Ophthalmosaurus icenicus*, the interclavicle is T-shaped and sits posterior to the clavicular strap and anterior to the coracoids (Text-fig. 31; Pl. 20). The T of the interclavicle consists of a transverse bar anteriorly, with a posteriorly-directed medial stem. The stem is usually longer than the transverse bar (e.g. NHMUK PV R4753), although in some smaller, and presumably juvenile specimens (e.g. LEICT 100’1949/27) this is greatly reduced; the latter specimen also has a median suture. Anteriorly, the clavicles cover the transverse bar, which is convex to fit into the posterior groove of the clavicles (see above) and each end tapers distally. The surface of the interclavicle is roughened and grooved, corresponding to the interior surface of the clavicle. A tuberosity is variably developed on the midline of the interclavicle that protrudes through a gap between the articulated clavicles. Kirton (1983) suggested this might have been a point of muscle attachment to the forelimb. The ventral edge of the transverse bar curves gently posteriorly to join the stem to the transverse bar. This narrows slightly into a neck, but then widens distally to form an elongate lateral flange. Proximally, the stem is convex laterally, becoming flatter distally as it becomes wider (Andrews 1910). Around the distal flange, a small ridge demarcates the edge, which tapers distally. The surface of this stem is roughened and longitudinally striated, particularly distally, and may have been the location for further muscle attachment. Along the midline of some specimens (e.g. NHMUK PV R4753), proximally, a low median ridge extends for about one-third of the length of the stem of the interclavicle; again this may have provided a point for muscle attachment.

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Internally, the anterior interclavicle is raised into a ridge dorsally that fits into the posterior groove on the clavicular arch (see above). This creates a channel posterodorsally along the transverse bar of the interclavicle that becomes less pronounced distally. The surface of this channel is rugose, although the posterior margin of the transverse bar may be smoother. Medially, the channel narrows posteriorly into a groove along the stem of the interclavicle, narrowing further in the neck. The surface of this groove is strongly striated longitudinally, but the channel broadens distally, and the striations cover the entirety of the distal flange. On this surface, the roughening likely indicates the application of cartilage or ligaments that intervened between the interclavicle and coracoid (Kirton 1983). Only in well-ossified individuals can a slight facet be seen on the coracoid (see below; Andrews 1910; Kirton 1983).

Coracoid. The coracoid, like the scapula, has a large variation in the degree of ossification and resulting morphology (Text-fig. 32; Pls 20, 21, Pl. 28, figs 5, 6, Pl. 30, figs 3, 4). The coracoid is a large, ovoid, plate-like bone with a rounded embayment-like notch laterally on the anterior border. Two broad and oblique, elongate facets are developed laterally and medially that give this bone a saddle shape: concave mediolaterally and convex anteroposteriorly. Almost the entire margin of the coracoidal plate is roughened and pitted, and with a slight groove indicating that it was likely surrounded by cartilage in life. Anteromedially, the coracoid projects forward into a broad, rounded process, where the marginal groove is particularly well developed. This portion of the coracoid, and the surrounding cartilage, would have come close to, or been fully articulated with the clavicles anteriorly (see above). Larger specimens have a triangular pitted region that would contact with the median stem of the interclavicle. The anterior notch forms lateral to this process, separating it from the lateral articular facet. The bone of the margin is smooth and rounded around the margin of the notch, unlike around the rest of the coracoid. Neither the dorsal nor ventral surfaces of the coracoid have any strong features on them. As mentioned above, they are both gently warped between the medial and lateral facets into a saddle shape. Kirton (1983) noted that the intercoracoidal facet is drawn dorsally and markedly raised dorsal to the dorsal surface, higher than the ventral portion, aiding in orienting and diagnosing the coracoid when it is disarticulated.

Much of the medial margin is broadened into a large, elliptical facet that articulates with the contralateral coracoid. The facet faces slightly dorsally, so that the long axis of the coracoids would be at an angle of *circa* 125° in articulation (Kirton 1983). However, the surface of the facet is strongly rugose and irregularly pitted throughout on both coracoids indicating that cartilage was present, intervening in the articulation. Some coracoids may fit well and closely, however, in some specimens the intercoracoidal facet is convex, so the two elements fit less closely (e.g. LEICT 100’1949/21). This makes it hard to determine the true angle between the coracoids in life. A similar facet is present on the coracoid laterally, also heavily pitted and slightly concave posteriorly to receive the proximal humerus (Seeley 1874b). This is generally not as strongly developed dorsoventrally as the intercoracoidal facet, and is oriented more perpendicular to the body of the coracoid. The anterior, triangular portion of the lateral facet is separated and slightly angled forward (*c*. 135°; Andrews 1910) to articulate with the coracoid facet of the scapula (see below). The size of the scapular facet is variable, but is often less than one-third the length of the lateral articular surface of the coracoid. When articulated, the median portion of the proximal margin of the scapula would have been placed against the anterior notch of the coracoid. This forms a fenestra that is also bordered anteriorly by the clavicles and probably was surrounded anteriorly by cartilage, although Andrews (1910) did not think that the scapular and coracoidal cartilages met. Johnson (1979, after Fürbringer 1876) referred to this as the *fenestra coracoscapularis*. Although this is not likely to be homologous to the coracoscapular fenestra in extant lizards, it might also be associated with the *M. scapulohumeralis anterior*, which attaches to the proximal scapula (Romer 1956; Kirton 1983; Maxwell & Druckenmiller 2011). Posterior to this, the larger part of the articular surface of the lateral facet on the coracoid forms the coracoidal portion of the glenoid articulation, opposite the scapular contribution. Kirton (1983, p. 90) noted that, in articulation, the scapula and coracoid do not form a well-defined socket for the humeral insertion, unlike in *Stenopterygius* (Johnson 1979). A large amount of cartilage was present between the scapula, coracoid, and humerus, so the true orientation of the latter cannot be determined. The posterior margin of the coracoid is variably rounded, connecting the medial and lateral facets: NHMUK PV R2148 has a straighter margin laterally, whereas NHMUK PV R2149 is regularly rounded, almost semicircular. Some coracoids from well-ossified individuals (e.g. CAMSM J63920) have a small excavation posterior to the glenoid articulation that may be surfaced in finished bone. This small excavation forms a slight concavity in the posterior margin of the coracoid, although not to the extent of the anterior notch or the posterior notch in the holotype (NHMUK PV R2133) and LEICT 100’1949/20 (see the Discussion of *Ophthalmosaurus icenicus* above).

Scapula. Proximally, the scapula takes part in the glenoid articulation with the coracoid and is expanded posteriorly for this structure (Text-fig. 31, Pl. 21, figs 5–8, Pl. 28, figs 3, 4, Pl. 30, figs 1, 2). The more distal portion narrows into a strap-like shank that is directed posterodorsally. The proximal end of the scapula is deeply pitted and has an elongate and shallow S-shape, which may be grooved, in proximal view. This surface is expanded posteriorly into a teardrop-like area that is straight medially, and convex laterally. This area articulates with the coracoid (forward portion) to form the glenoid facet, for which the scapula is greatly widened and heavily rugose: it is likely that much cartilage would have intervened in the glenoid articulation between the scapula, coracoid and the proximal humerus. Anteriorly, the proximal margin is strongly deflected laterally to form the acromion process, which forms a roughened ridge along the proximal one-half of the anterior margin of the scapula that may have been covered by cartilage. The middle section of the proximal margin is the thinnest part and was positioned opposite the anterior notch of the coracoid in life. This middle section of the proximal articulation of the scapula would not have directly articulated with the coracoid, but rather may have continued the cartilage surrounding the anterior notch of the coracoid posteriorly (see above). This portion of the proximal margin is usually roughened like the rest of the proximal scapular margin. However, in a few specimens (e.g. NHMUK PV R2140, R2152 and R2160; Pl. 21) the bone is smoothed to a rounded and slightly concave edge. The anterior margin of the scapula is convex in lateral view and often continuously curved. In more heavily ossified individuals, this is more strongly angled, separating the

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positions of the acromion process, midsection and coracoid and glenoid facets more clearly.

Posterior to the anterior curve of the S-shape of the anterior margin, the scapula is concave laterally, shallowing distally between the converging arms of the acromion process anteriorly and the expanded posterior facet. This concavity may have been the location of muscles connected to the humerus (*M. scapulohumeralis anterior*: Maxwell & Druckenmiller 2011), although there is little evidence of discrete attachment positions. The anterior margin of the scapula was gently concave and was covered anteriorly by the internal (posterodorsal) face of the distal clavicle (see above). Much of its surface is roughened and slightly flattened (e.g. PETMG R220) where it would fit into the posterodorsal channel of the clavicle (Seeley 1874b; Andrews 1910; Appleby 1956). The sharper posterior margin of the scapula is strongly concave in lateral view, particularly proximally, and forms a clear neck in the scapula that separates the proximal, articular portion and the distal blade. This blade is slightly curved dorsomedially around the rib cage, becoming slightly thinner distally, but may largely retain its dorsoventral height throughout (e.g. the holotype, NHMUK PV R2133), or may significantly broaden (e.g. NHMUK PV R2139 and R2140). Distally, the scapula is squared off, but this margin, and the surrounding bone, is pitted and grooved indicating that it would be continued by cartilage in life, the extent of which is uncertain. Laterally, the surface of the scapula is generally roughened, with rugose areas marking the attachment points of pectoral muscles. It is difficult to determine the true locations of muscle attachment, as has been attempted for *Stenopterygius* (Johnson 1979), as the requisite features are not clear. The medial surface is slightly concave proximally, and relatively featureless. Between the

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proximal and distal portions, there is a small development of shaft-like thickening along the midline of the scapular blade manifested as a triangular convexity. The medial surface of the distal blade is smoother and slightly concave proximodistally.

The scapula in *Ophthalmosaurus icenicus* shows a great degree of variation in its morphology, most likely due to its endochondral development. The middle portion of the proximal margin of the scapula, which would have been placed opposite the anterior notch of the coracoid in life, is often roughened, but is rounded and smoothed in NHMUK PV R2140. The acromion process is clearly offset anteriorly in some specimens, forming a strong emargination of the dorsal margin (e.g. NHMUK PV R1667 and PETMG R222). The dorsal margin is also occasionally straighter and confluent with the acromion process, which is more square proximally (e.g. NHMUK PV R2133). Maxwell & Druckenmiller (2011, p. 460) claim that the “morphological variation exhibited in the scapula of *Ophthalmosaurus icenicus* alone approaches the total amount of variation seen in the element among ophthalmosaurids as a whole”. The similarity between the pectoral girdles of different ophthalmosaurids makes it of little use taxonomically. Whether the extensive variation in *Ophthalmosaurus icenicus* is peculiar to this species, or a result of the relative glut of material is unclear. Great variation is also found in the pectoral girdles and forelimbs of other common ichthyosaurs, especially *Ichthyosaurus* and *Stenopterygius* (McGowan 1974b, 1979; Johnson 1979).

Forelimb. The forelimb is robust and strongly modified to a hydrodynamical shape (McGowan 1973b, 1992; Text-fig. 33g; Pl. 22). Disarticulation of much of the material from the Oxford Clay Formation has led to differing interpretations of the orientation and articulation of the forelimb elements. Efforts to solve this have focused on the humerus, which has the most distinct characteristics and asymmetries. The articulations and orientations of the more distal elements follow from the interpretation of the humerus. Seeley (1874b, p. 705, pl. 46, fig. 3) originally showed the humerus and forelimb inverted anteroposteriorly (compared to the orientation used in the following sections), so that the smallest facet was located posteriorly, equivalent to the right and left humeri being switched. Andrews (1910, pp. 51–53, fig. 36), apparently on the advice of Mr Alfred Leeds, reversed this orientation dorsoventrally, placing the dorsal process ventrally: the forelimb was placed on the correct side, but rotated 180° on its long axis. The orientation of the humerus was corrected by Kirton (1983, p. 96), following the interpretation of articulated specimens of *Stenopterygius* by Johnson (1979). Therefore, both Seeley (1874b, pl. 46, fig. 3) and Andrews (1910, fig. 36a, b) figured a left humerus (the paratype: NHMUK PV R2134) in dorsal view. Because of these re-orientations of the forelimb, the names given to more distal elements, particularly the epipodials and proximal carpals, have changed. Also, the configuration and homologies of the ichthyosaur forelimb have caused problems for several authors, particularly when the material studied is disarticulated (Kiprijanoff 1881; McGowan 1972a; Johnson 1979). Here, we follow the nomenclature of Motani (1999a, see especially fig. 7A), which follows Kirton (1983; Text-fig. 33g). For *Ophthalmosaurus icenicus*, confident reconstruction of the forelimb is largely based on a sketch made by Mr Alfred Leeds and kept in the NHMUK collections with specimen NHMUK PV R3702 (Kirton 1983, fig. 29). His knowledge, as one of the major collectors of material, generates more certainty in positioning these forelimb elements. In this interpretation, the forelimb of

Ophthalmosaurus icenicus possesses four primary digits and two accessory digits (see below).

Humerus. The short and robust humerus is an important element in the pectoral region of *Ophthalmosaurus icenicus* and ichthyosaurs generally (Text-fig. 33a–f, 34; Pls 22, 23, Pl. 28, figs 7, 8, Pl. 30, figs 5, 6). Proximally, the head is expanded to form a large surface for articulation with the glenoid facets of the coracoid and scapula. Distally, the humerus is expanded, particularly anteroposteriorly, and separated into three facets for articulation with the radius, ulna and an anterior accessory element. Between these extremities, the humerus is constricted slightly into a short shaft-like diaphysis, marked by anterior and posterior emarginations. The proximal surface is flattened but slightly convex and heavily pitted throughout in both small and even the largest individuals that show strong ossification in other elements, indicating that the epiphysis was covered by a large amount of cartilage (see also Scapula and Coracoid above). Some humeri referable to *Ophthalmosaurus icenicus* have a low marginal ridge around the proximal surface, creating a small internal channel. This is likely due to variation in the extent of ossification of the cartilaginous cap. In proximal view, the long axis of the proximal humerus is angled around 45° anteroventrally relative to the true anteroposterior orientation of the humerus (as given by the distal facets). Although superficially there appears to be torsion in the humeral shaft, this relates to the lateral expansion of the proximal head by the large dorsal and ventral trochanters (Kirton 1983). The dorsal process is situated about halfway along on the anteroposterior length of the humerus, and rises into a high, plate-like ridge. Proximally, the surface is pitted, a continuation of the proximal cartilaginous cap, but much of the distal surface is finished, although roughened for the attachment of the pectoral muscles. Distally, the dorsal process descends into the humeral diaphysis, extending slightly anteriorly along its length, for about half of the proximodistal length of the humerus. The larger ventral process is not as sharply demarcated from the main body of the humerus, and is positioned further anteriorly than the dorsal process, towards the anterior margin. It is analogous to the deltopectoral crest (Kirton 1983; *contra* Johnson 1979). The ventral process is a broad, rounded projection of the anteroventral portion of the humerus, extending the proximal surface of the humerus, and causing the apparent torsion described above. Much of the more distal surface is finished, but roughened for muscle attachment, however, in the paratype (NHMUK PV R2134), several unfinished pits descend onto the ventral surface from the proximal surface. This likely reflects variation in proximal ossification. The ventral process also extends over the diaphysis of the humerus for more than half of its length. This causes a broad proximal anterior surface on the humerus, slightly concave due to the strong anterior development of the dorsal process, which narrows distally. The anterior margin of the humerus is broad and rounded, compared to the narrower and sharper posterior margin; these features help in orientating isolated humeri (Kirton 1983). These two margins converge distally from the proximal head, forming the diaphysis, before rapidly diverging to form the long distal articular portion of the humerus. Kirton (1983, p. 94) noted that the posterior margin does not appear as strongly emarginated as the anterior margin. This is due in part to the greater anterior expansion of the anterior margin distally to accommodate the anterior distal facet.

Distally, the humerus is anteroposteriorly elongate, and slightly broadened, for the distal articulations with the three epipodials. The bone here is smoother than on the more proximal surfaces as there are no muscle attachment points in this region. In dorsal or ventral view, the distal margin of the humerus is separated into three parts by large obtuse angles. These mark the positions of the ridges that separate the three distal articular facets on the distal face of the humerus. The facets are broad, concave and heavily pitted for the application of cartilage that intervened between the articulations. The anterior facet is the smallest; it is angled slightly anteriorly, and articulates with the anterior accessory element. The anterior facet narrows anteriorly towards the anterior margin of the humerus, creating a triangular facet. The middle facet faces distally, is the largest facet and is a rectangular articulation for the radius. Towards the anteroposterior midline of this facet, the distal face of the humerus broadens dorsoventrally. Posterior to the radial facet, the posterior facet articulates with the ulna and is deflected slightly posteriorly. This facet has a broad pentagonal shape: the anterior portion is rectangular, but posterior to this, tapers with the posterior margin of the humerus, becoming rounded posteriorly. The irregular form of the ulnar facet is extended by the development of two tubera on the distal margin of the humerus dorsally and ventrally, at about the anteroposterior midline of that facet. These tubera are variably developed (compare NHMUK PV R2134 and R2173) and, in some cases, extend distally onto the ulna, but usually the ventral tuber is the largest (see below; Kirton 1983). Andrews (1910, p. 53) suggested that this variability might be sexually dimorphic, citing the approximately equal proportions of those specimens with and without these tubera. However, the humerus is invariably broadened here, whether the tubera are well developed or not. These prominences can also be variably developed between both humeri of a single individual (e.g. NHMUK PV R2138); it is more likely that their relative development is a result of individual variation rather than sexual dimorphism.

The humerus in *Ophthalmosaurus icenicus* shows a certain amount of variation, largely related to the extent of cartilage proximally and distally, and to its position as the largest part of the forelimb (Text-fig. 34; Table 4). The dorsal and ventral processes vary in size, although the latter is always larger, and thus the proximal dorsoventral expansion of the humerus corresponds to the development of these processes. Perhaps the most obvious instance of variation is found in the distal articular facets, which vary greatly in relative size (particularly the anterior accessory element facet) and orientation (Table 5). Fischer *et al*. (2012, table 2) considered the ratio anterior facet length/radial facet length to be of taxonomic importance in ophthalmosaurine ichthyosaurs. However, the values obtained for *Acamptonectes densus* fall into the range of variation exhibited by specimens referred to *Ophthalmosaurus icenicus* (0.173–0.778; Table 5), although the median value is slightly higher (0.414) in *Ophthalmosaurus*. Alongside variation in the distal facets, the constriction of the humeral diaphysis, which is generally strong in *Ophthalmosaurus icenicus*, varies in breadth. This creates a stronger separation of the proximal and distal heads in NHMUK PV R1668 than in R2853, for instance.

Forelimb epipodials. The radius and ulna articulate with the middle and posterior distal facets of the humerus respectively (Text-fig. 33; Pl. 22). The humerus also articulates with a pre-axial accessory element; this will be considered in the section Accessory digits, below. Following the re-orientation of the forelimb by Kirton (1983;

see Humerus above), note that the names of these elements are reversed from those published prior to this (as in Seeley 1874b; Andrews 1910).

Both the radius and ulna are short, strongly thickened, polygonal elements. The radius is smaller than the ulna and subpentagonal. It articulates with (right forelimb, clockwise from proximal in dorsal view) the humerus, pre-axial accessory element, radiale, intermedium, and ulna. For these articulations, the radius has a flattened proximal face and is pointed distally, taking the space between the proximal margins of the radiale and intermedium. The dorsal and ventral surfaces are finished, but slightly roughened, whereas the edges and the vertical faces, which articulate with the surrounding elements, are heavily pitted where thick cartilage would have intervened. Proximally, the radius follows the contours of its humeral articulation, and so becomes slightly thicker towards the centre of this surface. Andrews' (1910, p. 54, fig. 37) description shows the radius and ulna separated by an interosseous space. The size of the contacts between the radius, ulna and other elements are variable. In some specimens, the radius can be square from a lack of close contact, as in NHMUK PV R2853 and GLAHM V1893.

The anterior portion of the ulna is thickened, like the radius, but posteriorly it becomes narrower, along with the posterodistal humerus, tapering towards the posterior margin of the forelimb. This element is more square than the radius, articulating with (right forelimb, clockwise from proximal in dorsal view) the humerus, radius, intermedium, ulnare, and sometimes the proximalmost post-axial accessory element (= pisiform of Johnson 1979). The medial, proximal, and distal articular faces are large, and heavily pitted for the application of cartilage, as is the case with the radius. However, the facet for the post-axial accessory element is small and poorly developed, and, when in articulation, these two elements are not positioned as close together as the other surrounding bones. On the proximal, dorsal, and ventral margins, there may be a large tubercle, placed close to the corresponding tubercle on the humerus (see above; Kirton 1983). Posteriorly, the ulna becomes thinner, and the dorsal and ventral surfaces are slightly concave, reflecting this. The posterior margin, unlike all others on the ulna, is not pitted, but is comparatively smooth, although still roughened. This narrowing is only found in *Ophthalmosaurus* (Andrews 1910; Fischer *et al*. 2013). Seeley (1874b, p. 705) noted the nutritive foramina close to the articular margins on all bones of the forelimb.

Carpals. In *Ophthalmosaurus icenicus*, there are three proximal carpals: radiale, intermedium, and ulnare, and three distal carpals, supporting digits two, three, and four of the pentadactyl manus (Text-fig. 33; Pl. 22). Proximal carpal five and the entire first digit have been lost (Motani 1999a). The proximal carpals are of similar size and shape: the radiale and intermedium are clearly polygonal, with several facets for articulation with the surrounding elements. The radiale articulates with (right forelimb, clockwise from proximal in dorsal view) the proximal pre-axial accessory element, second pre-axial accessory element, distal carpals two and three, intermedium, and radius, while the intermedium articulates with the radius, radiale, distal carpals three and four, ulnare, and ulna. Like the radius proximally, these are strongly thickened elements, with roughened dorsal and ventral surfaces and heavily pitted vertical articular faces where cartilage was present. The intermedium is wedged between the radius and ulna proximally, and distal carpals three and four distally, so that both its proximal and distal margins are pointed. The ulnare has more rounded margins than the two more anterior proximal carpals and, like the ulna, narrows towards the posterior margin of the forelimb. This bone articulates with the ulna, intermedium, distal carpal four, metacarpal five, and the proximal post-axial accessory element (= pisiform of Johnson 1979). Kirton (1983, p. 101) noted that, when articulated, the proximal and distal borders of the radiale, intermedium, and ulnare align obliquely to the long axis of the forelimb. This is continued by more distal elements, but is less clear as these are rounded. Johnson (1979, pp. 75–76) suggested that this allowed flexibility without creating lines of weakness in the forelimb.

The three distal carpals (two, three, and four) represent smaller forms of the proximal carpals and are very similar in shape. Distal carpals three and four particularly are placed closely between the proximal carpals (radiale and intermedium, and intermedium and ulnare respectively) and so have pointed proximal margins. In all three elements, the distal margins are more rounded than in the more proximal limb elements. This reflects the transition to the more distal metacarpals and phalanges, which are all rounded, and were individually surrounded by thick cartilage (Kirton 1983). Both the proximal and distal carpals are thinner than the epipodials, but still have broad vertical faces for articulation with surrounding elements, particularly on the closely applied proximal margins.

Metacarpals. Following Motani (1999a), the four metacarpals present in *Ophthalmosaurus icenicus* represent the homologues of metacarpals two to five in the pentadactyl manus (Text-fig. 33; Pl. 22). This differs from Kirton’s (1983) interpretation, in which metacarpals one to four are present, and also in their position, due to the lack of a fourth distal carpal (see above). The metacarpals are more rounded and irregularly shaped than the more proximal elements in dorsoventral view, approaching the form of the phalanges. However, they retain obliquely angled margins, particularly proximally, for articulation with the distal carpals. Their shape and position suggest that they have lost close contact with adjacent elements. Many of the more distal limb elements would have been surrounded by cartilage, and the variable ossification of this creates heterogeneity in the forms of these elements. Each metacarpal supports a single digit distally (see below). From the metacarpals, the digits are directed slightly anteriorly due to the zigzag orientation of the distal faces of the distal carpals and metacarpals. As stated above, this may aid in reducing lines of weakness in the forelimb. Metacarpals two to four are more discoidal than the proximal elements. Their vertical faces retain the roughness and pitting associated with the cartilage surrounding each element.

The loss of the fifth distal carpal and reduction of distal carpals two, three, and four (see above) means that the fifth metacarpal is positioned more proximally than the line of the other three metacarpals, articulating proximally with the ulnare. In this position, it aligns with the distal carpal row, effectively replacing distal carpal five, and has taken on a sub-quadrate form, similar to the other distal carpals. Metacarpal five is noticeably larger and more equidimensional in dorsal and ventral view than the other three metacarpals and has a closer contact with the ulnare and distal carpal four proximally and anteroproximally respectively. It is also slightly thicker than the other metacarpals due to its more proximal position. The posterior margin is notably convex, and would articulate with the post-axial accessory digit, although this contact would probably not have been close.

Primary forelimb digits. The forelimb in *Ophthalmosaurus icenicus* possesses four primary digits, homologues of digits two to five of the pentadactyl manus, supported proximally by metacarpals two to five (McGowan 1972b; Text-fig. 33; Pl. 22). From Leeds' diagram (see Forelimb above), the proximal digital elements appear to be angled slightly anteriorly, curving distally to line up approximately with the long axis of the forelimb. At least seven phalanges were present in each digit, and eight in digit 4, but Kirton (1983) suggested that this is unlikely to be the full complement. The phalanges are rounded in dorsal and ventral view and decrease in size and thickness distally; the proximal phalanges are more elliptical and elongate anteroposteriorly than the distal elements. Like in more proximal elements, the margins of the primary digits are roughened and pitted and have a central groove along this face, creating a slight hourglass shape in anterior or posterior view. The phalanges remain dorsoventrally thick proximally, but narrow greatly in the distal forelimb, becoming more discoidal. This, and their relative spacing, indicates that a significant amount of cartilage was present between the individually ossified elements, particularly distally. As forelimb material is often disarticulated, variation in its configuration, common in Lower Jurassic taxa, is difficult to determine. Some reconstructions have been attempted, which show the possibility of digital bifurcation (e.g. NHMUK PV R2853, right forelimb; Andrews 1910; Kirton 1983), but this is circumstantial.

Accessory forelimb digits and elements. Two complete (extending a similar length to the primary digits) accessory digits are present in the forelimb of *Ophthalmosaurus icenicus*: an anterior accessory digit, of which the proximal element articulates with the anterior distal facet of the humerus, and a posterior accessory digit, of which the proximal element articulates proximally with a proximodistal facet on the ulna (Text-fig. 33; Pl. 22). Kirton (1983, fig. 30) further identified an isolated element in NHMUK PV R3702 that may be part of an incomplete second post-axial accessory digit. The proximal pre-axial accessory element – “olecranon” of Seeley (1874b, p. 703, pl. 46, fig. 3), “pisiform” of Andrews (1910, pp. 53, 54, fig. 37, pl. 2, fig. 4), and “extra zeugopodial element” of Motani (1999a, p. 39, fig. 7) – articulates proximally with the anterior distal facet of the humerus and with the radius, radiale and distal pre-axial accessory digit (anticlockwise from proximal in dorsal view). This element is triangular in dorsoventral cross section along the anteroposterior axis, corresponding to the shape of the distal humeral facet, and slightly rounded in dorsal or ventral view, becoming a little wider distally. The anterior narrowing of this element helps form a streamlined forelimb, as seen in many ichthyosaurs (McGowan 1992). Its other articular faces are thickened greatly, the posterior facet almost matching the thickness of the radius, and are heavily pitted for the application of cartilage between these articulations. The more distal elements of the pre-axial accessory digit match the corresponding rows along which they align, becoming thinner and more rounded distally. The decrease in size of the pre-axial accessory digit elements occurs more rapidly distally and there are often no more than six elements distal to the humerus. These narrow anteriorly to form a streamlined anterior margin to the forelimb. Like more posterior elements, the contacts are not necessarily close, particularly distally, so that only the proximal two elements have an angled posterior margin.

The proximalmost element of the post-axial accessory digit is usually homologized with the pisiform. This element articulates proximally with a small facet on the posterodistal ulna and with the posterior ulna. In dorsoventral view, the pisiform is teardrop-shaped, tapering proximally, and also narrows towards the posterior margin of the forelimb, as with the corresponding pre-axial element. The post-axial element immediately distal to the pisiform is also proximodistally elongate, but the elements distal to this are more rounded. As with the pre-axial digit, these elements are smaller than those in the rows they align with, although this digit may have eight elements.

Pelvic girdle. The pelvic girdle is very much reduced in comparison with the pectoral girdle, and has lost all bony contact with the vertebral column (Text-fig. 35). It comprises only two elements, a slender ilium and a fused, plate-like ischiopubis. Reconstructions of the position and articulations of the pelvic girdle are based upon mostly complete and articulated specimens of *Stenopterygius* from the Toarcian of south-western Germany (compare the reconstructions of Wiman 1921, figs 5 & 6, with Huene 1922a). As mentioned above (see Vertebral column), the lack of contact with the axial skeleton means that the position of the pelvic girdle, and associated sacral region, is uncertain. Buchholtz (2001) and Kirton (1983) placed this contact around vertebrae 39 and 42 respectively.

Ilium. The ilium is a short, curved and twisted rod of bone forming the dorsal portion of the pelvic girdle (Text-fig. 35a, b; Pl. 24, figs 1, 2). There is no direct connection to the vertebral column, but the pelves were likely attached by ligaments that connected dorsally. Kirton (1983) used this twisting to determine that the distal ilium is deflected medially to lie alongside the vertebral column. This allows the position of the pelvic girdle to be determined with reasonable certainty (see also Vertebral column above). The proximal end is a broad elliptical, pitted facet, capped by cartilage in life, that articulates with the anteroproximal portion of the ischiopubis (see below). This facet is larger than the corresponding facet on the ischiopubis, so that the posterior portion of the ilium forms part of the acetabulum. Andrews (1910) and Kirton (1983) disagreed on the relative size of the acetabular contribution, the former describing a larger face than the latter. This feature appears to be variable between specimens (compare GLAHM V1070, V1916, and NHMUK PV R2853), although the contribution of the ilium is always smaller than that of the ischiopubis (see below). The lateral surface of the ilium in some specimens (e.g. GLAHM V1899) is striated and may mark the origin of muscles that powered the hindlimb (Kirton 1983). Distal to this, the shaft of the ilium narrows along its length, flattening distally, and curves medially, so that the distal end is angled at about 30° to the vertical. The surface of this portion is smooth. Distally, the tip of the ilium is angled further medially than the curve of the bone more proximally. The medial surface is strongly rugose for the ligamentous and cartilaginous attachment to the vertebral column.

Ischiopubis. The ischium and pubis are fused along most of their proximodistal length, together forming an elongate plate (Text-fig. 35a, b; Pl. 24, figs 3–8). Their close association makes it reasonable to consider them together: no clear suture line is visible along their contact. The pubis is reduced to an anterior bar at the anterior of the ischiopubis, with the ischium forming much of the posterior, plate-like portion. This is shown by the retention of a narrow, proximodistally elongate obturator foramen close to the anterior edge of the ischiopubis (McGowan & Motani 2003, after Romer 1956). Kirton (1983, p. 104) did not consider this opening to be homologous with the obturator foramen, but the evolutionary sequence expounded by McGowan & Motani (2003, p. 56) suggests that this may be the case (see below). Proximally, the ischiopubis forms a broad, triangular articular surface that narrows posteriorly, for the ilium anteromedially and the acetabulum, which occupies most of this surface laterally and posteriorly. The surface is heavily pitted for the application of cartilage, and is convex; the acetabular portion faces slightly posteriorly and laterally, and the ilial facet is angled slightly ventrally. From this, the anterolateral face of the ischiopubis (formed by the pubis) is broadened where it meets the proximal articular surface, and slightly concave, becoming narrower and flatter distally. Laterally, the pubis is raised dorsal to the posterolateral face of the ischium, allowing identification of right and left contralateral elements; the surface is even medially. Distal to the proximal articulations, the ischiopubis narrows slightly, separating these facets from the distal plate-like portion, largely formed by the ischium. The ischium widens towards the distal margin, particularly as the thinner posterior margin is directed posterodistally. Posterior to the pubic portion of the ischiopubis, the obturator foramen forms the proximal portion of a proximodistally elongate channel that extends distally to the distal margin of the ischiopubis, marking the approximate line of fusion between the pubis and ischium. Close to the distal margin, along this line, one or two foramina are present in some specimens. These can be entirely enclosed in the ischiopubis or open distally forming a small notch in the distal margin of the ischiopubis. The occurrence, size, and position of these are variable between and within specimens (compare GLAHM V1070, V1916, and V1912). For instance, there are two foramina distally in GLAHM V1912, positioned posterior to the anterior margin. The distal margin of the ischiopubis is convex in lateral view, particularly anteriorly, pitted, and has a groove along its length indicating that it was extended by cartilage, with no direct contact between the two ischiopubes (Andrews 1910).

Hindlimb. The hindlimb is strongly reduced relative to the forelimb – the femur is about 0.6 times the length of the humerus – and there are far fewer elements in the hindlimb than in the forelimb (Text-fig. 36; Pl. 25, fig. 6). Unlike the forelimb, there are fewer specimens that have been recorded as articulated, although several specimens are mounted as such. Neither did Mr Alfred Leeds produce a sketch diagram as he did for the forelimb (see above). Because of this, the configuration of the hindlimb as a whole has been uncertain. Kirton (1983) accepted the reconstruction of Andrews (1907, 1910), who had discussions with Mr Alfred Leeds, although Kirton re-oriented the hindlimb. Andrews (1907, p. 208, fig. 5) originally oriented the femur with the smaller facet positioned anteriorly, and the smaller proximal process dorsally, later reversing this anteroposteriorly (Andrews 1910, p. 58, fig. 41). Kirton (1983, p. 105), following a similar pattern to her re-orientation of the humerus, reversed this dorsoventrally, so that the larger, more anterior proximal process is the ventral. In their interpretation, McGowan & Motani (2003, p. 42, fig. 65) invoked further characters and comparisons, such as the extent of the processes distally along the femur, orienting the femur so that the anterior margin is narrow and the ventral process is crest-like, thus accepting

Andrews' (1910) interpretation. Maxwell *et al*. (2012c, p. 1209, fig. 1P–T), used comparisons with articulated *Mixosaurus*, *Ichthyosaurus*, and the then undescribed *Cryopterygius kristiansenae*, to infer the orientation of the femur. Their interpretation reversed those of Andrews (1910) and McGowan & Motani (2003) anteroposteriorly, and reversed that of Kirton's (1983) dorsoventrally. Maxwell *et al.*'s (2012c) orientation is followed here: the femur is oriented with the broader, more anteriorly-positioned process dorsally; the narrower process, adjacent to the anterior concavity, is considered the ventral process; the tibial facet is typically larger than the fibular facet. The anterior face of the femur is broad, while the posterior margin is narrow and sharp, similar to the humerus (see above).

Femur. The femora take a similar form to the humeri, but differ in their dimensions (Text-fig. 36; Pl. 25, figs 1–5, Pl. 28, figs 9–12). Proximally, the articular surface is broad and more strongly convex and rounded than the proximal surface of the humerus. The surface is unfinished and heavily pitted for application of the acetabular cartilage. In proximal view, the extensive dorsal and ventral processes give this surface a triangular form: the anterior edge aligns dorsoventrally and is sinusoidal, convex dorsally and concave ventrally, following the contours of the anterior face. Posterior to this, the proximal surface narrows towards the posterior margin. The anterior face of the femur is wide dorsoventrally, due to the great extent of the dorsal and ventral processes, and is slightly concave. This makes the femur appear relatively more massive than the humerus proximally. The dorsal and ventral processes are angled slightly anteriorly at their greatest height, making the anterior face slightly concave, particularly proximally.

Distally, the anterior face narrows as these processes descend onto the diaphysis of the femur, giving it a spatulate appearance. Further distally, the anterior face of the femur becomes convex, reflecting the anteroposterior elongation of the distal femur. The dorsal process of the femur is the larger of the two and positioned anterodorsally, slightly anterior to the ventral process when viewed in dorsal or ventral view. This process is large and triangular, creating a slight convexity to the dorsal portion of the anterior margin. Proximally, the surface is heavily pitted for application of the articular cartilage. Distal to this, the dorsal process forms a prominent ridge just behind the anterior margin of the femur that descends distally onto the diaphysis for about half of the femoral length. The surface of this ridge is usually roughened for the attachment of muscles, but in some specimens (e.g. NHMUK PV R10031), the unfinished proximal surface extends distally. The ventral process of the proximal femur is slightly smaller and shorter proximodistally than the dorsal process. This process is narrower and more crest-like, being offset from the proximal surface by broad concavities in the ventral portion of the anterior face and the posteroventral face. The proximal surface continues the pitting for the articular cartilage, but the anterior and lateral faces are finished with cortical bone, although roughened for muscle attachment. The ventral process descends rapidly onto the femoral diaphysis for slightly less than half the length of the femur. Behind these two processes, two broad faces are oriented posterodorsally and posteroventrally respectively. These are slightly concave, particularly in their proximal portions, and meet at the narrow, sharp posterior margin of the femur, similar to the form in the humerus. In dorsal and ventral view, the femur is constricted slightly distally to one-half of its proximodistal length. This is caused by the concave anterior and posterior margins. Distally, the margins diverge to accommodate the distal portion and facets of the femur, with the anterior margin angled further anteriorly than the posterior margin is angled posteriorly.

Distally, the femur becomes elongate anteroposteriorly; the anterior margin is well rounded and convex, while the posterior margin becomes less sharply defined. Kirton (1983, pp. 106–107) noted that the anterodistal point of the femur is blunt and the surface unfinished, suggesting that it may have been continued in cartilage. The distal surface has two large facets that articulate with the epipodials. As with the humerus (see above), the two facets are oriented differently: the posterior facet faces slightly posteriorly relative to the anterior, forming a large obtuse angle between the two in dorsal and ventral views. This point marks where a dorsoventral ridge separates the two facets on the distal face. The two facets are sub-rectangular and concave, narrowing slightly toward the anterior and posterior ends of the femur, and are heavily pitted for the application of the intervening cartilage. The anterior facet is slightly longer and larger than the posterior facet, and articulates distally with the tibia (see below); the posterior facet is for articulation with the fibula. There are slight protuberances on the dorsal and ventral surfaces of the femur, just proximal to the fibular facet, and confluent with a slight bulge on the fibula, similar to those associated with the ulna on the humerus (see above). These are not developed to anywhere near the same extent, and may be a result of the rapid narrowing of the posterodistal femur.

Hindlimb epipodials. The hindlimb epipodials are similar in form to the forelimb epipodials, articulating proximally with the femur, and forming thickened discs that taper slightly towards the hindlimb margins, creating a hydrodynamical shape (Text-fig. 36; Pl.

25, fig. 6). The anterior element, the tibia, is the largest and it articulates with (right hindlimb, clockwise from proximal in dorsal view) the femur, distal carpal two, astragalus, and fibula respectively. This element is angled and polygonal for these articulations. The articular faces are pitted for the application of cartilage that, as with the forelimb, would intervene between each element. While the anterior face of the tibia is rather large, there is no certain evidence for an anterior accessory element; the extent to which the tibia may have been extended by cartilage is uncertain. The fibula articulates with (right hindlimb, clockwise from proximal in dorsal view) the femur, tibia, astragalus, and calcaneum. The anterior margin is straight for articulation with the tibia. However, posteriorly, the fibula becomes narrower and the posterior margin may be rather sharp, like the ulna (see above), and is not pitted. Unlike the ulna, the posterior margin of the fibula is convex and curved in dorsal and ventral views. Towards its anteroposterior midpoint, the proximal border of the fibula becomes slightly broader, matching the location of low protuberances on the femur; these may be points of muscle or ligamentous attachment as between the humerus and ulna (see above). The articular faces of the fibula are, like the tibia, pitted for cartilage or connective tissue.

Distal hindlimb elements. In the reduced hindlimb of *Ophthalmosaurus icenicus*, there are only about 10 elements certainly present distal to the epipodials; both Andrews (1910, fig. 41) and Kirton (1983, fig. 33) reconstructed the hindlimb with this many metapodial elements (based on NHMUK PV R4693–R4695; Text-fig. 36; Pl. 25, fig. 6). Apparently no example of the hindlimb of *Ophthalmosaurus icenicus* is more complete than NHMUK PV R4693–R4695, nor shows the configuration of these more distal elements. Kirton (1983, pp. 107–108) refrained from homologizing these elements; Caldwell (1997) homologized the proximal tarsal elements in *Stenopterygius* with (anterior to posterior) the centrale, astragalus, and calcaneum. The most basal ichthyosaurs, however, have lost or do not ossify the anterior proximal tarsal (centrale), and through their evolution, the second distal tarsal moves proximally to take its place (McGowan & Motani 2003). Here we treat the proximal metapodial row as containing (anterior to posterior) the second distal tarsal, astragalus, and calcaneum; these correspond to the tibiale, intermedium, and fibulare of Andrews (1910). These three elements are irregularly rounded and slightly thickened, with pitted articular faces, but the contact between them and other elements would not have been close. The second distal tarsal and astragalus are about the same size and slightly larger than the calcaneum, but all three elements are smaller and thinner than the epipodials; the calcaneum, like the fibula, becomes slightly narrower towards the posterior margin. The six elements more distal to these are arranged into three digits, with two, three, and two elements respectively (anterior to posterior). These are also rounded, discoidal elements that become smaller and thinner distally. They retain pitted margins, and there would have been thick cartilage separating these elements, forming the hydrodynamical contours of the hindlimb. Whether this example (NHMUK PV R4693–R4695) represents a complete hindlimb is uncertain.

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APPENDIX

INDETERMINATE ICHTHYOSAUR SPECIMENS FROM THE BRITISH MIDDLE AND UPPER JURASSIC

Below are listed specimens of ichthyosaurs that cannot be referred to one of the above taxa with certainty. The referral present on the specimen label is included. Abbreviations: **Bucks**, Buckinghamshire; **Cambs**, Cambridgeshire; **CF**, Cornbrash Formation; **CG**, Corallian Group; **KCF**, Kimmeridge Clay Formation; **Northants**, Northamptonshire; **Notts**, Nottinghamshire; **OCF**, Oxford Clay Formation; **Oxon**, Oxfordshire; **PSF**, Portland Stone Formation; **Suther**, Sutherland; **Wilts**, Wiltshire; **Yorks**, Yorkshire.

PLATE 1

Fig.		Page
	Ophthalmosaurus icenicus Seeley, 1874b Oxford Clay Formation of Peterborough, Cambridgeshire.	
1–3	Left maxilla (GLAHM V1921) in lateral, medial, and ventral (anterior is to the left) views.	
4, 5	Left nasal, lachrymal, and prefrontal (NHMUK PV R4753) in lateral and medial views	
	Scale bars represent 100 mm.	

PLATE 2

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2	Left prefrontal (GLAHM V1129) in dorsal and ventral views.
3, 4	Left postfrontal (NHMUK PV R3534) in dorsal and ventral views.
5–8	Left supratemporal (NHMUK PV R2146) in lateral, posterior, medial, and dorsal views.

Scale bars represent 50 mm.

PLATE 3

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Left parietal (LEICT 100’1949/198) in dorsal and ventral views.

3, 4 Right parietal (LEICT 100’1949/198) in dorsal and ventral views.

Scale bar represents 50 mm.

PLATE 4

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Right squamosal (GLAHM V1921) in lateral and medial views.

3, 4 Left postorbital (NHMUK PV R3893) in lateral and medial views.

5, 6 Left jugal (NHMUK PV R8653) in lateral and medial views.

7, 8 Sclerotic plates (NHMUK PV R8737) in external view.

9, 10 Sclerotic plates (NHMUK PV R8737) in internal view.

Scale bars represent 50 mm.

PLATE 5

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–4 Right vomer (NHMUK PV R4753) in lateral, medial, dorsal, and ventral views.

5, 6 Left palatine (NHMUK PV R4753) in dorsal and ventral views.

Scale bars represent 50 mm.

PLATE 6

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Left pterygoid (GLAHM V1921) in dorsal and ventral views.

3–5 Left quadrate with supratemporal portion (holotype: NHMUK PV R2133) in medial, lateral, and posterior views.

Scale bars represent 50 mm.

PLATE 7

Fig.		Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–6 Parabasisphenoid (part) (NHMUK PV R10023 = former Liverpool Museum 4524) in anterior, posterior, dorsal, ventral, right lateral, and left lateral views.

Scale bar represents 50 mm.

PLATE 8

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Left prootic (LEICT 100’1949/45) in external (anterior) and internal (posterior) views.

3–8 Left opisthotic (holotype: NHMUK PV R2133) in anteromedial, posterior, ventral, dorsal, medial, and lateral views.

Scale bars represent 20 mm.

PLATE 9

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–5 Supraoccipital (LEICT 100’1949/43) in anterior, posterior, ventral, dorsal, and right lateral views.

6–8 Left exoccipital (LEICT 100’1949/64) in medial, anterior, and posterior views.

9–11 Right exoccipital (LEICT 100’1949/64) in medial, anterior, and posterior views.

Scale bar represents 50 mm.

PLATE 10

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–6 Basioccipital (holotype: NHMUK PV R2133) in anterior, posterior, dorsal, ventral, right lateral, and left lateral views.

Scale bar represents 50 mm.

PLATE 11

Fig.		Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2	Left stapes (holotype: NHMUK PV R2133) in anterior and posterior views.	
3–6	Left stapes (LEICT 100'1949/45) in anterior, posterior, right ventral, and left dorsal views.	
	Scale bars represents 50 mm.	

PLATE 12

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Left splenial (GLAHM V1921, restored) in lateral and medial views.

3, 4 Right surangular (LEICT 100’1949/202, broken anteriorly) in lateral and medial views.

Scale bars represent 100 mm. Anterior is to the top.

PLATE 13

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2	Right angular (LEICT 100'1949/202, portion) in lateral and medial views.
3, 4	Left prearticular (GLAHM V1921, reconstructed) in lateral and medial views.

Scale bars represent 100 mm. Anterior is to the top.

PLATE 14

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Articulated partial right angular and surangular (NHMUK PV R2180) in lateral and medial views.

3, 4 Articulated left mandible (holotype: NHMUK PV R2133, posterior portion) in lateral and medial views.

5, 6 Articulated left mandible (NHMUK PV R2180, posterior portion) in lateral and medial views.

Scale bars represent 100 mm.

PLATE 15

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–6 Atlas-axis complex (LEICT 100’1949/75) in anterior, posterior, dorsal, ventral, left lateral, and right lateral views.

Scale bars represent 100 mm.

PLATE 16

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

Vertebral centra LEICT 100’1949/75.

1–3 Anterior cervical region (*c*. centrum 3) in anterior, dorsal, and left lateral views.

4–6 Middle cervical region (*c*. centrum 12) in anterior, dorsal, and left lateral views.

7–9 Posterior cervical region (*c*. centrum 25) in anterior, dorsal, and left lateral views.

Scale bars represent 50 mm.

PLATE 17

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

Vertebral centra LEICT 100’1949/75.

1–3 Anterior dorsal region (*c*. centrum 26) in anterior, dorsal, and left lateral views.

4–6 Middle dorsal region (*c*. vertebra 35) in anterior, dorsal, and left lateral views.

7–9 Posterior dorsal region (*c*. vertebra 41) in anterior, dorsal, and left lateral views.

Scale bars represent 50 mm.

PLATE 18

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–3 Anterior caudal vertebral centrum (LEICT 100’1949/75, *c*. vertebra 42) in anterior, dorsal, and left lateral views.

4, 5 Anterior cervical neural spines (GLAHM V1885, vertebrae 1–5) in left lateral and right lateral views.

6–8 Vertebra nine (NHMUK PV R8737) in anterior, posterior, and left lateral views.

9–11 Middle tail fluke vertebral centrum (GLAHM V1883) in anterior, dorsal, and left lateral views.

12 Anterior presacral vertebral centrum (GLAHM V1185) in left sagittal cross-sectional view (anterior to the left).

Scale bars represent 50 mm (Figs 1–8) and 20 mm (Figs 9–12).

PLATE 19

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Articulated clavicles and interclavicle portions (holotype: NHMUK PV R2133) in anterior and posterior views.

3, 4 Left clavicle (NHMUK PV R4753) in anterior and posterior views.

Scale bars represents 100 mm.

PLATE 20

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Interclavicle (NHMUK PV R4753) in anterior and posterior views.

3, 4 Left scapula and clavicle (holotype: NHMUK PV R2133) in lateral and medial views.

5, 6 Left coracoid (holotype: NHMUK PV R2133) in dorsal and ventral views.

Scale bars represent 100 mm.

PLATE 21

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Right coracoid (NHMUK PV R2149) in dorsal and ventral views.

3, 4 Right coracoid (NHMUK PV R2148) in dorsal and ventral views.

5, 6 Left scapula (NHMUK PV R2139) in lateral and medial views.

7, 8 Left scapula (NHMUK PV R2140) in lateral and medial views.

Scale bars represent 100 mm.

PLATE 22

Fig.		Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1 Left forelimb (paratype: NHMUK PV R2134) in dorsal view (anterior is to the bottom).

2 Right forelimb (NHMUK PV R2853) in ventral view.

3 Left forelimb (NHMUK PV R2853) in ventral view.

Scale bar represents 50 mm.

PLATE 23

Fig.		Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–6 Left humerus (paratype: NHMUK PV R2134) in dorsal, ventral, anterior, posterior, proximal, and distal views.

Scale bar represents 50 mm.

PLATE 24

Fig. Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Right ilium (GLAHM V1912) in lateral and medial views.

3, 4 Right ischiopubis (NHMUK PV R8737) in lateral and medial views.

5, 6 Right ischiopubis (NHMUK PV R8653) in lateral and medial views.

7, 8 Left ischiopubis (NHMUK PV R8653) in lateral and medial views.

Scale bars represent 50 mm.

PLATE 25

Fig.		Page

Ophthalmosaurus icenicus Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1–5 Right femur (NHMUK PV R10031) in dorsal, ventral, anterior, posterior, and proximal views.

6 Left hindlimb (NHMUK PV R4695) in ventral view.

Scale bars represent 50 mm.

PLATE 26

Fig.		Page

‘Ichthyosaurus megalodeirus’ Seeley, 1869

= *Ophthalmosaurus icenicus* Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Right premaxilla (CAMSM Ib3) in lateral and medial views.

3–6 Right nasal (CAMSM Ib5) in dorsal, lateral, ventral, and medial views.

7, 8 Right lachrymal (CAMSM Ib6) in lateral and medial views.

9, 10 Left narial region (CAMSM Ib2) in dorsolateral and ventromedial views.

Scale bars represent 50 mm.

PLATE 27

Fig. Page

‘Ichthyosaurus megalodeirus’ Seeley, 1869

= *Ophthalmosaurus icenicus* Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2	Right dentary (CAMSM Ia2) in lateral and medial views.
3, 4	Left splenial (CAMSM Ia6) in lateral and medial views.
5, 6	Left surangular (CAMSM Ia4) in lateral and medial views.
	Scale bars represent 50 mm. Anterior is to the top.

PLATE 28

Fig. Page

‘Ichthyosaurus megalodeirus’ Seeley, 1869

= *Ophthalmosaurus icenicus* Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Right clavicle (CAMSM IIa19) in anterior and posterior views.

3, 4 Left scapula (CAMSM IIa3) in lateral and medial views.

5, 6 Left coracoid (CAMSM IIa1) in dorsal and ventral views.

7, 8 Left humerus (CAMSM IIa5) in dorsal and ventral views.

9, 10 Right femur (CAMSM IIa22) in dorsal and ventral views.

11, 12 Left femur (CAMSM IIa23) in dorsal and ventral views.

Scale bars represent 50 mm.

PLATE 29

Fig.		Page

‘*Ophthalmosaurus monocharactus*’ Appleby, 1956

= *Ophthalmosaurus icenicus* Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Skull roof (PETMG R220) in dorsal and ventral views (anterior is to the left).

3 Basicranium (PETMG R220) in posterior view.

Scale bars represent 50 mm. Images copyright Vivacity–Peterborough Museum and Art Gallery.

PLATE 30

Fig. Page

‘*Ophthalmosaurus monocharactus*’ Appleby, 1956

= *Ophthalmosaurus icenicus* Seeley, 1874b

Oxford Clay Formation of Peterborough, Cambridgeshire.

1, 2 Right scapula (PETMG R220) in lateral and medial views.

3, 4 Right coracoid (PETMG R220) in dorsal and ventral views.

5, 6 Right humerus (PETMG R220) in dorsal and ventral views.

Scale bars represent 50 mm. Images copyright Vivacity–Peterborough Museum and Art Gallery.

TEXT-FIGURE CAPTIONS

Text-fig. 1. Mounted remains of *Ophthalmosaurus icenicus* Seeley, 1874b from the Oxford Clay Formation of Peterborough, Cambridgeshire, UK; presently on display in the main foyer of the Natural History Museum, London, UK. Composed of three specimens (Andrews 1915): NHMUK PV R3702, R3893 and R4124; mounted by Mr L. T. Parsons. Note that the forelimbs are anteroposteriorly reversed based on the interpretation at the time (see Forelimb below). Photograph courtesy Natural History Museum, London.

Text-fig. 2. Map of major Middle and Upper Jurassic rock outcrop ~~in the UK~~of Great Britain, with important ichthyosaur-producing localities indicated. Scale bar represents 100 km. Illustration by Benjamin Moon.

Text-fig. 3. Summarized British stratigraphy from the Bathonian to Portlandian indicating formations (**boldface**) that have produced ichthyosaur remains. International stage boundary ages are from the International Chronostratigraphic Chart v2014/02 (Cohen *et al*. 2013) and ammonite biozones are from Cox (1990), with approximate boundaries from Cope *et al*. (1980). The chart is scaled to equal ammonite biozones.

Text-fig. 4. *Ophthalmosaurus icenicus* Seeley, 1874b: reconstruction of the skull in left lateral (**a**) (based upon NHMUK PV R3893 and R4753) and dorsal (**b**) views (based upon NHMUK PV R3893 and GLAHM V1129). Abbreviations: **an**, angular; **bo**, basioccipital; **d**, dentary; **en**, external narial opening; **ex**, exoccipital; **fr**, frontal; **j**, jugal; **l**, lachrymal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, premaxilla; **pa**, parietal; **pf**, postfrontal; **po**, postorbital; **pr**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **s**, supratemporal; **sa**, surangular; **sc**, sclerotic ring; **sf**, supratemporal fenestra; **so**, supraoccipital; **sq**, squamosal; **st**, stapes. Scale bar represents 200 mm. Illustrations by Angela Kirton and Benjamin Moon.

Text-fig. 5. *Ophthalmosaurus icenicus* Seeley, 1874b: reconstruction of the skull roof in ventral view (**a**) (based upon GLAHM V1129) and the cranium in palatal view (**b**) (based upon NHMUK PV R2180, R3893 and GLAHM V1129). Abbreviations: **al**, alveolar groove; **bo**, basioccipital; **bs**, basisphenoidal portion of parabasisphenoid; **fep**, epipterygoidal facet on the parietal; **fl**, lachrymal facet of the nasal; **fm**, maxillary facet of the nasal; **fop**, opisthotic facet on the supratemporal; **fpa**, parietal facet on the parietal; **fpo**, postorbital facet on the supratemporal; **fq**, quadrate facet of the supratemporal; **fr**, frontal; **fso**, supraoccipital facet on the parietal; **fsq**, squamosal facet on the supratemporal; **icf**, internal carotid foramen; **ich**, impression of the cerebral hemisphere; **in**, internal narial opening; **iob**, impression of the olfactory bulb; **iop**, impression of the optic lobe; **j**, jugal; **m**, maxilla; **ma**, muscle (*M. adductor mandibulae internus pterygoideus)* attachment location; **ml**, muscle (*M. levator pterygoidei*) attachment point; **n**, nasal; **na**, external naris flared edge; **np**, narial projection; **p**, premaxilla; **pa**, parietal; **pal**, palatine; **pf**, postfrontal; **pr**, prefrontal; **ps**, parasphenoidal portion of parabasisphenoid; **pt**, pterygoid; **q**, quadrate; **qc**, articular condyle of the quadrate; **qj**, quadratojugal; **s**, supratemporal; **sl**, lateral flange of the supratemporal; **smf**, medial flange of the supratemporal; **st**, stapes; **v**, vomer, **va**, vascular channel. Scale bars represent 100 mm (**a**) and 200 mm (**b**). Illustrations by Angela Kirton and Benjamin Moon.

Text-fig. 6. *Ophthalmosaurus icenicus* Seeley, 1874b: right quadratojugal (NHMUK PV R4753) in lateral (**a**) and medial (**b**) views. Abbreviations: **fj**, jugal facet; **fpo**, postorbital facet; **fq**, quadrate facet; **fsq**, squamosal facet; **li**, attachment point of ligaments binding quadrate to quadratojugal. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 7. *Ophthalmosaurus icenicus* Seeley, 1874b: left vomer (NHMUK PV R4753) in lateral (**a**) and dorsal (**b**) views and left vomer (GLAHM V1129) in dorsal (**c**) and medial (**d**) views. Abbreviations: **ch**, choana medial wall; **fp**, premaxillary facet; **fpl**, palatine contact; **fpt**, pterygoid facet; **fvo**, vomer facet; **gpt**, groove for pterygoid; **nb**, internal naris medial border; **ri**, ridge separating vestibulum and choanal tube; **sp**, spinous projections; **vn**, wall of vestibulum nasi; **vpr**, vertical projection. Scale bar represents 100 mm. Illustrations by Angela Kirton.

Text-fig. 8. *Ophthalmosaurus icenicus* Seeley, 1874b: left palatine (NHMUK PV R4753) in ventral (**a**) and dorsal (**b**) view. Abbreviations: **fm**, maxillary facet; **fpt**, suture with the pterygoid; **fvo**, vomer facet; **in**, internal narial opening; **nu**, nutritive foramina and grooves; **pr**, ascending projection. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 9. *Ophthalmosaurus icenicus* Seeley, 1874b: right quadrate (GLAHM V1878) in anterior (**a**), lateral (**b**) and posterior (**c**) views. Abbreviations: **ac**, articular condyle; **far**, articular facet; **foq**, quadrate foramen; **fpt**, pterygoid facet; **fqj**, quadratojugal facet; **fs**, supratemporal facet; **fsa**, surangular facet; **fst**, stapedial facet; **me**, muscle (*M. adductor mandibulae externus*) attachment point; **mp**, muscle (*M. adductor mandibulae posterior*) attachment point; **ocl**, occipital lamella; **ptl**, pterygoid lamella; **tu**, tubercle for ligamentous attachment to pterygoid. Scale bar represents 100 mm. Illustrations by Angela Kirton.

Text-fig. 10. *Ophthalmosaurus icenicus* Seeley, 1874b: basisphenoid portion of the parabasisphenoid (NHMUK PV R4522) in anterior (**a**), left lateral (**b**), dorsal (**c**) and ventral (**d**) views. Abbreviations: **btp**, basipterygoid process; **ds**, *dorsum sellae*; **fbo**, basioccipital facet; **fst**, stapedial facet; **gr**, median groove; **icf**, internal carotid foramen; **no**, notch marking anterior extremity of upturned notochord; **npa**, groove for palatine ramus of facial (VII) nerve; **pif**, pituitary fossa; **pma**, pit for muscle origin; **ps**, base of the parasphenoid rostrum; **tr**, impressions of trabecular cartilage. Scale represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 11. *Ophthalmosaurus icenicus* Seeley, 1874b: right prootic (NHMUK PV R4522) in anterior (**a**) and posterior (**b**) views. Abbreviations: **iaa**, impression of the ampulla of the anterior vertical semicircular canal; **ihc**, impression of the horizontal canal; **isa**, impression of the sacculus; **iut**, impression of the utriculus; **ivc**, impression of the anterior vertical semicircular canal; **mj**, ridge for attachment of the jaw adductor muscles. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 12. *Ophthalmosaurus icenicus* Seeley, 1874b: right opisthotic (NHMUK PV R4522) in anterior (**a**), posterior (**b**), medial (**c**), ventral (**d**) and dorsal (**e**) views. Abbreviations: **fbo**, basioccipital facet; **fs**, supratemporal facet; **fst**, stapedial facet; **hy**, groove for transmission of hyomandibular branch of facial (VII) or glossopharyngeal (XI) nerve; **ihc**, impression of horizontal semicircular canal; **ipc**, impression of posterior vertical semicircular canal; **ma**, axial muscle attachment point; **me**, muscle (*M. adductor mandibulae externus*) attachment point; **pam**, impression of posterior ampulla; **poc**, paroccipital process; **vf**, vagus foramen. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 13. *Ophthalmosaurus icenicus* Seeley, 1874b: left exoccipital (NHMUK PV R4522) in lateral (**a**) and medial (**b**) views. Abbreviations: **fbo**, basioccipital facet; **fhy**, foramina conveying branches of the hypoglossal (XII) nerve; **fop**, opisthotic facet; **fso**, supraoccipital facet; **mo**, muscle (occipital muscles) attachment point; **vf**, vagus foramen. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 14. *Ophthalmosaurus icenicus* Seeley, 1874b: basioccipital (NHMUK PV R4522) in anterior (**a**), dorsal (**b**), posterior (**c**) and left lateral (**d**) views. Abbreviations: **ac**, articular condyle; **eca**, extracondylar area; **fbs**, basisphenoid facet; **fex**, exoccipital facet; **fom**, floor of the foramen magnum; **fop**, opisthotic facet; **fst**, stapedial facet; **icd**, impressions of the cochlear duct; **n**, ventral notch; **no**, notochordal pit. Scale bar represents 100 mm. Illustrations by Angela Kirton.

Text-fig. 15. *Ophthalmosaurus icenicus* Seeley, 1874b: right stapes (NHMUK PV R4522) in anterior (**a**), posterior (**b**), dorsal (**c**) and ventral (**d**) views. Abbreviations: **fbo**, basioccipital facet; **fbs**, basisphenoid facet; **fop**, opisthotic facet; **fps**, facet for pterygoid and supratemporal; **fpt**, pterygoid facet; **fq**, quadrate facet; **hp**, hyoid process; **hy**, groove for hyomandibular branch of facial (VII) or glossopharyngeal (IX) nerve; **ms**, muscle scar; **sta**, path of stapedial artery. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 16. *Ophthalmosaurus icenicus* Seeley, 1874b: reconstruction of the skull in posterior view (**a**) (based upon NHMUK PV R2133, R2161, R3893, R4753 and GLAHM V1901) and the occipital region in left lateral view (**b**) (based upon NHMUK PV R2161). Abbreviations: **ac**, articular condyle of the quadrate; **bo**, basioccipital; **bs**, basisphenoid; **btp**, basipterygoidal processes of the basisphenoid; **cf**, carotid foramen; **eca**, extracondylar area of the basioccipital; **ex**, exoccipital; **fm**, foramen magnum; **fmd**, dorsal (supraoccipital) portion of foramen magnum; **fop**, foramen in the opisthotic for transmission of the glossopharyngeal (IX) or facial (VII) nerve; **fso**, foramen in the supraoccipital for the passage of a vein; **j**, jugal; **ms**, muscle scar on the stapes; **msv**, muscle (sub-vertebral) attachment point on the pterygoid; **npa**, groove for palatine ramus of facial (VII) nerve; **op**, opisthotic; **opp**, paroccipital process of the opisthotic; **pa**, parietal; **poc**, paths of the otic capsule soft tissues (dashed lines); **pr**, prootic; **pt**, pterygoid; **q**, quadrate; **qf**, quadrate foramen; **qj**, quadratojugal; **s**, supratemporal; **so**, supraoccipital; **spr**, pterygoid ramus of the supratemporal; **sps**, posterior shelf on the supratemporal; **sq**, squamosal; **sqf**, quadrate facet on the stapes; **st**, stapes; **ts**, posterolateral tubera on the supratemporal; **vf**, vagus foramen; **regular dots** indicate regions of cartilage. Scale bars represent 100 mm (**a**) and 50 mm (**b**). Illustrations by Angela Kirton.

Text-fig. 17. *Ophthalmosaurus icenicus* Seeley, 1874b: reconstructed lower right jaw ramus (based on NHMUK PV R3893 and GLAHM V1893) in lateral (**a**) and medial (**b**) views with cross-sections (**1**–**5**) in anterior view. Abbreviations: **al**, alveolar groove; **an**, angular; **ar**, articular; **d**, dentary; **fct**, foramen for chorda tympani; **fsa**, fossa surangularis; **gl**, jaw glenoid, articulation facets with the quadrate; **gr**, longitudinal groove on dentary; **m**, Meckelian Canal; **mc**, symphysial portion of Meckelian Canal on the dentary; **me**, muscle (*M. adductor mandibulae externus*) attachment point; **mi**, muscle (*M. adductor mandibulae internus*) attachment point; **ms**, muscle (*M. adductor mandibulae externus superficialis*) attachment point; **msy**, posterior portion of mandibular symphysis on the splenial, symphysial facet; **pcp**, paracoronoid process of the surangular; **pra**, prearticular; **sa**, surangular; **saf**, surangular foramen; **sp**, splenial; **dashed lines**, positions of cross-sections **1**–**5**. Scale bars represent 200 mm (**a**, **b**) and 100 mm (**1**–**5**). Illustrations by Angela Kirton and Benjamin Moon.

Text-fig. 18. *Ophthalmosaurus icenicus* Seeley, 1874b: anterior right (**a**, **b**), middle left (**c**, **d**) and middle right (**e**) positioned teeth (from GLAHM V1129) in mesial (**a**, **c**, **e**), distolingual (**b**) and distal (**d**) views. Abbreviations: **ce**, cementum; **cr**, crown; **de**, smooth dentine covered by acellular cementum; **ra**, root abnormality; **rp**, resorption pit; **wf**, wear facet. Scale bar represents 10 mm. Illustrations by Angela Kirton.

Text-fig. 19. *Ophthalmosaurus icenicus* Seeley, 1874b: atlas-axis complex (GLAHM V1916) in anterior (**a**), posterior (**b**), left lateral (**c**) and right lateral (**d**) views. Abbreviations: **dat**, atlas diapophysis; **dax**, axis diapophysis; **fna**, neural arch facets on the atlas-axis; **nat**, atlas neural spine; **nax**, axis neural spine; **nc**, neural canal; **pat**, atlas parapophysis; **pax**, axis parapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 20. *Ophthalmosaurus icenicus* Seeley, 1874b: vertebral centrum height/length ratios for PETMG R340, OUMNH J50496 (anterior presacral region) and CAMSM J65093–J65140 (caudal portion). Data for PETMG R340 from Buchholtz (2001). Figure by Benjamin Moon.

Text-fig. 21. *Ophthalmosaurus icenicus* Seeley, 1874b: anterior (**a**, **b**) and posterior (**c**, **d**) presacral vertebral centra (GLAHM V1916) in anterior (**a**, **c**) and left lateral (**b**, **d**) views. Abbreviations: **cd**, central depression; **dp**, diapophysis; **fna**, neural arch facet on the centrum; **nc**, neural canal; **pp**, parapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 22. *Ophthalmosaurus icenicus* Seeley, 1874b: anterior presacral vertebra centra 1–7 (GLAHM V1611) in left lateral (**a**) and ventral (**b**) views. Abbreviations: **at**, atlas-axis complex; **dp**, diapophysis; **fus**, ridge marking the line of fusion between the atlas and axis; **k**, ventral keel on anterior vertebral centra; **pit**, pits marking paths of vessels; **pp**, parapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 23. *Ophthalmosaurus icenicus* Seeley, 1874b: middle presacral vertebral centra (GLAHM V1611) showing transition from ‘cervical’ to ‘dorsal’ regions by separation of the neural arch facet and diapophysis: (**a**) centra 22–27 in left lateral view and (**b**) centrum 27 in ventral view. Abbreviations: **dp**, diapophysis; **k**, ventral keel; **pit**, pits marking paths of vessels; **pp**, parapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 24. *Ophthalmosaurus icenicus* Seeley, 1874b: presacral–caudal transitional vertebral centra 39–44 (GLAHM V1611) in left lateral view, showing the fusion of the diapophysis and parapophysis into the synapophysis. Abbreviations: **dp**, diapophysis; **pit**, pits marking paths of vessels; **pp**, parapophysis; **r**, ridge between parapophysis/synapophysis and anterior margin of the vertebral centrum; **sp**, synapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 25. *Ophthalmosaurus icenicus* Seeley, 1874b: anterior neural arches and spines (GLAHM V1894) 1–6 in left lateral view (**a**) and 1, 2, 4 and 6 respectively in anterior (**b**–**e**) and posterior (**f**–**i**) views. Only the right half of the atlantal neural spine is shown in **b** and **f**. Abbreviations: **ats**, atlas neural spine; **axs**, axis neural spine; **fc**, central facet on the neural arch; **fus**, line of fusion between right and left sides of arch and spine; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis. Dashed lines mark complete element outlines. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 26. *Ophthalmosaurus icenicus* Seeley, 1874b: middle presacral to middle caudal (left to right) neural spines and arches (GLAHM V1916) in left lateral (**a**–**f**), anterior (**g**–**l**) and posterior (**m**–**r**) views. Abbreviations: **fc**, central facet on the neural arch; **fus**, line of fusion between right and left sides of arch and spine; **g**, dorsal groove on the neural spine; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis. Incomplete portions indicated by dashed line. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 27. *Ophthalmosaurus icenicus* Seeley, 1874b: anterior (**a**–**c**) and middle (**d**–**f**) caudal vertebral centra (GLAHM V1916) in anterior (**a**, **d**), left lateral (**b**, **e**) and ventral (**c**, **f**) views. Abbreviations: **cd**, central central depression; **fh**, haemal arch facets; **fna**, neural arch facet; **nc**, neural canal; **pit**, pit marking path of vessel; **sp**, synapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 28. *Ophthalmosaurus icenicus* Seeley, 1874b: apical centra 71–74 (GLAHM V1916) in anterior view (**a**–**d**) and articulated in left lateral view (**e**) showing the curve created. Abbreviations: **cd**, central centrum depression; **fha**, haemal arch facet;

fna, neural arch facet; **nc**, neural canal; **pm**, procoelous margin; **r**, rib; **sp**, synapophysis; **θ**, approximate tail bend angle. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 29. *Ophthalmosaurus icenicus* Seeley, 1874b: apical neural arches 71–75 (GLAHM V1916) in anterior view (**a**–**e**) and left lateral view (**f**–**j**). Abbreviations: **cc**, pitting indicating a cartilage cap to the neural spine; **fc**, central facet on the neural arch; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 30. *Ophthalmosaurus icenicus* Seeley, 1874b: middle presacral to posterior caudal right lateral ribs (GLAHM V1916) in anterior (**a**–**f**), posterior (**g**–**l**) and dorsal (**m**–**o**) views. **a**, **g**: middle presacral region (proximal portion only); **b**, **h**: posterior presacral region; **c**, **i**: anterior caudal region; **d**, **j**, **m**: middle caudal region; **e**, **f**, **k**, **l**, **n**, **o**: posterior caudal region. Abbreviations: **ca**, capitulum; **cc**, attachment point of cartilaginous cap; **gr**, groove; **sh**, sheet between tuberculum and capitulum; **sp**, synapophysial articulation on the rib; **tu**, tuberculum; **tub**, muscle tubercle. Scale bar represents 50 mm. Illustrations by Angela Kirton.

Text-fig. 31. *Ophthalmosaurus icenicus* Seeley, 1874b: pectoral girdle (NHMUK PV R2137) in anterior (**a**), dorsal (**b**) and left lateral (**c**) views. Abbreviations: **ano**, anterior notch of the coracoid; **cl**, clavicle; **co**, coracoid; **fgc**, glenoid (humeral) facet of the coracoid; **fgs**, glenoid facet of the scapula; **fsc**, scapular facet of the coracoid; **ic**, interclavicle; **sc**, scapula; **t**, tubercle on interclavicle. Scale bar represents 100 mm. Illustrations by Angela Kirton.

Text-fig. 32. *Ophthalmosaurus icenicus* Seeley, 1874b: outlines of referred coracoids in dorsal view: **a**, type specimen: NHMUK PV R2133; **b**, LEICT 100'1949/20; **c**, holotype specimen of *Ophthalmosaurus monocharactus* Appleby, 1956: PETMG R220; **d**, GLAHM V1872. Abbreviations: **ano**, anterior notch; **fcc**, coracoidal facet on the coracoid; **fgc**, glenoid (humeral) facet on the coracoid; **fsc**, scapular facet on the coracoid; **pi**, posterior invagination ('notch'). Dashed lines mark complete element outlines. Scale bar represents 100 mm. Illustrations by Angela Kirton (**a**, **b**, **d**) and Benjamin Moon (**c**).

Text-fig. 33. *Ophthalmosaurus icenicus* Seeley, 1874b: left humerus (GLAHM V1893) in dorsal (**a**), ventral (**b**), proximal (**c**), distal (**d**), anterior (**e**) and posterior (**f**) views; reconstructed right forelimb (NHMUK PV R3702) in dorsal view (**g**). Abbreviations: **af**, anterior accessory element facet of humerus; **dp**, dorsal process; **h**, humerus; **i**, intermedium; **m**, muscle tubercle; **p**, pisiform; **pa**, pre-axial accessory element; **r**, radius; **rd**, radiale; **rf**, radial facet of humerus; **u**, ulna; **ul**; ulnare; **uf**, ulnar facet of humerus; **vp**, ventral process (deltopectoral crest); **arabic numerals**, distal carpals; **roman numerals**, metacarpals. Scale bars represent 100 mm. Illustrations by Angela Kirton.

Text-fig. 34. *Ophthalmosaurus icenicus* Seeley, 1874b: outlines of referred humeri in dorsal view: **a**, NHMUK PV R2132, right humerus; **b**, NHMUK PV R2135, left humerus; **c**, NHMUK PV R2173, right humerus; **d**, **e**, NHMUK PV R2138, left and right humeri; **f**, NHMUK PV R2186, left humerus. **b**, **d** and **f** have been reflected to appear as a right humerus in dorsal view for comparison. Humeri have been aligned to maintain a vertical long axis. Abbreviations: **af**, anterior distal facet; **rf**, radial facet; **uf**, ulnar facet. Dashed lines mark complete element outlines. Scale bar represents 100 mm. Illustrations by Benjamin Moon.

Text-fig. 35. *Ophthalmosaurus icenicus* Seeley, 1874b: pelvic girdle (GLAHM V1916) in lateral (**a**) and medial (**b**) views and reconstructed left hind paddle (NHMUK PV R4693–5) in ventral view (**c**). Abbreviations: **as**, astragalus; **cal**, calcaneum; **dc**, distal carpal 2; **f**, femur; **fac**, acetabular (femoral) facet on the ischiopubis; **fai**, acetabular (femoral) facet on the ilium; **fi**, fibula; **fis**, ilial facet on the ischiopubis; **fsi**, ischiopubic facet on the ilium; **il**, ilium; **is**, ischiopubis; **lig**, area of ligamentous attachment to the vertebral column; **n**, notch; **obf**, obturator foramen; **t**, tibia; **vp**, ventral process. Dashed lines mark complete element outlines. Scale bars represent 100 mm (**a**, **b**) and 50 mm (**c**). Illustrations by Angela Kirton.

Text-fig. 36. *Ophthalmosaurus icenicus* Seeley, 1874b: right femur (GLAHM V1916) in dorsal (**a**), ventral (**b**), proximal (**c**), anterior (**d**), posterior (**e**) and distal (**f**) views. Abbreviations: **ap**, anterior blunt projection; **dp**, dorsal process; **ff**, fibular facet of the femur; **m**, muscle scar; **tf**, tibial facet of the femur; **vp**, ventral process. Scale bars represent 50 mm. Illustrations by Angela Kirton.

TABLE CAPTIONS

Table 1. Specimens referable to *Ophthalmosaurus icenicus* Seeley, 1874b. Abbreviations: **Bucks**, Buckinghamshire; **Cambs**, Cambridgeshire; **KCF**, Kimmeridge Clay Formation; **Lincs**, Lincolnshire; **OCF**, Oxford Clay Formation; **Oxon**, Oxfordshire; **Wilts**, Wiltshire.

Table 2. Selected measurements (in mm) of cranial material referred to *Ophthalmosaurus icenicus* Seeley, 1874b. Typical measurements for adult specimens are included. Few elements are complete enough to permit extensive comparisons.

Table 3. Measurements (in mm) of the width of the extracondylar area of basioccipitals referred to *Ophthalmosaurus icenicus* Seeley, 1874b. Compare with *Brachypterygius extremus* (Boulenger, 1904) in Table 8.

Table 4. Measurements (in mm) of humeri referred to *Ophthalmosaurus icenicus* Seeley, 1874b. Humeri referred to CAMSM TN948 are uncertain and do not necessarily belong to this specimen. Abbreviations: **L**, left; **R**, right.

Table 5. Measurements (in mm) of distal facets of humeri referred to *Ophthalmosaurus icenicus* Seeley, 1874b. Humeri referred to CAMSM TN948 are uncertain and do not necessarily belong to this specimen. Abbreviations: **ARF**, ratio of length of anterior distal facet/radial facet; **L**, left; **R**, right.

BRITISH MIDDLE AND UPPER JURASSIC ICHTHYOSAURS