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A SECOND SPECIMEN OF *PROTOICHTHYOSAURUS APPLEBYI* (REPTILIA: ICHTHYOSAURIA) AND ADDITIONAL INFORMATION ON THE GENUS AND SPECIES

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ABSTRACT

Three isolated, partial skulls from historic collections, previously identified as *Ichthyosaurus communis* are herein assigned to *Protoichthyosaurus prostaxalis*. A fourth, nearly complete skull is referred to *Protoichthyosaurus applebyi*, only the second known specimen of the species. It provides additional information on the posterior portion of the skull and mandible. The diagnosis of *P. applebyi* is emended to include a postorbital that is dorsoventrally long but anteroposteriorly narrow relative to its length. It separates most of the jugal dorsal ramus from the orbit margin and makes up much more than half of the orbit posterior margin. The genus *Protoichthyosaurus* can be most easily distinguished from its sister taxon, *Ichthyosaurus*, by the forefin morphology, with three primary digits (II-IV) in the former and four primary digits (II-V) in the latter. In addition, the pineal in *Protoichthyosaurus* is bordered posteriorly by the parietals rather than being entirely enclosed by the frontals as in *Ichthyosaurus*. Many skull features, although not unique to *Protoichthyosaurus*, can together distinguish it from *Ichthyosaurus*. These include: a low-crowned skull with a long, slender rostrum; a large, posteriorly high, triangular external naris; an asymmetric maxilla with a long anterior process; a dorsoventrally long prefrontal anterior process that separates the dorsal process of the lacrimal from the orbit margin; and tooth roots with deep grooves that extend to the base of the crown. However, these characters vary among individuals and are often difficult to assess because of orientation, completeness, or preservation. Characters that distinguish individual species of *Protoichthyosaurus* from individual species of *Ichthyosaurus* are less subjective and often more easily evaluated.

INTRODUCTION

Recent work has shown that the Lower Jurassic genus *Protoichthyosaurus* Appleby, 1979, is valid and can be distinguished from the more common and better known genus *Ichthyosaurus* De la Beche and Conybeare, 1821, on the basis of a unique forefin (Lomax et al., 2017). Without the presence of a forefin, determining the identification of an isolated skull or other elements of the postcranial skeleton as either *Protoichthyosaurus* or *Ichthyosaurus* can be difficult. *Protoichthyosaurus*, however, possesses several skull characters that are not found together in any species of *Ichthyosaurus* (Lomax et al., 2017), although each species shares some characters. In this paper, we review the combination of features of the skull that distinguish the two genera and discuss the variation in those features.

The genus has two species: *Protoichthyosaurus prostaxalis*, first described by Appleby (1979), and *P. applebyi*, recently recognized by Lomax, et al. (2017). Differences in skull morphology can distinguish the two species from each other and from species of *Ichthyosaurus*. Here we report on four specimens, isolated partial skulls that had previously been identified as *Ichthyosaurus communis*, but can be assigned to species of *Protoichthyosaurus*. One skull is only the second specimen known of *P. applebyi* and provides additional information on the skull morphology of the species. This paper also presents a summary of skull characters that can distinguish species of *Ichthyosaurus* from species of *Protoichthyosaurus*. Species identifications are often necessary to confirm the generic assignment if the proximal forefin is not preserved.

Institutional abbreviations—BRLSI, Bath Literary and Scientific Institution, UK; **BU** (formerly BIRUG), Lapworth Museum, University of Birmingham, UK; **GPIT**, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Germany; **LEICT**, Leicester Arts and Museums Service, New Walk Museum and Art Gallery, UK; **NHMUK** (formerly BMNH), The Natural History Museum, London, UK; **NMING**, National Museum of Ireland – Natural History, Dublin; **NMW**, National Museum of Wales, Cardiff, UK; **SOMAG** (formerly AGC), Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street, Somerset, UK; **TTNCM**, Somerset County Museum, Taunton, UK; **UNM**, University of Nottingham Museum, UK.

MATERIALS

The specimens of *Protoichthyosaurus* described here are from historic collections, as are almost all referred specimens and the holotypes of the two species (Lomax et al., 2017). Although all four are preserved in three dimensions, only one or two aspects of the skull of each specimen are sufficiently well-preserved to provide information on morphology. None of the skulls are complete.

NMING:F16625 (Figure 1) was part of the William Lee Collection (acquired by the Royal Dublin Society by purchase in 1867, incorporated into the state-run Dublin Science and Art Museum, Ireland, in 1877, now the National Museum of Ireland), although the specimen and species list of the original acquisition is missing (Nigel Monaghan, pers. comm.). The present museum label suggests that it is probably specimen "o" cited by Lydekker (1891, p. 50) in his catalogue of specimens at the Dublin Science and Art Museum. Two old NMING labels affixed to the specimen indicate that it is from Barrow-upon-Soar, Leicestershire, which is also the location indicated by Lydekker (1891) for specimen "o". The preservation and bone color of the specimen is consistent with the preservation style from that locality. The specimen is the middle portion of a skull and mandible, from about the middle of the orbit to several centimeters anterior to the external naris, preserved in three dimensions. Bones comprising the anterior, dorsal, and ventral margin of the orbit and those surrounding the external naris are well preserved in right lateral view, but the skull is broken posterior to that. In left lateral view, the bones are fragmented and portions of their surfaces have been sheared off, and so this side of the skull provides little information. The dorsal side preserves mainly the nasals and the anterior portions of the left prefrontal, parietal and frontal, but the same elements from the right side are damaged, displaced, or missing. The ventral side of the skull is poorly preserved and damaged, so does not provide any useful information.

NMING:F8756 (Figure 2) is a poorly preserved, isolated skull in three dimensions, but the anterior portion of the rostrum and some portions of the posterior part of the skull are missing. As with the previous specimen, it is from the William Lee Collection. Information with the specimen identify it as Lydekker's (1891, p. 49-50) specimen "k" from Barrow-upon-Soar, Leicestershire. Lydekker's (1891) comment on the "large size of the teeth" supports this attribution because the teeth are large and very prominent on the specimen. NMING:F8756 has a similar bone color and preservation style as NMING:F16625. The specimen was removed from plaster in 1988 and presently is in four pieces. The right lateral view provides the most information, although the skull is broken across the lacrimal and maxilla anterior to the orbit. The second break is in the premaxillary portion of the rostrum, and the third break is at the anterior end of the rostrum forming a very small anterior piece. In right lateral view, a portion of the left mandible is exposed, which is presumably due to taphonomic distortion. In left lateral view, only the portion of the skull anterior to the orbit is present, but it is more poorly preserved than the right side. In dorsal view, the entire posterior half of the left side of the skull is missing, although the dorsal surface provides some information. In ventral view, the right mandible is preserved for the entire length of the specimen but the left mandible is absent on the posterior piece. Mediolateral crushing has moved the two sides of the mandible so that they touch for the entire rostrum length anterior to the maxilla.

FIGURE 1: NMING:F16635, *Protoichthyosaurus prostaxalis* preorbital-narial region of skull, probably from Barrow-upon-Soar, Leicestershire, UK. Although the specimen is preserved in three dimensions, the other views are too poorly preserved to provide information. Anterior to the right. Scale = 10 cm.

GPIT 1796/1 (Figure 3) is an isolated skull from the Lyme Regis area, Dorset, one of only three specimens of *Protoichthyosaurus* from that location. The anterior portion of the rostrum is missing. The left side and dorsal surface are poorly preserved, but the right side and ventral surface preserve much of the original bone surface. This results in a clear difference in color, with the eroded surface being much lighter (tan) than the other (brown).

NHMUK R1164 (Figure 4) is another isolated skull from the Lyme Regis area, Dorset (Lydekker, 1889, p. 46). Interestingly, the specimen was mentioned and figured by Motani (2005, p. 341-342, fig. 3D-F), who suggested that it was not *Ichthyosaurus*, but probably represented a new genus or species. The skull is in three-dimensions but laterally compressed, and it is almost entirely removed from matrix. The anterior tip of the rostrum, probably

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FIGURE 2: NMING:F8756, nearly complete skull of *Protoichthyosaurus prostaxalis*, probably from Barrow-upon-Soar, Leicestershire, UK, in right lateral view. Anterior end of rostrum is missing. Although the specimen is preserved in three dimensions, the other views are too poorly preserved to provide information. Scale = 10 cm. Photo courtesy of National Museum of Ireland.

less than 5 mm, is missing. Five cervical centra and partial neural spines are articulated with the skull, one of which might be the atlas-axis, but it is poorly preserved and partially buried. The skull is best preserved in right lateral view, although the ventral portion of the lacrimal is missing (Figure 4), exposing the dorsal portion of the maxilla that is normally overlain by the lacrimal and subnarial process of the premaxilla. The left side preserves only the rostrum, with almost the entire post-narial portion of the skull missing. The dorsal side does not provide much information but shows the strong lateral compression of the rostrum. The portion of the skull posterior to the nasals is missing except for a few poorly preserved bones on the right side. In ventral view, the posterior half of the left mandible is missing, and the remaining bones provide little useful information.

In addition, as part of this study, we located an additional specimen of the genus, an isolated articulated forefin (TTNCM: 59/2000) collected from the shoreline at Lilstock, Somerset, U.K. The humerus is damaged, but the rest of the fin is nearly complete. The specimen has three primary digits (II-IV), a bifurcation of digit II in the metacarpal row, a second more distal bifurcation of digit II, and the posterior metacarpal of digit II nearly separates distal carpals two and three. These features are diagnostic for the genus. The specimen is not discussed further.

SYSTEMATIC PALEONTOLOGY

ICHTHYOSAURIA de Blainville, 1835
ICHTHYOSAURIDAE Bonaparte, 1841
PROTOICHTHYOSAURUS Appleby, 1979

Revisions to the Diagnosis—Diagnosis as emended in Lomax et al. (2017), but with the following additions and corrections to the "unique combination of characters": pineal bordered posteriorly by parietals; prefrontal anterior process separates most, if not all, of dorsal process of lacrimal from anterior orbit margin (shared with *Ichthyosaurus larkini*, *I. somersetensis*); large external naris, usually somewhat triangular (much higher posteriorly than anteriorly); strongly asymmetric maxilla with long, slender anterior process; prominent grooves on tooth root extend to base of crown (shared with *Temnodontosaurus*, *I. somersetensis*); three primary digits (II, III, IV) in forefin (shared with *Stenopterygius*, *Temnodontosaurus*, and others, but not *Ichthyosaurus*); digital bifurcation of digit II results in five digits in forefin (shared with *Ichthyosaurus*).

Additional Referred Specimen—TTNCM: 59/2000, a left forefin and associated partial scapula, ribs, and vertebrae collected *ex situ* at Lilstock, Somerset, UK.

Remarks—The emended diagnosis in Lomax et al. (2017) stated that the jugal anterior process does not extend beyond the anterior edge of the orbit. This is incorrect. The anterior extent of the jugal anterior process varies among specimens of *P. prostaxalis* and so it is not diagnostic for the genus. Additionally, Lomax et al. (2017) stated that a long internasal foramen was always present, but we have found that the presence and size varies among specimens and thus is likely the result of individual variation or preservation. The midline of the nasals is often filled with matrix, making it difficult to confirm the presence of a foramen. As also identified by Maisch and Matzke (2000), a depression along the midline of the nasals usually occurs in specimens that preserve the skull roof. The depression is usually broader and deeper posteriorly. The feature seems to be more common in *Protoichthyosaurus* than in *Ichthyosaurus*.

In addition, an error in the terminology used by Lomax et al. (2017) resulted in an error stating that the forefin of *Protoichthyosaurus* had five primary digits,

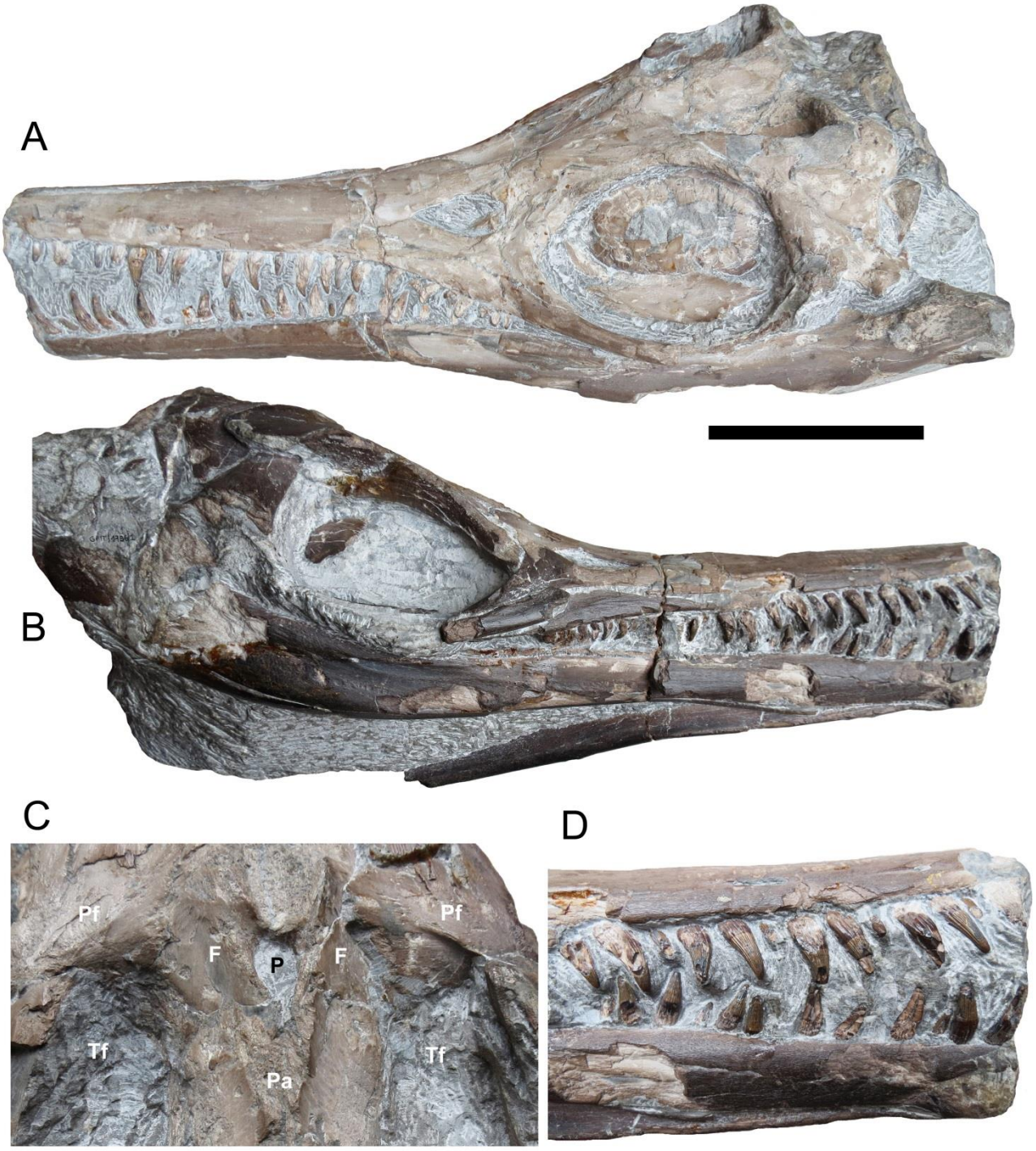

FIGURE 3: GPIT 1796/1, isolated skull of *Protoichthyosaurus prostaxalis* from the Lyme Regis area, Dorset, UK. A. Skull in left lateral view, but exposing some of the skull roof. B. Right lateral view of the same. C. Close-up of the skull roof, showing the pineal foramen between the frontals and parietal. D. Close-up of some of the teeth figured in 'B'. Abbreviations: F, frontal; P, pineal foramen; Pa, parietal; Pf, postfrontal; Tf, temporal fossa. Scale = 10 cm.

which it shared with *Ichthyosaurus*. Both genera have anterior digital bifurcations in the forefin, resulting in five digits (as defined by Cooper et al., 2007, fig.1). However, *Ichthyosaurus* has four primary digits (II, III, IV, V) whereas *Protoichthyosaurus* has only three (II, III, IV), regardless of the number of bifurcations. In *Protoichthyosaurus*, a proximal bifurcation results in two metacarpals associated with digit II. Thus four elements are in the metacarpal row (fourth row of the forefin), the same number that usually occurs in *Ichthyosaurus*. However in *Ichthyosaurus*, metacarpal five and distal carpal four contact the distal edge of the ulnare; whereas in *Protoichthyosaurus*, distal carpals three and four contact the ulnare, and metacarpal five is absent (Motani, 1999; Lomax et al., 2017). The combination of three primary digits (II-IV) and an anterior digital bifurcation in *Protoichthyosaurus* is unique among parvipelvian ichthyosaurs.

Finally, one of the specimens described here confirms that the pineal opening is between the frontal and parietal (Figure 3C), as suggested by Lomax et al. (2017), a feature shared by *Leptonectes*, *Stenopterygius*, *Temnodontosaurus* and others (McGowan & Motani, 2003, fig. 69; Motani, 2005). This is different from *Ichthyosaurus*, where the pineal is at the posterior edge of the frontal, but completely enclosed by it (Motani, 2005; Massare and Lomax, 2017). Preservation can often make this difficult to discern.

SKULL FEATURES OF *PROTOICHTHYOSAURUS*

In addition to the position of the pineal opening, which is not frequently preserved, several skull characters can distinguish *Protoichthyosaurus* from *Ichthyosaurus*, but only in combination: (1) *Protoichthyosaurus* has a low skull, with a low slope of the crown from the temporal region to the external naris. Skulls of *Ichthyosaurus* vary, but usually have a higher crown, especially *I. larkini* and *I. conybeari*. (2) *Protoichthyosaurus* has a long slender rostrum, similar to *I. larkini*, but not as robust as the long rostra in *I. anningae* and some specimens of *I. communis*. The difference is not easily quantified because the slenderness is not reflected in the snout ratio (as defined by McGowan, 1973). (3) In lateral view, the prefrontal of *Protoichthyosaurus* is dorsoventrally long anteriorly, and extends along part of the anterior orbit margin, separating most (if not all) of the dorsal process of the lacrimal from the orbit margin, as in *Ichthyosaurus larkini* and *I. somersetensis*. By itself, it cannot distinguish the genus from *Ichthyosaurus*. (4) Uncrushed skulls of *Protoichthyosaurus* usually have a large, triangular external naris that is distinct from that of *Ichthyosaurus* because it is dorsoventrally very high posteriorly. Some specimens of *Ichthyosaurus*, notably *I. somersetensis*, have a triangular naris, but the difference in height between the posterior and anterior ends is not as great. The dorsoventral height of the naris in *Protoichthyosaurus* is greater than in *Ichthyosaurus*, making it appear much larger. *Ichthyosaurus conybeari* and *I. breviceps* also have dorsoventrally high nares, but they are shorter anteroposteriorly than in *Protoichthyosaurus*. The amount of flattening and the orientation of the skull, however, can distort the shape of the naris and its dorsoventral height, so the naris shape is not distinctive in all specimens. In some specimens, it is an elongated oval rather than triangular, so the lack of a triangular shape does not rule out the genus. (5) *Protoichthyosaurus* has an asymmetric maxilla with a long, slender anterior process in lateral view, measured from the maximum height of the maxilla, and extends well beyond the naris. This is similar to *I. conybeari*. Many specimens of other species of *Ichthyosaurus* have maxillae with anterior processes that extend beyond the external naris. The asymmetry is the important feature in recognizing *Protoichthyosaurus*, but even then, the difference from *I. conybeari* is subtle. The orientation of the skull, however, can affect the apparent lengths; a more ventral orientation can make processes appear longer; a more dorsal orientation can make processes look shorter. (6) *Protoichthyosaurus* and some species of *Ichthyosaurus* have prominent grooves and ridges in the tooth roots. In *Protoichthyosaurus* and *I. somersetensis*, the grooves extend to the base of the crown and are continuous with the ornamentation of the crown itself (Figure 4C). It does not occur on every tooth of every specimen, largely because of preservation. In other species of *Ichthyosaurus*, the root is usually smooth at the base of the crown. Because of the large roots and wide bases of the crowns, the teeth of *Protoichthyosaurus* often look massive in comparison to the slenderness of the snout.

Most of these characters are qualitative and difficult to assess. They are all variable, in part because of individual variation, but also the result of differences in completeness, orientation, and preservation. A given specimen might not display the typical morphology of every feature, making a generic assignment difficult, especially on poorly preserved skulls. Individual species of each genus, however, have unique combinations of characters that distinguish them from each other, and sometimes species can be more readily identified than the genus, thus allowing assignment to *Ichthyosaurus* or *Protoichthyosaurus* (see below).

PROTOICHTHYOSAURUS PROSTAXALIS Appleby, 1979

Holotype—BRLSI M3553 (formerly B. 1963'5/OS), a partial skull, pectoral girdle, and both forefins, preserved in ventral view.

Additional Referred Specimens— NMING: F16625, the middle portion of a skull preserved in three dimensions. NMING:F8756, a poorly preserved, isolated skull in three dimensions. GPIT 1796/1, an isolated skull in three dimensions, missing the anterior portion of the rostrum.

Locality and horizon—NMING:F16625 and NMING:F8756 are probably from Barrow-upon-Soar, Leicestershire, England, UK, as are some other referred specimens of *P. prostaxalis* (Lomax et al., 2017). Specimens from that locality might be from the Tilmanni Ammonite Zone (Martin et al., 1986; but see Page, 2010; Weedon et al., 2017), but as with most historical specimens, specific stratigraphic information is not available. GPIT 1796/1 is from Lyme Regis, specifically from the Bucklandi Ammonite Zone (lower Sinemurian) according to the label with the specimen. This confirms the occurrence of the genus and species in the lower Sinemurian.

Diagnosis—As emended in Lomax et al. (2017).

Remarks—Only fragmentary hind fins of *Protoichthyosaurus prostaxalis* are known, but they indicate that three primary digits (II, III, IV) are present. This feature is shared with *Ichthyosaurus* (note error in terminology in Massare and Lomax, 2017), and it might prove to be a genus characteristic for *Protoichthyosaurus* as well. Hindfins of *Ichthyosaurus* have a proximal bifurcation of digit II in the metacarpal or first phalangeal row (Massare and Lomax, 2018). Whether a similar bifurcation occurs in either species of *Protoichthyosaurus* is unknown.

DESCRIPTION

None of the specimens herein referred to *Protoichthyosaurus prostaxalis* preserves a forefin with the diagnostic features of the genus. NMING:F16625 (Figure 1) has a large, triangular external naris that is high posteriorly and tapers anteriorly. NMING:F16625 might also have an internasal foramen or at least a depression in the nasals at the midline of the skull, but the area is filled with matrix. The maxilla is dorsoventrally high and roughly triangular, although its dorsal edge is somewhat rounded and partially covered by matrix. The maxilla morphology is most similar to that of BU 5323, a referred specimen of *P. prostaxalis*. Furthermore, the narrow anterior process of the maxilla extends well beyond the external naris and is much longer than the posterior process, measuring from the maximum height of the maxilla. The high, asymmetric maxilla in lateral view in NMING:F16625 is characteristic of *P. prostaxalis*. *Ichthyosaurus somersetensis* can have a long anterior process (e.g., ANSP 15766), but the very slender posterior process is even longer, resulting in the opposite sense of asymmetry as *P. prostaxalis*. *Ichthyosaurus communis* can also have a long anterior process of the maxilla (e.g., NHMUK R1162, SMNS 13111), but on such specimens, the posterior process is also long, making the maxilla nearly symmetric. In NMING:F16625, because of damage to the anterior ends of the maxilla and nasal, it is unclear whether the maxilla extends as far as the nasals in lateral view. The left maxilla is too poorly preserved to provide any useful information. The lacrimal is triradiate, as also occurs in most species of *Ichthyosaurus*, but the dorsal process is much longer than the anterior process, a diagnostic feature of *P. prostaxalis* (Lomax et al., 2017). The anterior process of the lacrimal would have contacted the damaged subnarial process of the premaxilla slightly posterior to the mid-point of the ventral margin of the external naris. The dorsal process of the lacrimal is dorsoventrally high and has a long contact with the prefrontal. The posteroventral process of the lacrimal is longer than both the dorsal and anterior processes, as in *P. prostaxalis* and some species of *Ichthyosaurus*. However, disarticulation or the orientation of the skull can affect the extent of exposure of the posteroventral process, and thus its perceived length relative to the other processes. The prefrontal has a dorsoventrally long anterior process that separates the dorsal process of the lacrimal from the anterior border of the orbit, as in *Protoichthyosaurus*, *I. somersetensis*, and *I. larkini* (Lomax and Massare, 2017; Lomax et al., 2017). The jugal extends anteriorly beyond the anterior edge of the orbit, as in NHMUK R36958, another specimen of *P. prostaxalis*, although it might be displaced anteriorly in NMING F16625. In other specimens of *P. prostaxalis*, the jugal extends just to the anterior edge of the orbit or only slightly beyond (e.g. BU5323, BRLSI M3555, GPIT 1796/1). Thus the position of the anterior extent of the jugal is variable and is not diagnostic of the genus (contrary to Lomax et al., 2017). The anterior termination of the jugal in NMING:F16625 is blunt rather than pointed and does not look damaged, similar to the shape in NHMUK R36958. *Ichthyosaurus larkini* has a similar blunt termination of the jugal, but in that species, the jugal extends much farther anteriorly than in NMING:F16625 and it separates the lacrimal from the maxilla. The extent of the prefrontal, the asymmetric maxilla with a long anterior process, and the large, triangular external naris identifies the specimen is *Protoichthyosaurus*. The dorsoventrally high maxilla and relative size of the dorsal and anterior processes of lacrimal identifies NMING:F16625 as *P. prostaxalis*.

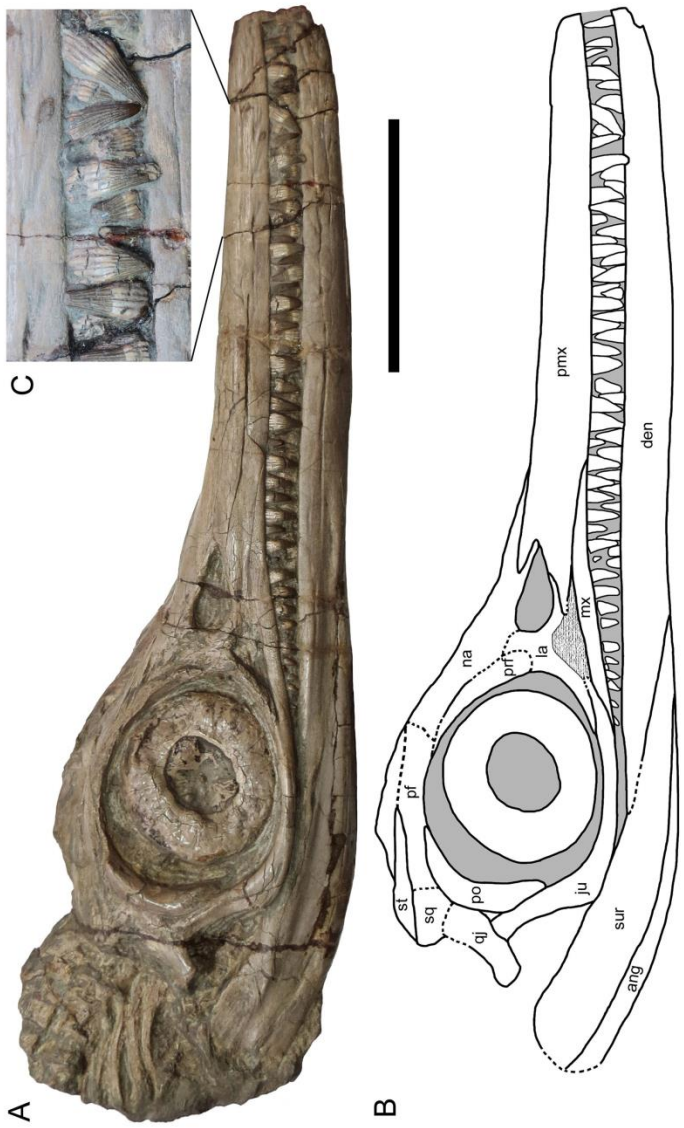

FIGURE 4: NHMUK R1164, nearly complete skull of Protoichthyosaurus appleby from the Lyme Regis area, Dorsett, UK. A. Right lateral view, anteriormost tip of rostrum is missing. Although the specimen is preserved in three dimensions the other views are too poorly preserved to provide informtion. B. Interpretive illustration of skull. Stippled region indicates wehre lacrimal is missing, exposing bones that weree beneath it. Gray areas are matrix. C. Close-up of nterior premaxillary teeth. Abbreviations: ang, angular; den, dentary; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pf, postfrontal; po, postorbitalpmx, premaxilla; prf, prefrontal; qj, quadratojugal; sq, squamosal; st, supratemporal; sur, surangular. Scale = 10 cm.

NMING:F8756 (Figure 2) has a low skull with a long slender rostrum. The preserved length is 49 cm, with a preorbital length of 34.5 cm, although an unknown length of the anterior rostrum is missing. The preserved mandible length is 54 cm (snout ratio > 0.64). The external naris is triangular, but not as high posteriorly as is typical of *Protoichthyosaurus*. The dorsoventrally high maxilla is asymmetric, with a long, slender anterior process that extends well beyond the external naris, as is diagnostic of *P. prostaxalis*. On the right side of the skull, the maxilla appears to contact the ventral margin of the external naris because the lacrimal process and subnarial process of the premaxilla are broken or worn off. On the left side, although damaged, it is clear that the anterior process of the lacrimal and subnarial process of the premaxilla separate the maxilla from the ventral margin of the external naris. On the left side of the skull, the dorsal process of the lacrimal is noticeably longer than the anterior process, a characteristic of *P. prostaxalis*, although the lacrimal processes and subnarial process of the premaxilla are poorly preserved. On the right side, the anterior process of the prefrontal is dorsoventrally high and separates the dorsal process of the lacrimal from the anterior margin of the orbit, a diagnostic feature of *Protoichthyosaurus*, but also present in *Ichthyosaurus larkini* and *I. somersetensis*. The sclerotic ring is complete (height=6.5 cm, length=7.0 cm) and fills just under 50% of the orbit (height=8.7 cm; length=11 cm). The anterior process of the jugal is broken. The jugal dorsal ramus makes up about half of the posterior orbit margin, and has a broad contact with the ventral edge of the postorbital as in BU 5323 and BRLSI M3555, referred specimens of *P. prostaxalis* (Lomax et al., 2017). The postorbital makes up no more than half of the posterior orbit margin, as in *P. prostaxalis*, *Ichthyosaurus communis*, and *I. breviceps*. It is roughly rectangular, but slightly anteroposteriorly wider dorsally than ventrally, with both the anterodorsal and anteroventral edges tapering to narrow processes, as in BU 5323. In right lateral view, the surangular is exposed to just beyond the external naris. The angular makes up only a small portion of the posterior part of the mandible, and appears to extend anteriorly slightly beyond the surangular, although this could be due to the orientation or damage of the skull (Figure 2). No teeth are preserved well enough to describe, however, the diameters of the roots appear fairly large for the rostrum length. In dorsal view, only the right nasal is complete, articulated with part of the left nasal. It does not appear to have an internasal foramen, although that portion of the skull is damaged and most of the left side is missing. Only the right temporal fenestra is present and is an anteroposteriorly elongated oval. The surrounding elements are poorly preserved and broken, and it is difficult to confidently interpret sutures. NMING F8756 can be referred to *Protoichthyosaurus* on the basis of a long rostrum, a prefrontal that separates the dorsal process of the lacrimal from the orbit margin, and the asymmetric maxilla with a long slender anterior process. It is identified as *P. prostaxalis* because of the dorsoventrally high maxilla that extends well beyond the external naris, and a dorsoventrally short, but anteroposteriorly wide, postorbital that makes up no more than half of the posterior orbit margin.

GPIT 1796/1 (Figure 3) has a preserved skull length of 41 cm and jaw length of 43 cm. It has been described in detail by Maisch and Matzke (2000), but we disagree with some of their interpretations. The prefrontal anterior process is dorsoventrally wider and extends ventrally to at least the level of the ventral edge of the external naris, contrary to their illustration (Maisch and Matzke, 2000, fig. 3). They also suggested that the lacrimal anterior process makes up the entire ventral margin of the external naris and extends beyond it. However, the subnarial process of the premaxilla makes up most of the ventral margin and the anterior process of the lacrimal is short, although it is damaged on both sides of the skull. Maisch and Matzke (2000) also describe the presence of a septomaxilla in the posteroventral part of the external naris. This might be part of a salt gland structure (Wahl, 2012). Several features of this specimen clarify previously unknown morphology of the skull roof. The pineal opening is enclosed largely in the frontals but continues slightly posteriorly, beyond the posterior edge of the complete left frontal (as seen in LEICT G729.1889.1 and can be inferred in BU 5323 and NHMUK R36958). Thus, although the anterior parietals are damaged, it is clear that they made up the posterior border of the pineal, as noted by Maisch and Matzke (2000). The nasals lack an internasal foramen but there is a depression along the midline (Maisch and Matzke, 2000). GPIT 1796/1 is assigned to *Protoichthyosaurus* on the basis of the slender rostrum, large triangular external naris, a prefrontal that separates most of the lacrimal dorsal process from the orbit margin, and large tooth roots with prominent grooves that extend to the base of the crown. It is assigned to *P. prostaxalis* because of the dorsoventrally high, asymmetric maxilla, a wide postorbital that makes up about half of the posterior border of the orbit, and a squamosal with a triangular posteroventral process (Figure 3).

PROTOICHTHYOSAURUS APPLEBYI Lomax, Massare, and Mistry 2017

Holotype—UNM.G.2017.1 (formerly UON VR159), a nearly complete skull and skeleton, although the posterior portion of the tail has most likely been added (Lomax et al., 2017).

Referred Specimen—NHMUK R1164, a nearly complete, isolated skull with a few articulated cervical vertebrae.

Locality and Horizon—No locality or horizon information is known for the holotype, but the preservation style suggests that it might be from the Lower Jurassic of Nottinghamshire or Leicestershire (Lomax et al., 2017). NHMUK R1164 is from Lyme Regis, Dorset, England, UK, generally assumed to be Hettangian-Sinemurian in age, although strata from the Rhaetian-Pliensbachian are preserved in the area (Benton and Spencer, 1995, fig. 5.3; Gallois, 2007; Page, 2010). As with most historic specimens, the stratigraphic horizon is unknown.

Emended Diagnosis—*P. applebyi* is distinguished from *P. prostaxalis* and all species of *Ichthyosaurus* by a unique combination of characters listed in Lomax et al. (2017) to which is added: postorbital makes up much more than half of orbit posterior margin (as in *I. conybeari*, *I. anningae*, *I. larkini*, and *I. somersetensis*, but unlike *P. prostaxalis*); postorbital dorsoventrally long but anteroposteriorly narrow relative to its length (similar to *I. somersetensis* and *I. conybeari*).

DESCRIPTION OF NHMUK R1164

NHMUK R1164 (Figure 4) is a larger skull than that of the holotype (UNM.G.2017.1), and thus likely represents a more mature individual. Of particular note, this specimen is about the same size (mandible length 44.0 cm; Table 1) as several specimens assigned to *P. prostaxalis* (Lomax et al. 2017, table 2; and herein). This demonstrates that the morphological differences between the two species are not ontogenetic. *Protoichthyosaurus applebyi* is not a juvenile of *P. prostaxalis*.

The dorsal skull roof of NHMUK R1164 is poorly preserved. However, the most important feature of the dorsal surface is a depression along the midline of the nasals, made more prominent because the left side has been pushed upward with respect to the right. An internasal depression occurs on specimens of *Protoichthyosaurus prostaxalis* that preserve the dorsal skull, but this is the first specimen of *P. applebyi* on which it is preserved. The presence of an internasal foramen cannot be confirmed because of compression of the skull.

The remaining description is from the right lateral view, unless otherwise stated (Figures 4A, B). The post-orbital region of the skull and posterior portion of the mandible are much better preserved than on the holotype and provide new information.

The subnarial and supranarial processes of the premaxilla make up the anterior margin of the external naris. The subnarial process extends about half the external naris length, but makes up the anterior quarter of the naris ventral margin. For much of its length, it is separated from the naris by the thin anterior process of the lacrimal. The supranarial process extends less than half the external naris length and is separated from the dorsal margin of the naris by a thin sliver of the nasal. The supranarial process does not seem to be broken, and thus the nasal makes up all of the dorsal margin of the naris.

The low maxilla is more bar-like than triangular, a feature that distinguishes *P. applebyi* from *P. prostaxalis* (Lomax et al., 2017). However, a portion of the lacrimal is missing and the end of the subnarial process is broken, exposing a small length of the maxilla that is usually covered. This makes the maxilla appear higher and more triangular than it would be on an undamaged skull (compare Figures 4A and B). The maxilla is separated from the margin of the external naris by processes of the lacrimal and premaxilla. The posterior process of the maxilla narrows abruptly, and does not extend very far below the orbit. Its anterior process extends at least ½ naris length beyond the external naris, a much longer extent than in the holotype of *P. applebyi* and similar to that in *P. prostaxalis*. In lateral view, the maxilla appears to extend beyond the nasals, which is not the case in the holotype, but the skull is distorted and the nasals are pushed inward (seen in lateral and dorsal views).

The large, triangular external naris that tapers anteriorly is diagnostic of the genus (Lomax et al., 2017). The lacrimal is triradiate, and the anterior process extends more than half the length of the ventral margin of the external naris, although it is very slender in the anterior portion. The dorsal process of the lacrimal is damaged so its length relative to the anterior process, a feature that distinguishes *P. prostaxalis* from *P. applebyi*, is not evident. It probably makes up most of the posterior margin of the external naris, but a tiny process on the nasal makes up the posterodorsal edge, as is seen in other specimens of the genus (Lomax et al., 2017, fig. 4). The prefrontal makes up at least half of the dorsal margin of the orbit, which was also suggested in the holotype (Lomax et al., 2017). Anteriorly, it separates the dorsal process of the lacrimal from the anterior orbit margin.

The sclerotic ring in NHMUK R1164 is complete and undistorted, and fills 62% of the orbit. Fernández et al. (2005) suggested that the sclerotic ring nearly

filled the orbit in juveniles, but occupied less of the orbit in adults, at least in ophthalmosaurid ichthyosaurs. For comparison, in large *Caypullisaurus* specimens (skull length 1.0-1.5 m), presumably adults, the sclerotic ring was 54-60% of the area of the orbit (Fernández et al., 2005).

The jugal does not extend beyond the anterior margin of the orbit, but seems to be separated into two pieces by a groove that exposes matrix, so it might have been damaged. The dorsal ramus bends at nearly a right angle and is narrow for most of its length. Although it extends dorsally for about half of the orbit height, it is largely separated from the posterior margin of the orbit by the postorbital and makes up only a small portion of the posterior orbit margin. A long contact between the jugal and postorbital extends for almost half of the length of the jugal dorsal ramus.

The crescentic postorbital is tall and narrow, and makes up about three-quarters of the posterior margin of the orbit. The shape and extent of the postorbital is entirely different from that of *P. prostaxalis*, and distinguishes the two species (Lomax et al., 2017). The postorbital shape and extent is somewhat similar to that of *I. somersetensis*, but the jugal of that species has only a slight bend of the dorsal ramus and the postorbital makes up more of the posterior orbit margin (Lomax and Massare, 2017). The postorbital of *I. conybeari* is also high, but it is narrower relative to its height than that of *P. applebyi.*

Most of the quadratojugal is exposed, but the dorsal portion is crushed and damaged. The shaft narrows, forming a slightly bulbous ventral end for the quadrate facet. This is similar to the morphology in *P. prostaxalis* (NMW 2012.23G.1; Lomax et al., 2017). A deep embayment between the jugal dorsal ramus and quadratojugal results in a high lower temporal arch, which appears to be more prominent than what occurs in *P. prostaxalis* and *Ichthyosaurus*.

The angular makes up about one third of the posterior end of the mandible in lateral view, the remaining portion being the surangular. Both bones taper anteriorly, with the angular terminating at a position slightly anterior to the middle of the orbit, and the surangular extending to a position posterior to the middle of the external naris. The posterior end of the dentary extends at least to the middle of the orbit.

Many well-preserved teeth are present. The teeth have large roots with prominent longitudinal grooves that extend to the base of the crown in well preserved teeth (Figure 4C). The portion of the root between the grooves becomes the base of the longitudinal striations of the crown, suggesting that the crown striations are formed by folds in both the enamel and dentine layers in *Protoichthyosaurus*, rather than just in the enamel layer. The tooth crown itself has an acute but rounded apex, and the longitudinal striations do not extend all the way to the apex. When the entire tooth is preserved, the crown is small relative to the root, even on premaxillary teeth.

NHMUK R1164 is assigned to *Protoichthyosaurus* because of a combination of features that include: a large, triangular external naris, a long slender rostrum, a strongly asymmetric maxilla with a long anterior process, the prefrontal anterior process separating the lacrimal dorsal process from the orbit margin, and tooth roots with prominent longitudinal grooves that extend to the base of the crown. It is assigned to *P. applebyi* because the maxilla is dorsoventrally low and the postorbital is high and narrow, making up more than half of the posterior margin of the orbit.

THE STATUS OF *ICHTHYOSAURUS FORTIMANUS*

Owen (1849-1884) described a new species of *Ichthyosaurus*, *I. fortimanus*, defined on the basis of a forefin that was missing the humerus. The main distinguishing characters were the number of digits, size of the elements, the angular shape of phalanges, and the width of the fin relative to its length. Almost a century later, McGowan (1974) synonymized *I. fortimanus* with *I. communis*.

The specimen figured by Owen (1849-1884, pl 30, fig. 1) is no doubt NHMUK R1063 (Figure 5). It possesses the diagnostic characters of *Protoichthyosaurus*: only digits II, III, and IV are present, with digit V missing, unlike in *Ichthyosaurus*; a bifurcation in the metacarpal row results in two metacarpals associated with digit II; the posterior metacarpal two is proximodistally long, nearly separating distal carpal two from distal carpal three; and a distal bifurcation of digit II results in a total of five digits in the forefin, the same number as in many specimens of *Ichthyosaurus.* Lomax et al. (2017) assigned the specimen to the genus without realizing that it was the holotype of *I. fortimanus*. Additionally, they expanded the diagnosis of *P. prostaxalis* to include additional characters of the paratypes and referred specimens. NHMUK R1063, however, possesses only features characteristic of the genus.

NHMUK R1063 is from Lyme Regis, Dorset, as is GPIT 1796/1, a specimen of *P. prostaxalis*, and the new specimen of *P. applebyi* (NHMUK R1164). The Lyme Regis location encompasses strata along the coast that range from Rhaetian (uppermost Triassic) to Pliensbachian (upper Lower Jurassic; Benton and Spencer, 1995). Although the stratigraphic horizon is known for GPIT 1796/1, the stratigraphic horizon is unknown for the other two specimens, as is common with historical specimens. Thus, we cannot confirm that either species occurs at the same stratigraphic horizon or location as *I. fortimanus*. On the other hand,

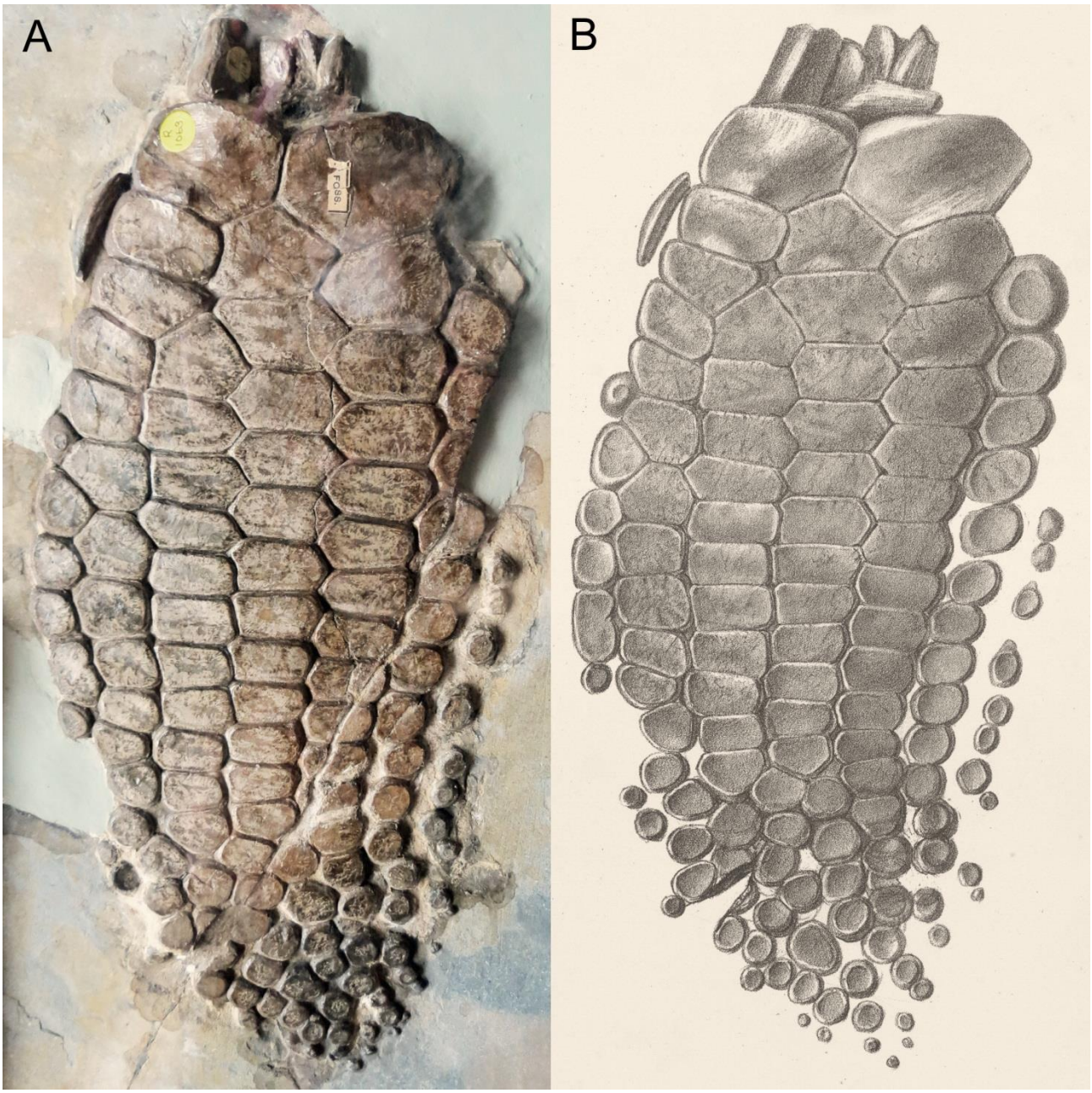

FIGURE 5: NHMUK R1063, isolated forefin of *Protoichthyosaurus fortimanus* (Owen, 1849-1884). A. Photograph of the specimen, on display and behind glass at the NHMUK. B. Illustration from Owen, 1849-1884, *Ichthyosaurus* plate 30, reversed from the original publication. The forefin displays only genus characters and cannot be distinguished from either *P. prostaxalis* or *P. applebyi*.

the size of NHMUK R1063 is more similar to *P. prostaxalis*, a seemingly larger species than *P. applebyi*. The isolated forefin, however, does not possess any diagnostic characters of either *P. prostaxalis* or *P. applebyi*. It is possible that *P. prostaxalis* or *P. applebyi* is a junior synonym of *P. fortimanus*, but it is impossible to determine with only a single forefin. Thus, pending the discovery of features of the forefin that can distinguish species of *Protoichthyosaurus*, *P. fortimanus* must be retained as a separate species of the genus.

DISTINGUISHING SPECIES OF *PROTOICHTHYOSAURUS* AND *ICHTHYOSAURUS* FROM SKULL MORPHOLOGY

For Lower Jurassic taxa that are not monotypic (e.g., *Stenopterygius*, *Temnodontosaurus*), postcranial

characteristics, especially forefin morphology, identify the genera more readily than skull characteristics. In *Stenopterygius*, for example, few skull characteristics define the genus, whereas differences in skulls are useful to identify species (McGowan and Motani, 2003; Maisch, 2008; Maxwell, 2012). Of the characters selected for distinguishing species in this study, *Stenopterygius quadriscissus* shares six skull characters with some species of *Ichthyosaurus*, although four or less with species of *Protoichthyosaurus* (Table 1; Maxwell, 2012, fig. 1). *Protoichthyosaurus* is similar in that the skull features of the genus are not as objectively assessed as those that distinguish individual species of *Protoichthyosaurus* from individual species of *Ichthyosaurus*. Thus a species assignment can often be made with confidence, whereas assignment to a genus is more equivocal without a species assignment.

TABLE 1: Measurements of NHMUK R1164, *Protoichthyosaurus applebyi*. * Anteriormost tip of the rostrum is missing so these measurements might be slight underestimates.

Dimension	Measurement in cm
Skull length	39.7*
Preorbital length	26.7*
Prenarial length	22.9*
Premaxillary length	19.5*
Jaw length	44.0*
Maxilla length	10.7
Orbit length	8.5
Orbit height	7.3
Sclerotic ring length	6.3
Sclerotic ring height	6.1
Naris length	3.6
Naris maximum height	1.5

The species of *Protoichthyosaurus* can be distinguished from each other and from species of *Ichthyosaurus* by a combination of characters, but the portion of the skull around the external naris and orbit must be well preserved in lateral view so that several bone shapes and contacts can be evaluated (Table 2). For example, in *P. applebyi*, the postorbital is a dorsoventrally long element that makes up nearly all of the posterior margin of the orbit, similar to *I. conybeari*, *I. somersetensis*, *I. anningae*, and *I. larkini* (Lomax and Massare, 2015, 2017; Massare and Lomax, 2016). This is also similar to *Stenopterygius quadriscissus*, where the long, narrow postorbital makes up the entire posterior margin of the orbit (Maxwell, 2012, fig. 3). In *P. prostaxalis*, on the other hand, the postorbital makes up no more than half of the posterior orbit margin, similar to *I. communis* and *I. breviceps* (Massare and Lomax, 2017), although the postorbital is roughly rectangular in *P. prostaxalis* rather than crescentic as it is in the other two. By examining additional characters, process of elimination will lead to a species identification. In this way, both species of *Protoichthyosaurus* can be distinguished from each other and all species of *Ichthyosaurus* (Table 2). Of course, identification becomes complicated if critical portions of the skull are missing or not well-preserved (see below). Furthermore, the extent of intraspecific variation has yet to be determined for individual skull bones.

Table 2 compares useful characters for distinguishing species for skulls preserved in lateral view. For these traits, *Protoichthyosaurus prostaxalis* is most similar to *Ichthyosaurus breviceps* sharing seven of nine characters. *Protoichthyosaurus prostaxalis* can easily be distinguished from *I. breviceps* by a much longer rostrum. In addition, the anterior process of the prefrontal is dorsoventrally long and separates the dorsal process of the lacrimal from the anterior margin of the orbit, and an asymmetric maxilla with a long anterior process that extends well beyond the external naris.

Based on the same characters (Table 2), the skull of *Protoichthyosaurus applebyi* is most similar to that of *I. larkini*, and *I. somersetensis*, sharing six and seven of nine characters, respectively. *P. applebyi* has a lower crowned skull compared to *I. larkini*, although both species have fairly long rostra. The teeth of *P. applebyi* have prominent longitudinal grooves on the roots that extend to the base of the crown, This is not the case for *I. larkini*. The species can also be distinguished in lateral view by the symmetry of the dorsoventrally low maxilla: in *P. applebyi*, the anterior process is much longer than the posterior process whereas in *I. larkini*, the two processes are about equal in length. *P. applebyi* has a dorsoventrally high external naris, whereas *I. larkini* has a dorsoventrally low external naris that is very elongated anteroposteriorly. Of course, naris shape is greatly influenced by orientation and taphonomic flattening of the skull. *P. applebyi* can be distinguished from *I. somersetensis* by a much longer rostrum and, as with *I. larkini*, by the shape of the maxilla. The maxilla of *P. applebyi* is dorsoventrally low, with a much longer anterior process compared to the posterior process; whereas the maxilla of *I. somersetensis* is dorsoventrally high, with a much longer and more slender posterior process compared to the anterior process.

Preservation can also affect how skull characters are evaluated. As the extent of crushing and orientation varies from specimen to specimen, it is inevitable, that skull features will also vary among specimens of the

TABLE 2: Skull characters that can, in combination, distinguish species of *Ichthyosaurus* from species of *Protoichthyosaurus*. Abbreviations: comm, *I. communis*; brev, *I. breviceps*; cony, *I. conybeari*, anni, *I. anningae*, lark, *I. larkini*, some, *I. somersetensis*, pros, *P. prostaxalis*, appl, *P. applebyi*; quad, *Stenopterygius quadrissicus*.

Skull character	comm	brev	cony	anni	lark	some	pros	appl	quad
Postorbital makes up more than half of posterior margin of orbit	no	no	yes	yes	yes	yes	no	yes	yes
Postorbital dorsoventrally long and much narrower anteroposteriorly	no	no	yes	yes	yes	yes	no	yes	yes
Prefrontal excludes all or most of lacrimal dorsal process from anterior orbit margin	no	no	no	no	yes	yes	yes	yes	no
Lacrimal dorsal process longer than anterior process	yes	yes	yes	?	no	no	yes	no	no
Maxilla taller than distance between dorsal edge of maxilla and external naris	rarely	rarely	no	yes	no	yes	yes	no	yes
Maxilla is approximately symmetric - processes are about the same height and length from tallest point of maxilla.	yes	no	no	yes	yes	no	no	no	no
Prominent grooves in tooth root	no	yes	no	no	no	yes	yes	yes	no
Grooves in tooth root extend to base of crown and merge with striations in enamel	no	no	no	no	no	no	yes	yes	no
Angular exposure much less than half of surangular exposure at posterior end of mandible	yes	yes	yes	yes	yes	yes	yes	yes	no

same species. For example, Lomax and Sachs (2017) reported a very large specimen of *Ichthyosaurus somersetensis* in which the lacrimal dorsal process was larger and more robust than in the holotype, and the characteristic shelf at the base of the lacrimal dorsal process was somewhat obscured due to crushing, especially if viewed directly in lateral view. However, the triradiate shape of the lacrimal, its dorsal extent, its exclusion from the orbital margin, and the extent of its anterior process were all consistent with *I. somersetensis*. A slight difference in view/orientation can easily distort an element so that it looks different than what is expected for the species. Individual variation can also result in slightly different morphologies of individual bones. Thus, for these reasons, a single character should not be used to refer a specimen to a specific species, and nor should a slight difference in a single feature be considered representative of something new.

CONCLUSIONS

Without the presence of a forefin, *Protoichthyosaurus* and *Ichthyosaurus* can be distinguished on the basis of skull characters, but only in combination. Thus, in poorly preserved or incomplete skulls, generic identification can be especially difficult and often species identifications can be more readily discerned. The recognition of four new specimens of *Protoichthyosaurus* expands information on the genus. One specimen, GPIT 1976/1, extends the geographic range of *Protoichthyosaurus prostaxalis* to the Lyme Regis area, and more importantly, confirms that the genus/species persisted to the lower Sinemurian (Bucklandi Ammonite Zone). It also confirms that the pineal foramen is between the frontals and parietals, as suggested by Lomax et al. (2017). Another specimen, NHMUK R1164, is only the second known specimen of *P. applebyi*, and extends its geographic range to the Lyme Regis area, Dorset. Furthermore, it provides new information on the post-orbital region of the skull and posterior portion of the mandible that adds to the original species diagnosis. It also confirms Motani's (2005) suggestion that NHMUK R1164 represented something different from *Ichthyosaurus*. The specimens described herein bring the number of specimens assigned to *Protoichthyosaurus* to 27, including the missing paratype. Seventeen specimens

can be assigned to *P. prostaxalis*, and two can be assigned to *P. applebyi*.

This work further illustrates the importance of historic collections in the search for additional, unrecognized specimens of *Protoichthyosaurus*. Because *Protoichthyosaurus* was not recognized until 1979 (Appleby, 1979), isolated skulls of *Ichthyosaurus* and *Protoichthyosaurus* were confused with each other in the early literature and collections from the 19th century. In fact, Lydekker (1891, p. 49; 1889, p. 46) identified two specimens discussed here (NMING F8756, NHMUK R1164) as *I. communis*. It would not be surprising to find more '*I. communis*' specimens in historic collections that are actually *Protoichthyosaurus*.

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