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First evidence of vampyromorph cephalopod jaw structures from the Sinemurian, Lower Jurassic of Dorset

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A new specimen of the Coleoidea from the Charmouth Mudstone Formation of the Dorset Coast has been identified as *Loligosepia bucklandi* (Voltz, 1840). The specimen includes the gladius and jaw fragments, which represent one of few records of its kind, but the head area, arms, hooks and suckers are not discernible. It can be favourably compared to other *L. bucklandi* fossils in the Natural History Museum in London and the J.F. Jackson Collection in the National Museum Wales in Cardiff. The range of *L. bucklandi* is determined to be from the Turneri Zone, Brooki Subzone to the Obtusum Zone, Stellare Subzone of the lower Sinemurian, with the new specimen stratigraphically a little older than the precisely located specimens in the J.F. Jackson Collection.

Key words: Jurassic, Sinemurian, Dorset, Coleoidea, *Loligosepia*

INTRODUCTION

Loligosepiina Jeletzky, 1965, a group of fossil coleoid cephalopods, play a central role in the evolution of the Coleoida (e.g., Fuchs and Weis, 2008; Fuchs et al., 2013; Marroquín et al., 2018; Fuchs, 2020). The original specimen of *Loligosepia bucklandi* was collected by Mary Anning from the Lias of Lyme Regis (Dorset, UK). It was recorded as "fossil *Loligo*" by William Buckland (1836: p. 306). This specimen which, by this time, was in the Oxford University Museum (OUM J3530), was named by Voltz (1840) only on the basis of Buckland's illustration (1836: pl. 30). This specimen (Fig. 1), is therefore, the holotype (see Donovan and von Boletzky, 2014). Since that time further specimens have been recorded (e.g., Fraas,1889) and some are in the collections of the Natural History Museum in London and the National Museum Wales in Cardiff. An early description of ''*Loliginites zitteli*'' provided by Fraas (1889), re-drawn by Naef (1922) and more recently figured and described by Fuchs et al. (2013) shows arm stumps, a lower mandible; eye, cephalic cartilage; funnel and mantle. In recent years there have been further descriptions of *Loligosepia* by Fuchs and Weis (2008), Donovan and von Boletzky (2014) and Rowe et al., (2023) examining both soft tissue preservation and the place of *Loligosepia* in coleoid phylogeny.

Nevertheless, apart from representatives of the Belemnoidea, fossil remains of the Coleoidea are rare (e.g., Rowe et al., 2023) and well-preserved coleoid beaks are exceedingly rare (Dzik, 1986; Klug et al., 2005). Klug et al. (2005) do show upper and lower "beaks" of coleoids, from the Kimmeridgian and Klug and Fuchs (2009) also note beaks for a specimen from the Hettangian of Somerset Coast, but it is not shown in detail (or convincing). Rarity may, in part, be related to the chitin of the beak requiring a moderately early mineralization and a low rate of decay to become fossilized (Allison, 1988).

GEOLOGICAL SETTING

Exposed along the Dorset coast (Fig. 2) between Lyme Regis and Seatown (Dorset, UK) are marine sediments of the Charmouth Mudstone Formation of Sinemurian and Pliensbachian age that have been investigated extensively in terms of their biostratigraphy (e.g., Lang and Spath, 1926; Cope et al., 1980; Simms, 2004), lithostratigraphy and sedimentology (e.g., Sellwood, 1972; Hesselbo and Jenkyns, 1995; Cox et al., 1999) and fossil content (e.g., Bennett et al., 2012; Donovan and von Boletzky, 2014; Hart et al., 2020). The sediments of the Charmouth Mudstone Formation are divided into five members (Fig. 3). The lowermost Shales-with-Beef Member (from which the specimen was derived, see below) consists of finely laminated and organic-rich dark grey mudstone beds with a few bands of limestone nodules (e.g., the Birchi Nodules) and thin beds of fibrous calcite, or "beef", which give the member its

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Fig. 1. *Loligosepia bucklandi* (Voltz), the holotype, OUM J3530, gladius, anterior to left

Scale bar 5 cm; Oxford University Museum digital image, PAL-J3530

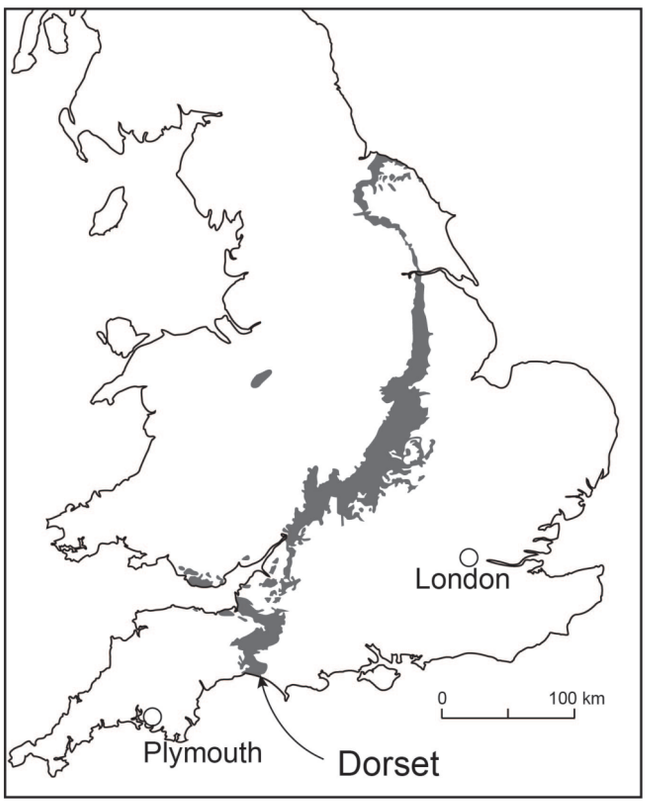

Fig. 2. Outcrop map for the Lias Group in England and Wales and showing the location of Dorset, UK (after Cox et al., 1999)

name (Hesselbo and Jenkyns, 1995; Simms, 2004; Cope, 2016). The Shales-with-Beef Member was deposited in a fully marine environment and represents part of the fill of a half-graben system that constitutes a segment of the Wessex Basin (Chadwick, 1986; Hesselbo and Jenkyns, 1995).

With respect to the holotype (Buckland, 1836: p. 304) there was, however, no locality or other geological information attached to it other than it was from Lyme Regis. Many of the other specimens listed by Donovan and von Boletzky (2014: appendix 1) also lack stratigraphical information, although they appear to come from the Shales-with-Beef and Black Ven Marls members of the Charmouth Mudstone Formation (Figs. 2 and 3). The most precisely located specimens are those in the J.F. Jackson Collection (National Museum Wales) which are recorded as coming from the Flatstones and the Stellare Nodules of the Sinemurian Black Ven Marls of Lyme Regis. The bed numbers used by Lang and Spath (1926: p. 160) were reported by Donovan and von Boletzky (2014) based on Cope (2012: p. 56). Specimen NMW G250 is recorded as being associated with the Lower Flatstones (bed 83d) while specimen NMW G3528a is from the Upper Flatstones (bed 83h). The new specimen, representing part and counterpart (Figs. 4 and 5), is within a loose nodule that was found in Chippel Bay (Lyme Regis) ~200 m east of Seven Rock Point: see Cope (2016: fig. 9) for a locality map. This would place it from within the Shales-with-Beef Member (which underly Black Ven Marls) of the of the Charmouth Mudstone Formation (Turneri Zone, *Microderoceras birchi* Subzone, lower Sinemurian) near to the Birchi Tabular or Birchi Nodules (Lang and Spath, 1926: beds 76–83; Palmer, 1984).

Chippel Bay lies within the Pinhay Bay to Fault Corner Geological Conservation Review Site (GCR) that was described by Simms (2004: pp. 60–82). This account illustrates the succession in three important logs of the Liassic sequence (Simms, 2004: figs. 2.6a, b, 2.8 and 2.11), three of which were also reproduced by Cope (2016: figs. 13, 16 and 18). The specimen NMW G3658, which is a near-complete gladius (though missing some shelly material) from the Stellare Nodules, is nearly identical to the specimen in our Figure 5. The gladius is a chitinous structure in the dorsal mantle of living Vampyromorpha (Octobrachia) that provides support during the contractions involved in swimming by "jet propulsion" (Fuchs and Iba, 2015). Jurassic species appear to have had a gladius preserved in apatite (Fuchs and Weis, 2008), although this has not been confirmed in the new specimen. The form of the gladius has been described in detail by both Fuchs and Weis (2008) and Donovan and von Boletzky (2014: fig. 4). Two other specimens in the Jackson Collection (NMW G3528 and NMW G250) are more fragmentary with only a partial gladius (again with shell material missing). If all the specimens in the Jackson Collection and the NHM (see Donovan and von Boletzky, 2014) are conspecific with the new specimen, then the range of *L. bucklandi* is from the Turneri to the Obtusum zones, Brooki to the Stellare subzones of the lower Sinemurian. This would date the new specimen as a little older than the specimens in the Jackson Collection of the National Museum Wales.

Institutional abbreviations. – NMW – National Museum Wales, Cardiff; NHM – Natural History Museum, London

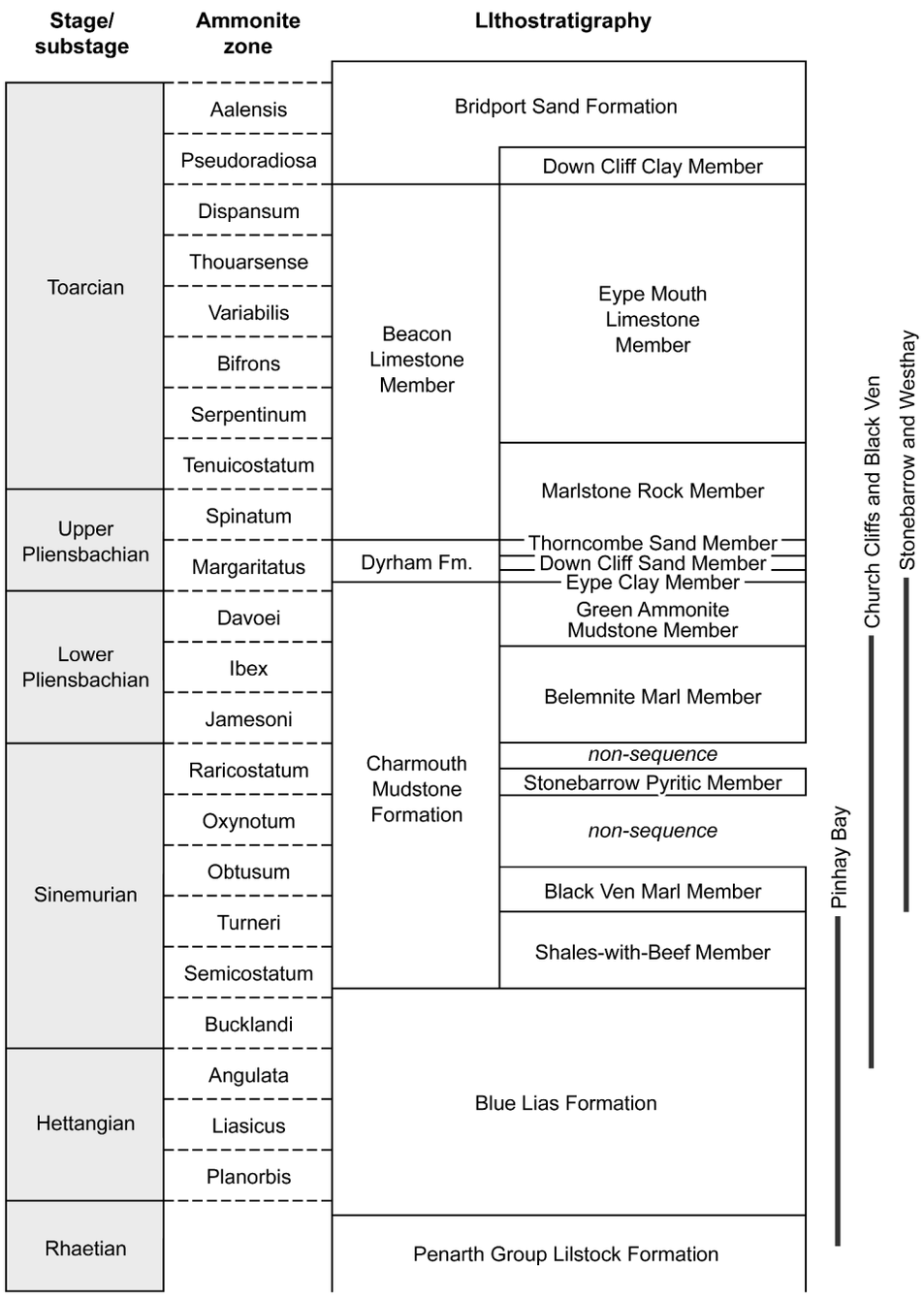

Fig. 3. Stratigraphical succession of the Jurassic strata exposed on the Dorset Coast, West Dorset (modified from Simms, 2004)

SYSTEMATIC PALAEONTOLOGY

Class Cephalopoda Cuvier, 1797
Superorder Octobrachia Haeckel, 1866
Order Vampyromorpha Robson, 1929
Genus *Loligosepia* Quenstedt, 1839

T y p e s p e c i e s. – *Loligo aalensis* Schübler in v. Zieten (1832: p. 24) by subsequent designation by van Regteren Altena (1949, p. 57); ICZN Opinion 1914, 1999. Type species from the Lower Toarcian of southern Germany.

Loligosepia bucklandi (Voltz, 1840)

M a t e r i a l. – The new specimen (Figs. 4A and 5) shows the gladius, some jaw fragments and an area surrounding the jaw fragments that may have been part of the head and the arms. No details of the latter are apparent. Owing to the similarities in the gladius shape and the parameters listed by Fuchs

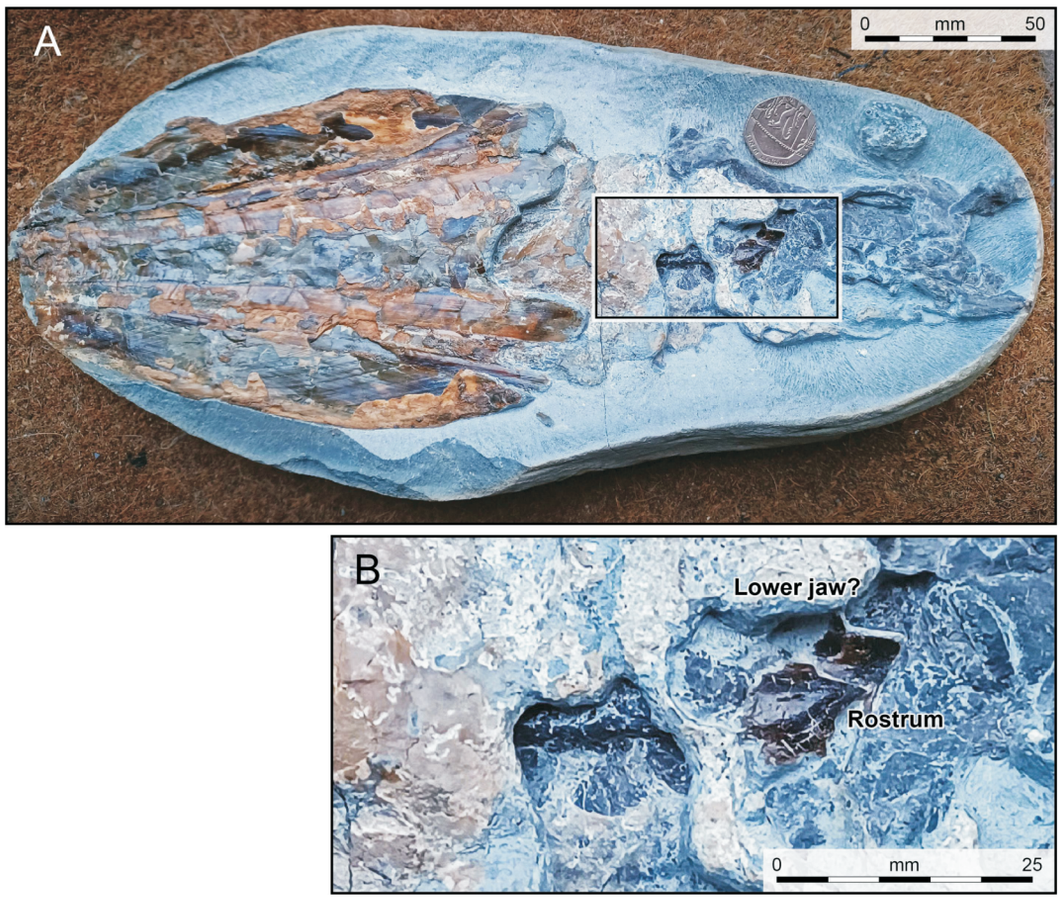

Fig. 4. Vampyromorph cephalopod *Loligosepia bucklandi* (Volz, 1840) from a loose nodule that may have come from the Turneri Zone (Microderoceras birchi Subzone), Shales-with-Beef, Charmouth Mudstone Formation (Sinemurian) of Monmouth Beach, Lyme Regis

The gladius (**A**) and jaw fragments (black in colour) and an area (**B**) which may represent the disturbed remains of the head and arms; the jaw fragments include the "rostrum" of the upper jaw together with part of the lower jaw; within the gladius, the median field and the paired lateral fields are visible

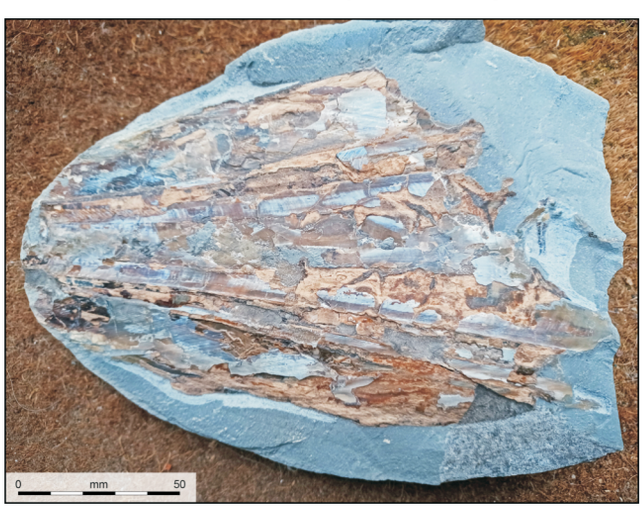

Fig. 5. Vampyromorph cephalopod *Loligosepia bucklandi* (Volz, 1840) from a loose nodule that may have come from the Shales-with-Beef, Charmouth Mudstone Formation (Sinemurian) of Monmouth Beach, Lyme Regis

The gladius of the specimen shown in Figure 4A; the median field is visible as well as the paired lateral fields (with growth lines at a distinct angle to the edge of the median field)

(2020) the gladius is considered to belong to a vampyromorph coleoid, *Loligosepia*.

Current status and depository. – The specimen described in this paper is currently being cleaned into a final condition, with further investigations planned. Discussions are on-going about its final location in a suitable collection within the area of the Dorset Coast. The status of some of the fossils from this area *vis-à-vis* the proposed on-line 'Jurassic Coast Collection' of the Dorset and East Devon World Heritage Site is also being considered.

Description. – Similar to the earlier records mentioned above, this specimen includes and an almost unfragmented and three dimensionally preserved gladius (length = 16 cm), head and arm crowns (Fig. 4). The jaw fragments include the "rostrum" of the upper jaw together with part of the lower jaw. Figure 5 shows the median field in a central position between the paired lateral fields (*sensu* Jeletzky, 1966). The slightly sinusoidal character of the growth lines in the hyperbolar zone is quite distinct. In comparison, the general appearance of this specimen closely resembles that illustrated by Fuchs and Weis (2008, fig. 3) and the specimens figured by both Fuchs and Weis (2008, fig. 4A) and Donovan and von Boletzky (2014: fig. 1A, C and fig. 2A): see also Fuchs (2016).

Remarks. – The jaw fragments (Fig. 4A, B) are up 17 mm in length. They show the 'rostrum' (sharp tip) of the upper

jaw and a part of the lower jaw, following Tanabe et al. (2017). The position of the jaw fragments and preservation has not permitted the rostral, hood, crest and wing length, as well as the width of outer lamella to be determined (cf. Clarke, 1962, 1986; Clarke and Maddock, 1988; Tanabe et al., 2017). Indeed, as this rostrum is in a cementstone nodule it cannot be extracted further without damage. Hence further comparisons with Tanabe et al. (2017) for example are not possible. Nevertheless, this specimen represents one of the few records of the jaw in *Loligosepia* (family Loligosepiidae). There are some undetermined 'black features' posterior of the jaw fragments and the area anterior of the jaw fragments should contain evidence of the arms, though this is unclear in both normal and UV light.

A specimen in the University Museum in Florence, recorded as *Geoteuthis bollensis* Münster 1843 would probably be placed in *Loligosepia* following Fuchs and Weis (2008). This specimen may be the first record of the jaw in *Loligosepia* (family Loligosepiidae) from Jurassic strata, although there are other occurrences described by Tanabe (2012) and Keupp and Mitta (2013). Triassic 'beaks' have been described by Doguzhaeva et al. (2022). A full discussion of cephalopod 'beaks' is provided by Clarke (1962, 1986); Clarke and Maddock (1988); and Klug et al. (2010, 2020). There are some undetermined 'black features' posterior of the jaw fragments and the area anterior of the jaw fragments should contain evidence of the arms, though this is unclear in both normal and UV light. It must be noted that none of the *L. bucklandi* specimens in the NMW and NHM collections preserve evidence of the head area, arms, hooks or suckers. In all these specimens, the gladius is less well-preserved than the new specimen.

It may only be a 'coincidence' but Clarke (2003: fig. 15) described a statolith (Jurassic sp. B) from this part of the Dorset coast succession. Clarke's material was provided by amateur fossil collectors Mr and Mrs Hiscock, who were based in Somerset. They collected and prepared the samples which were used to demonstrate that Jurassic sp. B (see Hart et al., 2015: fig. 2C, D) is widespread across Dorset and Somerset, including their location XII (see Hart et al., 2015: fig. 1) near Lyme Regis. This statolith probably came from near, or within, Bed 88f in the upper part of the Asteroceras stellare Subzone. This is the same stratigraphical level as specimen NMW G3658 in the Jackson Collection of the National Museum Wales. It is possible, therefore, that statolith Jurassic sp. B may come from *L. bucklandi* although other coleoids (belemnites and phragmoteuthids) are known from the same bed, and such an interpretation is therefore speculative. The statolith Jurassic sp. B coming from *L. bucklandi* cannot be confirmed without a macrofossil specimen that has the statolith *in-situ*. Other examples of Jurassic sp. B have been recorded in the adjacent strata.

Stratigraphic and geographic range. – This specimen and those in the collections of the National Museum Wales and the Natural History Museum indicate a stratigraphical range from the Microderoceras birchi Subzone to the Asteroceras stellare Subzone of the Lower Sinemurian and a distribution that is currently that of the Lyme Regis area of West Dorset.

CONCLUSIONS

A new specimen of *Loligosepia bucklandi* (Volz, 1840) from Chippel Bay, west of The Cobb in Lyme Regis, UK, has been cleaned and prepared. It reveals many of the diagnostic features of both the genus and species, especially in the shape and structure of the gladius. The jaw fragments include a clear view of the rostrum, although the details of the head, arms and any suckers are missing. Apart from representatives of the Belemnoidea, fossil remains of the Coleoidea are rare and such well-preserved coleoid jaw fragments are exceedingly rare (Dzik, 1986; Klug et al., 2005). If all the specimens in the Jackson Collection and the NHM are conspecific with the new specimen described here, then the range of *L. bucklandi* is likely to be from the Turneri to the Obtusum zones, Brooki to the Stellare subzones of the Lower Sinemurian. This would place the new specimen stratigraphically a little older than the precisely located specimens in the Jackson Collection of the National Museum Wales.

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REFERENCES

Allison, P.A., 1988. Konservat–Lagersätten: cause and classification. Paleobiology, **14**: 331–344. https://doi.org/10.1017/S0094837300012082

Bennett, S.P., Barrett, P.M., Collinson, M.E., Moore-Fay, S., Davis, P.G., Palmer, C.P., 2012. A new specimen of *Ichthyosaurus communis* from Dorset, UK, and its bearing on the stratigraphical range of the species. Proceedings of the Geologists' Association, **123**: 46–154. https://doi.org/10.1016/j.pgeola.2011.07.001

Buckland, W., 1836. Geology and Mineralogy Considered with Reference to Natural Theology. vol 1: vi-xvi, William Pickering, London. https://doi.org/10.5962/bhl.title.125523

Chadwick, R., 1986. Extension tectonics in the Wessex Basin, southern England. Journal of the Geological Society, **143**: 465–488. https://doi.org/10.1144/gsjgs.143.3.0465

Clarke, M.R., 1962. The identification of cephalopod "beaks" and the relationship between beak size and total body weight. Bulletin of the British Museum (Natural History), Zoology, **8**: 419–480.

Clarke, M.R., 1986. A Handbook for the Identification of Cepahlopod Beaks. Oxford University Press, Oxford, UK.

Clarke, M.R., 2003. Potential of statoliths for interpreting coleoid evolution: a brief review. Berliner Paläobiologische Abhandlungen, **3**: 37–47.

Clarke, M.R., Maddock, L., 1988. Beaks of living coleoid Cephalopoda. In: The Mollusca, Volume 12, Palaeontology and Neontology of Cephalopods (eds. M.R. Clarke and E.R. Trueman): 121–131. Academic Press, San Diego.

Cope, J.C.W., 2012. Geology of the Dorset Coast (1st Edition). Geologists' Association Guide no. 22, London.

Cope, J.C.W., 2016. Geology of the Dorset Coast (2nd Edition). Geologists' Association Guide no. 22, London.

Cope, J.C.W., Getty, T.A., Howarth, M.K., Morton, N., Torrens, H.S., 1980. A Correlation of Jurassic Rocks in the British Isles. Part One: introduction and Lower Jurassic. Special Report of the Geological Society of London, **14**: 1–73.

Cox, B.M., Sumbler, M.G., Ivimey-Cook, H.C., 1999. A formational framework for the Lower Jurassic of England and Wales (onshore area). British Geological Survey, Research Report, RR/99/01.

Doguzhaeva, L.A., Summesberger, H., Brandstaetter, F., Gruber, D., Tintori, A., 2022. Triassic coleoid beaks and other structures from the Calcareous Alps. Acta Palaeontologica Polonica, **67**: 655–666. https://doi.org/10.4202/app.00953.2021

Donovan, D.T., 1977. Evolution of the dibrachiate Cephalopoda. Symposia of the Zoological Society of London, **38**: 15–48.

Donovan, D.T., von Boletzky, S., 2014. Loligosepia (Cephalopoda: Coleoidea) from the Lower Jurassic of the Dorset coast, England. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **273**: 45–63. https://doi.org/10.1127/0077-7749/2014/0415

Dzik, J., 1986. Uncalcified cephalopod jaws from the Middle Jurassic of Poland. Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 1986: 405–417.

Fraas, E., 1889. *Loliginites (Geoteuthis) zitteli* Eb. Fraas – Einvollstandig erhaltener Dibranchiate aus den Laibsteinen des Liasepsilon. Jahreshefte des Vereins für vaterländische Naturkundein Württemberg **45**: 217–232.

Fuchs, D., 2016. Part M, Coleoidea, Chapter 9B: the gladius and gladius vestige in fossil Coleoidea. Treatise Online, **83**: 1–23. https://doi.org/10.17161/to.v0i0.6488

Fuchs, D., 2020. Part M, Coleoidea, Chapter 23G: systematic descriptions: Octobrachia. Treatise Online, **138**: 1–52. https://doi.org/10.17161/to.vi.14661

Fuchs, D., Weis, R., 2008. Taxonomy, morphology and phylogeny of Lower Jurassic loligosepiid coleoids (Cephalopoda). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **249**: 93–112. https://doi.org/10.1127/0077-7749/2008/0249-0093

Fuchs, D., Iba, Y., 2015. The gladiuses in coleoid cephalopods: homology, parallelism, or convergence? Swiss Journal of Palaeontology, **134**: 187–197. https://doi.org/10.1007/s13358-015-0100-3

Fuchs, D., Keupp, H., Schweigert, G., 2013. First record of a complete arm crown of the Early Jurassic coleoid Loligosepia (Cephalopoda). Paläontologische Zeitschrift, **87**: 431–435. https://doi.org/10.1007/s12542-013-0182-4

Hart, M.B., Clarke, M.R., De Jonghe, A., Price, G.D., Page, K.N., Smart, C.W., 2015. Statoliths from the Jurassic succession of south-west England, United Kingdom. Swiss Journal of Palaeontology, **134**: 199–205. https://doi.org/10.1007/s13358-015-0080-3

Hart, M.B., Arratia, G., Moore, C., Ciotti, B., 2020. Life and death in the Jurassic seas of Dorset, Southern England. Proceedings of the Geologists' Association, **131**: 629–638. https://doi.org/10.1016/j.pgeola.2020.03.009

Hesselbo, S.P., Jenkyns, H.C., 1995. A comparison of the Hettangian to Bajocian successions of Dorset and Yorkshire. In: Field geology of the British Jurassic (ed. P.D. Taylor): 105–150. Geological Society, London.

Jeletzky, J.A., 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea. University of Kansas Paleontological Contributions, Mollusca, **7**: 1–162.

Keupp, H., Mitta, V., 2013. Cephalopod jaws from the Middle Jurassic of central Russia. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **270**: 23-54. https://doi.org/10.1127/0077-7749/2013/0356

Klug, C., Fuchs, D. 2009. An earliest Hettangian (Jurassic belemnitid from Great Britain with a preserved proostracum. In: Cephalopods Present and Past (eds. K. Tanabe, Y. Shigeta, T. Sasaki and H. Hirano): 181–185. Tokai University Press, Tokyo.

Klug, C., Schweigert, G., Dietl, G., Fuchs, D., 2005. Coleoid beaks from the Nusplingen Lithostratigraphic Limestone (Upper Kimmeridgian, SW Germany). Lethaia, **38**: 173–192. https://doi.org/10.1080/00241160510013303

Klug, C., Schweigert, G., Fuchs, D., Dietl, G., 2010. First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany). Lethaia, **43**: 445–456. https://doi.org/10.1111/j.1502-3931.2009.00203.x

Klug, C., Etter, W., Hoffmann, R., Fuchs, D., De Baets, K., 2020. Jaws of a large belemnite and an ammonite from the Aalenian (Middle Jurassic) of Switzerland. Swiss Journal of Palaeontology, **139**: 7. https://doi.org/10.1186/s13358-020-00207-7

Lang, W.D., Spath, L.F., 1926. The Black Marl of Black Ven and Stonebarrow, in the Lias of the Dorset coast. Quarterly Journal of the Geological Society, **82**: 144–187. https://doi.org/10.1016/S0016-7878(32)80024-6

Marroquín, S.M., Martindale, R.C., Fuchs, D., 2018. New records of the Late Pliensbachian to Early Toarcian (Early Jurassic) gladius-bearing coleoid cephalopods from the Ya Ha Tinda Lagerstätte, Canada. Papers in Palaeontology, **4**: 245–276. https://doi.org/10.1002/spp2.1104

Naef, A., 1922. Die fossilen Tintenfische. Jena: Gustav Fischer-Verlag. https://doi.org/10.5962/bhl.title.2082

Palmer, C.P., 1984. A note on the Birchi Beds, Lower Jurassic, at Lyme Regis, Dorset. Geological Magazine, **121**: 645–647. https://doi.org/10.1017/S001675680003079X

Rowe, A.J., Kruta, I., Villier, L., Rouget I., 2023. A new vampyromorph species from the Middle Jurassic La Voulte-sur-Rhône Lagerstätte. Papers in Palaeontology, **9:** e1511. https://doi.org/10.1002/spp2.1511

Sellwood, B.W., 1972. Regional environmental change across a Lower Jurassic stage boundary. Palaeontology, **15**: 125–157.

Simms, M.J., 2004. The Wessex Basin (Dorset and central Somerset). In: British Lower Jurassic Stratigraphy (eds. M.J. Simms, N. Chidlaw, N. Morton and K.N. Page): 53–109. Geological Conservation Review Series, No. 30, Joint Nature Conservation Committee, Peterborough.

Tanabe, K., 2012. Comparative morphology of modern and fossil coleoid jaw apparatuses. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **266**: 9–18. https://doi.org/10.1016/j.cretres.2016.10.009

Tanabe, K., Misaki, A., Hikida, Y., Nishimura, T., 2017. New records of coleoid cephalopod jaws from the Upper Cretaceous of Hokkaido, Japan, and their paleobiogeographic and evolutionary implications. Cretaceous Research, **70**: 128–141. https://doi.org/10.1016/j.cretres.2016.10.009

Voltz, P.L., 1840. Observations sur les Belopeltis ou lames dorsales des bélemnites. Mémoires de la Société du Muséum d'Histoire naturelle de Strasbourg, **3**: 1–38.