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THE FIRST CENOZOIC OCTOPOD: A LOWER EOCENE RECORD FROM BOLCA, NORTHEASTERN ITALY

ALEKSANDR MIRONENKO[1*], LUCA GIUSBERTI[2], GIOVANNI SERAFINI[3], ROBERTO ZORZIN[4] & ALEXANDRE F. BANNIKOV[5]

[1]Geological Institute of the Russian Academy of Sciences, Pyzhevski Lane 7, Moscow 119017, Russia. E-mail: paleometro@gmail.com
[2]Department of Geosciences, Via G. Gradenigo 6, 35131 Padova, Italy. E-mail: luca.giusberti@unipd.it
[3]Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, 41125 Modena, Italy. E-mail: giovanni.serafini@unimore.it
[4]Museo Civico di Storia Naturale di Verona. Lungadige Porta Vittoria 9, 37129 Verona, Italy. E-mail: zorzin.geol@gmail.com
[5]Borissiak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia. E-mail: aban@paleo.ru
[*]Corresponding Author.

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Abstract. To date, soft-tissue remains of extinct incirrate octopods have been described exclusively from Upper Cretaceous deposits. Here, three specimens of an incirrate octopodid with well-preserved soft tissue imprints are described for the first time from Paleogene strata. This material originates from the upper Ypresian (lower Eocene) fish-bearing levels of the Bolca *Konservat-Lagerstätte* in the Pesciara of Bolca in north-eastern Italy. Previously, these specimens had tentatively been interpreted as teuthids. Based on a detailed study of their anatomical structure, a new genus and species of octopodid, *Bolcaoctopus pesciaraensis*, belonging to the extant family Octopodidae, are here erected. *Bolcaoctopus* gen. nov. may be distinguished from the Late Cretaceous genus *Styletoctopus* by the presence of long and thin arms and an elongated body shape with a narrowed apical end and covered by longitudinal wrinkles. Although finds of fossil octopuses in the Bolca *Konservat-Lagerstätte* remain extremely rare, it is worth noting that Cenozoic marine vertebrate localities constitute an important potential source of additional finds of coleoid cephalopods, the study of which may shed light on a poorly understood period in the evolutionary history of these molluscs.

Introduction

Octopods (Cephalopoda, Octopoda), represented in modern faunas by two suborders, Cirrata and Incirrata, are widely distributed in present-day seas, ranging from shallow coastal waters to ultra-abyssal depths. They play an important role in various marine ecosystems (e.g., Lima et al. 2020; Roura et al. 2023). However, their fossil record is extremely scanty. For over a century, the sole known extinct octopod was *Palaeoctopus newboldi*, described by Woodward (1896) from Santonian limestones in Lebanon. Two additional genera of fossil incirrate

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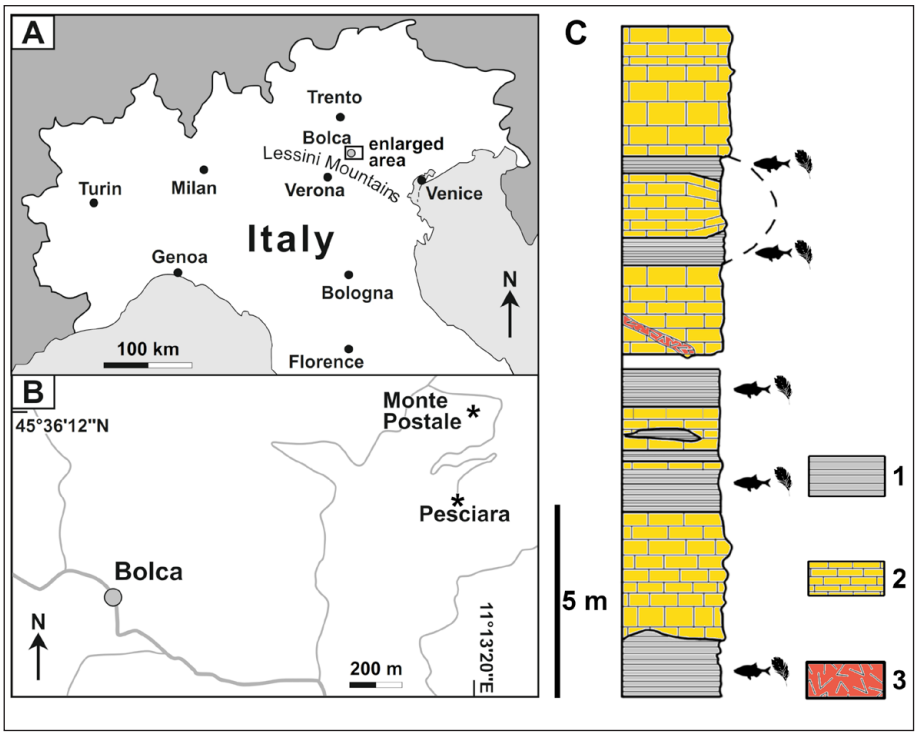

Fig. 1 - A, B) Map of the fossiliferous sites of Pesciara and Monte Postale in the vicinity of the township of Bolca (Verona, north-eastern Italy). C) Stratigraphical log of the Pesciara *Lagerstätte*. Legend: (1) fine-grained laminated limestones with fishes and plants; (2) coarse-grained biocalcarenite-biocalcirudite limestones with benthic fauna; (3) volcanic and basaltic rocks. Modified from Vescogni et al. (2016) and Calzoni et al. (2023).

octopuses, *Keuppia* and *Styletoctopus*, have recently been described from the Upper Cretaceous (Cenomanian) of Lebanon (Fuchs et al. 2009). All three genera of Upper Cretaceous incirrate octopuses named above are represented by well-preserved soft body imprints and constitute representatives of two octopod families, differing in the structure of the gladius vestige. *Palaeoctopus* and *Keuppia* belong to extinct Palaeoctopodidae, while *Styletoctopus* is assigned to the extant family Octopodidae (Fuchs et al. 2009; Fuchs 2020). This demonstrates that already in the Late Cretaceous octopuses were relatively diverse. However, until now, imprints of fossil octopod bodies were unknown from Cenozoic strata. Only peculiar fossilised shell-like egg cases of representatives of the family Argonautidae had been recorded from several Cenozoic rocks, starting from the lower Eocene (for a review, see Fuchs 2020).

The presence of octopuses in Cenozoic seas is also confirmed by the finds of specific drill holes in shells of various molluscs, crabs and barnacles (Klompmaker et al. 2013, 2014, 2019; Fuchs 2020). In modern marine ecosystems such drill holes are made by incirrate octopuses in hard shells of their prey items (Saunders et al. 1991). These boreholes, with a very characteristic oval-elongated shape and attributed to the ichnotaxon *Oichnus ovalis* Bromley, 1993, are known from Upper Cretaceous (Campanian) strata and upwards (Fuchs 2020; Klompmaker & Landman 2021; note that similar traces were recorded from the Ordovician by Fatka et al. 2022, but their connection with cephalopod-produced traces is highly doubtful). Unequivocal octopod drillings are still unknown from pre-Campanian deposits, but the discovery of *Styletoctopus* in Cenomanian beds, which has a completely modern structure of vestige gladius (stylets), suggests that the family Octopodidae had already arisen by the mid-Cretaceous, and without any doubt existed throughout the Cenozoic. However, actual finds of such octopuses had not been described to date.

In the present paper, three unique body imprints of incirrate octopuses from the Eocene *Lagerstätte* of Pesciara of Bolca in north-east Italy are described. The Pesciara, known since the mid-sixteenth century (Sorbini 1972; Romano & Carnevale 2023), is exceptionally rich in marine fishes, especially acanthomorphs, with a bewildering diversity (e.g., Bannikov 2014; Carnevale et al. 2014; Friedman & Carnevale 2018). Other vertebrates and invertebrates from Bolca (the so-called "minor fauna" *sensu* Sorbini 1972) are much less abundant, but three specimens of soft-bodied cephalopods were found in the upper Ypresian (lower Eocene) laminites at this locality (Broglio Loriga & Sala Manser-

vigi 1973; Giusberti et al. 2014). Initially, these were tentatively interpreted as teuthids (Metateuthoidea *sensu* Naef, 1921) on account of the narrow apically pointed body shape. However, a detailed study of their anatomical structure has now allowed us to re-interpret them as representatives of a new octopod genus and species in the family Octopodidae.

Geological setting

The specimens studied come from the Pesciara, the main fossiliferous outcrop in the vicinity of the township of Bolca, which is located in the Lessini Mountains about 30 km from the city of Verona (north-eastern Italy; Fig. 1A, B). Fish remains have long been collected from two approximately coeval sites at Bolca (i.e., Pesciara and Monte Postale; Fig. 1B), in close proximity to each other, but with different fish assemblages and representing different depositional contexts (Marramà et al. 2016). The calcareous limestone succession of the Pesciara site, a large olistolith embedded into volcanic deposits, has traditionally been referred to as 'Calcari Nummulitici', an informal unit of early-middle Eocene age that is widely distributed in north-eastern Italy (e.g., Papazzoni & Trevisani 2006). The Pesciara succession (Fig. 1C) consists of a cyclic alternation of about 20 metres of finely laminated micritic limestones (containing exquisitely preserved fishes, plants and invertebrates) and coarse-grained, *Alveolina*-dominated biocalcarenites/biocalcirudites. Based on their larger benthic foraminiferal and calcareous nannofossil content, the fish-bearing limestones of Pesciara have been referred to the uppermost part of SBZ 11, corresponding to the basal portion of NP 14 and CNE 6, dated between 48.96 and *c.* 48.5 Ma (latest Ypresian; Papazzoni et al. 2017). Results of quantitative palaeoecological analysis by Marramà et al. (2016) have suggested that the Pesciara fish assemblage was characterised by a sharp oligarchic structure dominated by planktivorous fishes (mostly clupeoids). Sedimentological and taphonomic features also suggest that the fossiliferous sedimentary rocks accumulated in a shallow intraplatform basin in which anoxic conditions and the development of a biofilm at the bottom were conducive to high-quality fossil preservation (see also Papazzoni & Trevisani 2006). Apart from the specimens described herein, the only coleoid currently known from the Pesciara is represented by a small apical portion of a phragmocone belonging to the sepiid *Spirulirostra georgii* (Mellini & Quaggiotto 1999).

Materials and methods

The present study is based on three individuals preserved on six slabs in the collections of the Museo Civico di Storia Naturale, Verona (MCSNV lB12/lB13; in part and counterpart), the Sezione di Geologia e Paleontologia del Museo della Natura e dell'Uomo dell'Università degli Studi di Padova (MGP-PD 31434, in single plate), and the Museo dei Fossili di Bolca (MFB IG23682, in single plate, counterpart to MGP-PD 31434; MFB IGVR71417/IGVR71418, in part and counterpart). These specimens have been studied using stereomicroscopes and photographs made under ultraviolet light. MGP-PD 31434 and the other specimens were exposed to a combination of different UV radiation wavelengths to highlight imprints of the mantle tissue from the surrounding matrix. UV-A (peak emission at 368 nm), UV-B (peak emission at 318 nm) and UV-C (peak emission at 254 nm) wavelengths were produced with a 95 W discharge lamp from WayTooCool LLC. Pictures were taken with a Canon EOS 700D and 1000D with a 50-mm lens.

Institutional abbreviations: MCSNV, Museo Civico di Storia Naturale, Verona; MFB, Museo dei Fossili di Bolca; MGP-PD, Sezione di Geologia e Paleontologia del Museo della Natura e dell'Uomo (Università degli Studi di Padova).

Systematic palaeontology

Subclass **COLEOIDEA** Bather, 1888
Superorder **Octobrachia** Fioroni, 1981
Order **Octopoda** Leach, 1818
Suborder **Incirrata** Grimpe, 1916
Family Octopodidae d'Orbigny, 1840

Genus *Bolcaoctopus* gen. nov.

Diagnosis: Gladius vestige developed as narrow stylets; arms long and thin; body shape elongated, with narrowed apical end, covered by longitudinal wrinkles.

Etymology: From the Bolca township, in the vicinity of which the type series was found.

Type species: *Bolcaoctopus pesciaraensis* sp. nov., by present designation.

Composition*:* Type species only.

Bolcaoctopus pesciaraensis sp. nov.

Figs. 2-5

1975 dibranchiate Cephalopod: Broglio Loriga & Sala Manservigi, p. 166, pl. VIII, figs. 1, 2 (originally published as offprint in 1973).
2014 teuthoid: Giusberti et al., p. 82, fig. 7d.

Holotype: MGP-PD 31434 and MFB IG23682, part and counterpart (Figs. 2, 4).

Diagnosis*:* As for genus.

Etymology*:* From the Pesciara site, the main *Lagerstätte* in the Bolca area.

Paratypes: MCSNV lB12/lB13, part and counterpart (Fig. 3) and MFB IGVR71417/ IGVR71418, part and counterpart (Fig. 5).

Type locality and horizon: laminites of Pesciara site (Bolca, Verona, northeastern Italy); uppermost SBZ 11 and basal NP 14 and CNE 6 zones, dated between 48.96 and *c.* 48.5 Ma (latest Ypresian; Papazzoni et al. 2017).

Description. The holotype comprises a near-complete body including mantle and arms, with exception of the rear part of the mantle (Fig. 2). The preserved part of the mantle has a length of 55 mm, but since the posterior end is missing, the original length of the animal was about 10 mm longer. The mantle becomes narrower towards the head, the posterior end also tapers upwards; the maximum width of the mantle is at the level of the lower end of the stylets (Fig. 2A). The mantle and especially its posterior end are covered by longitudinal wrinkles (Figs. 2A, B; 4A). Along these wrinkles throughout the mantle numerous pyrite grains are located in rows; they possibly represent mineralised traces of the original pigmentation of the mantle (Fig. 4A). In the upper part of the mantle, the anterior part and ventral bend of one of the stylets (right) are visible under UV light (Figs. 2D(s); 4B). The visible length of the stylet is 5 mm, but its posterior part is hidden by matrix, and the total length is presumably 8 mm. The fins are absent. The head and eyes are large; the mineralised pigmentation of the eyeballs is well preserved (Fig. 2B, D). The head length is about 20 mm, the width 17 mm, and eye length 12 mm. Slightly above and between the eyes, near the remnants of cephalic cartilage, the statoliths are visible (Figs. 2D; 4C). They are oval and massive, but a detailed study of their shape is complicated by the fact that they are recrystallised into calcite. The jaws seem to be small (2–3 mm long), but likely these are not completely preserved. Eight arms are clearly visible (see Fig. 2D); these are thin and long, part of them lying in loops. The arms are of the same length: approximately 50 mm in a straightened length; the structure of their surface is poorly distinguishable, and the suckers are not clearly visible (Fig. 2D). The ink sac is located in the middle part of the mantle, closer to the head (Fig. 4D). The length of the ink sac is 10 mm; in front of it there is a thin ink duct 12 mm long. In UV images, a spot of leaked ink is visible around the ink sac, increasing its apparent size by one and a half times.

The imprint of the mantle is poorly reactive under UV light but appears sufficiently distinct from the surrounding matrix (Fig. 2A, B). It is currently unclear if the reported contrast is just a feature of the sediment enhanced by UV exposition or if a fluorescence of what might be remnants of the soft tissues truly occurred. Contrary, the putative remnants of pigmentation are more reactive under short UVs (Fig. 4A–C), possibly on account of their unique mineralogical substitution.

Paratype MCSNV lB12/lB13 is comprised of a complete body including mantle and arms, but the specimen is about half the size of the holotype (Fig. 3). The mantle is oval, elongated, and pointed towards the rear. The length of the mantle is 35 mm; its maximum width is 13 mm. The head is 12 by 12 mm in length and width; the eyes 5 by 2.5 mm, respectively. The surface of the mantle, as in the holotype, appears to be covered with longitudinal wrinkles, possibly with mineralised remnants of pigment visible under UV light (Fig. 3A, B). The ink sac is 7 mm long, but due to the leaked ink in the mantle cavity, it looks almost twice as long. Seven arms are visible in front and on the sides of the head, they are partially intertwined with each other. The arms are 30–35 mm in length. The eighth arm is possibly located behind the head near the mantle (Fig. 3D). Poorly preserved paired structures, possibly stylets, are visible in the upper part of the mantle (Fig. 3D(s?)).

Paratype IGVR 71417/71418 is a relatively large, but not a completely preserved specimen (Fig. 5). The preserved part of its mantle is 40 mm long and 38 mm wide, but the apical end with stylets is missing. The preserved part of the ink sac is 13 mm in length; its adoral ink duct is 12 mm long. They are surrounded by a stain of leaked ink (Fig. 5A, B). Large eyes are clearly visible, measuring 11 mm in length and 8 mm in width. Of the arms, only six are visible, with a maximum length of about 70 mm, but their ends are not preserved (Fig. 5D). The remaining arms are either hidden in the matrix or were bitten off by a predator before burial. The jaws are

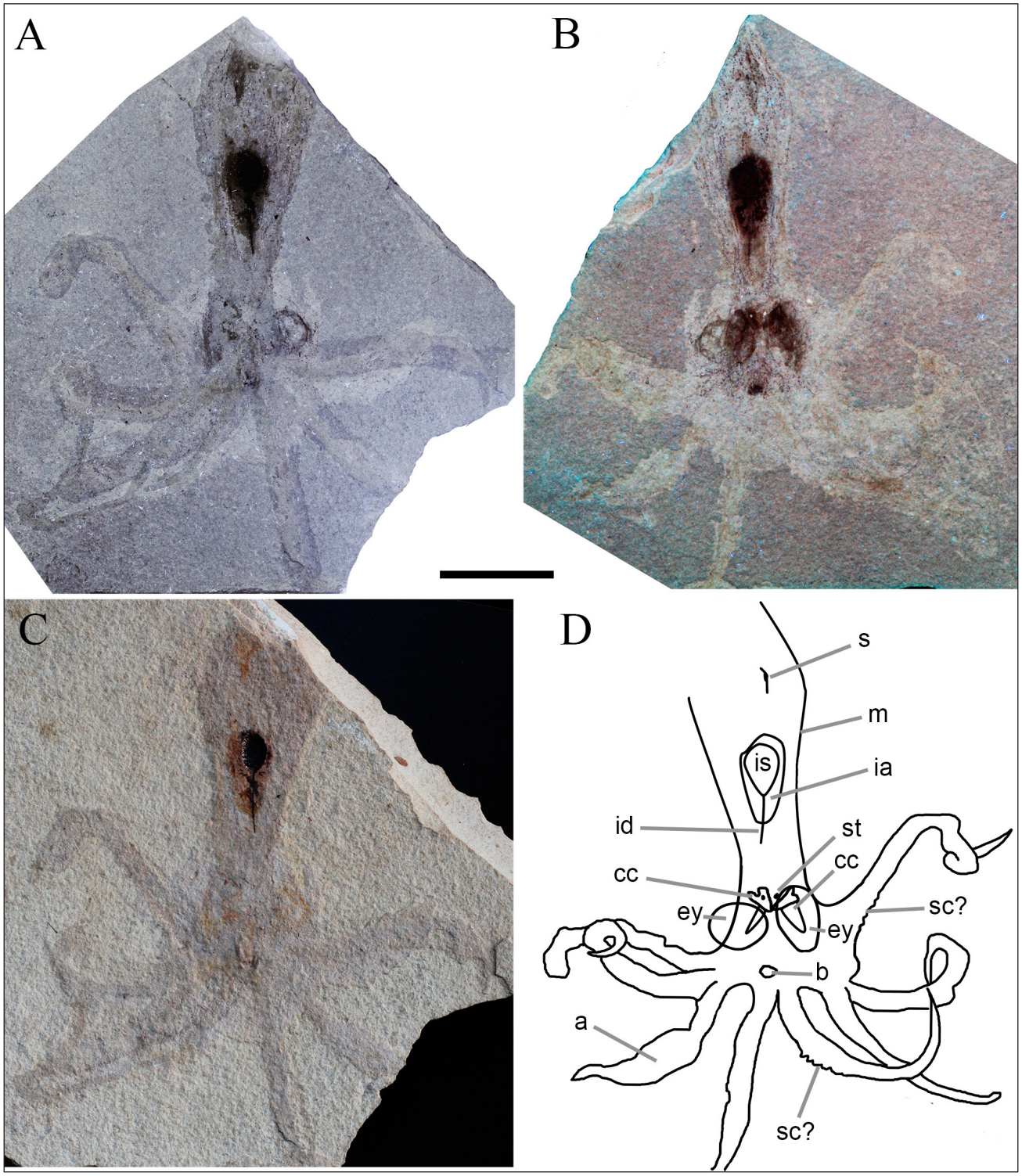

Fig. 2 - *Bolcaoctopus pesciaraensis* gen. nov., sp. nov. from the lower Eocene of Bolca, the holotype. A) Specimen MFB IG23682, under UV light. B) Counterpart specimen MGP-PD 31434, under UV light. C) Specimen MFB IG23682, under natural light. D) Schematic drawing mainly based on B (MGP-PD 31434). Letters of references: a - arms, b - beak, cc – cephalic and ocular cartilage, ey - eyes, ia - leaked ink around the ink sac, id - ink duct, is - ink sac, m - mantle, s - stylet, sc - remnants of sucker cups?, st – statoliths. Scale bar equals 20 mm.

preserved, but the structural details are not recognisable. The specimen is much more reactive under both long and short UV wavelengths than the holotype and the other paratype, possibly implying a better and structurally distinct preservation of the mantle tissues (Fig. 5A, B). Future compositional studies might shed light on the soft-tissue preservation of these unique specimens.

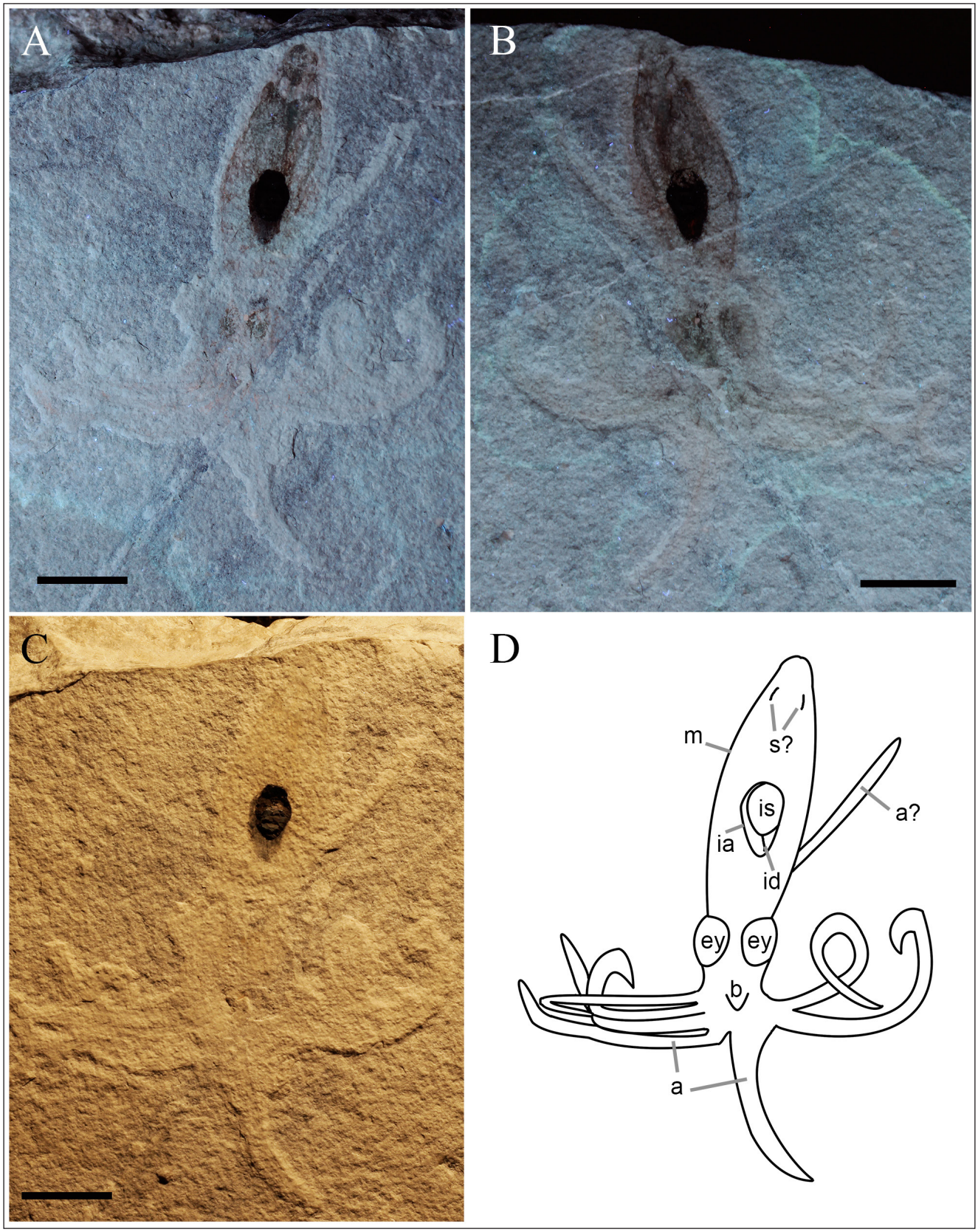

Fig. 3 - *Bolcaoctopus pesciaraensis* gen. nov., sp. nov. from the lower Eocene of Bolca, the paratype. A) MCSNV lB13 under UV light. B) Counterpart, MCSNV lB12 under UV light. C) MCSNV lB13 under natural light. D) Schematic drawing mainly based on (A) (MCSNV lB13). Letters of references: a - arms, b - beak, ey - eyes, ia - leaked ink around the ink sac, id - ink duct, is - ink sac, m – mantle, s? - possible stylets. Scale bars equal 10 mm.

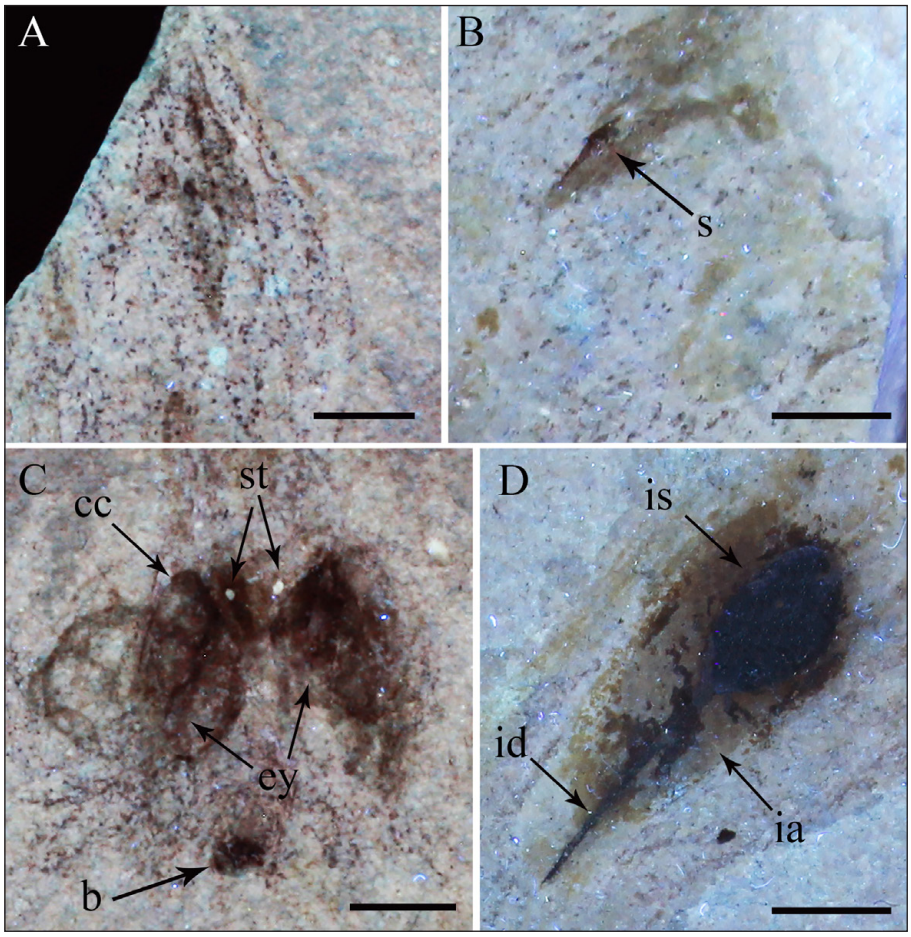

Fig. 4 - *Bolcaoctopus pesciaraensis* gen. nov., sp. nov. from the lower Eocene of Bolca, details of the holotypic structure under UV light. A) Apical part of the body, MGP-PD 31434. B) The right stylet (s), MFB IG23682. C) The head with beak (b), cephalic and ocular cartilage (cc), eyes (ey), and statoliths (st), MGP-PD 31434. D) The ink sac (is), ink duct (id), and leaked ink around the ink sac (ia). MFB IG23682. Scale bars equal 5 mm.

Differential diagnosis*: Bolcaoctopus pesciaraensis* gen. nov., sp. nov. considerably differs from the Upper Cretaceous (Cenomanian) genus *Styletoctopus* (the sole known fossil representative of the extant family Octopodidae) in that it has a more elongated body shape with a tapered apical end, longer arms and a proportionately larger ink sac. *Bolcaoctopus* gen. nov. differs from representatives of the family Argonautidae, whose shells (egg cases) occur in the fossil record from the Oligocene onwards (Fuchs 2020), by the presence of well-developed stylets, which are absent in argonautids (Bizikov 2008).

Remarks. Comparison with modern species is hampered by the limited number of features preserved in the fossil state. The stylets are not clearly visible, and the statoliths are recrystallised; the radula is not visible or not even preserved, which also makes comparisons difficult.

Discussion

The three individuals of coleoid cephalopod available differ in size by almost a factor of two. However, they are nearly identical in structural features and likely belong to the same species. Initially, they were tentatively interpreted as teuthids (Metateuthoidea *sensu* Naef 1921) based on their narrow and apically pointed body shape (Broglio Loriga & Sala Manservigi 1973; Giusberti et al. 2014). However, the presence of eight arms, the absence of the main teuthid feature, i.e., a gladius, and the presence of well-defined gladius vestige (stylets) indicate that these coleoids are in fact octopuses. The general shape of the body and of the stylets allow these octopuses to be assigned to the extant incirrate family Octopodidae. The oldest member of that family, *Styletoctopus* Fuchs, Bracchi & Weis, 2009, was described from the Upper Cretaceous (Cenomanian) deposits of Lebanon (Fuchs et al. 2009). Therefore, this family was undoubtedly represented in Eocene seas. The length of stylets (estimated at 8 mm) is approximately 12 per cent of the length of the mantle (estimated at 65 mm), which is quite consistent with a range typical of octopodids (Bizikov 2008: table 5).

The mantle of all three specimens is oval in shape: it is not only pointed posteriorly, but also tapers anteriorly. Therefore, the anterior end of the mantle of all specimens tapers towards the head, and its border with the head is indistinguishable.

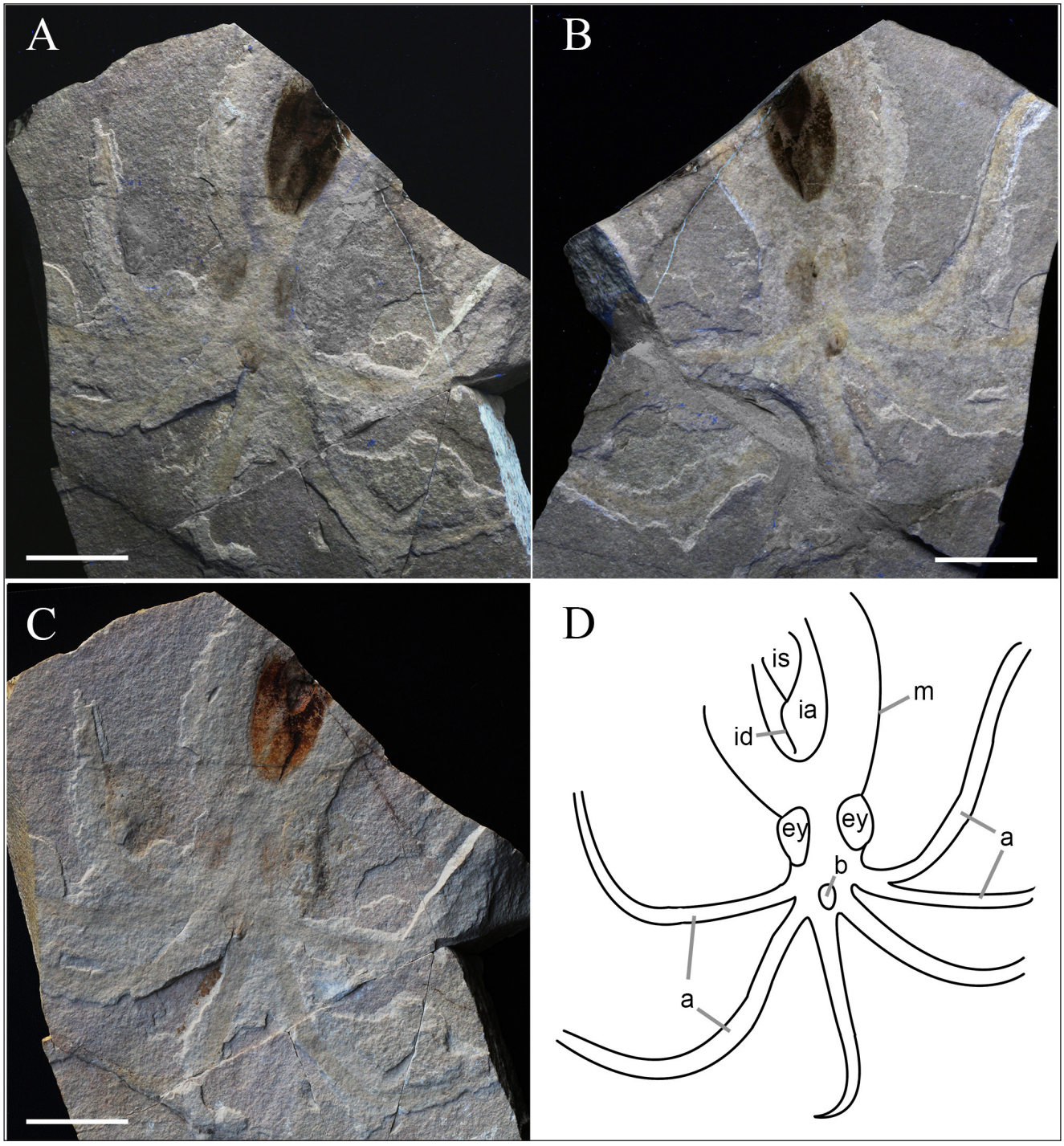

Fig. 5 - *Bolcaoctopus pesciaraensis* gen. nov., sp. nov. from the lower Eocene of Bolca, the paratype. A) MFB IGVR71417 under UV light. B) Counterpart, MFB IGVR71418 under UV light. C) MFB IGVR71417 under natural light. D) Schematic drawing mainly based on (B) (MFB IGVR71418). Letters of references: a - arms, b - beak, ey - eyes, ia - leaked ink around the ink sac, id - ink duct, is - ink sac, m - mantle. Scale bars equal 20 mm.

This feature, characteristic of fossil and modern octopods, clearly distinguishes these specimens from the recently described first fossil loliginid squid from the lower Oligocene of Russia, in which the mantle is conical and widens towards the head (Mironenko et al. 2021). Unlike the specimens described herein, the anterior end of the mantle of that particular squid is not connected to the head; there is a noticeable gap between them (Mironenko et al. 2021: fig. 2). These differences also suggest that the Bolca cephalopods are octopods.

All three specimens have a relatively large ink sac, large eyes, thin arms without a connecting membrane between them – taken together, these characteristics indicate that they were inhabitants of shallow waters. The posterior part of the fusiform body of these octopuses, pointed upwards, apparently had a colour pattern, the mineralised remains of which are visible under UV light.

Conclusions

Discoveries of the taxon of octopus, *Bolcaoctopus pesciaraensis* gen. nov., sp. nov. from the Pesciara of Bolca *Konservat-Lagerstätte* have augmented our knowledge of extinct octopuses. These findings show that during the early Eocene octopuses inhabited the Tethyan seas in southern Europe. Judging by the shape of their stylets and the general shape of the body these octopuses belonged to the extant family Octopodidae.

These Eocene octopuses and previously described Oligocene squid (Mironenko et al. 2021) were both found at those localities where rocks rich in fishes crop out; these have been extensively studied by specialists in vertebrate palaeontology. These findings indicate that fossil coleoids, including well-preserved fossilised soft bodies of squids and octopods, although rare, can be found in such types of sites (*Konservat-Lagerstätten*). While coleoids are extremely rare at these localities, possibly having been occasional visitors to the areas, where fish-bearing sedimentary rocks formed, their study is very important since it sheds light on a poorly understood period of coleoid evolutionary history in the first half of the Cenozoic. Therefore, we wish to recommend that researchers of fossil coleoids around the world pay attention to Cenozoic strata that are rich in fish fossils. It is quite possible that the fossil collections from these localities contain specimens of coleoids that still remain unstudied and undescribed; perhaps such specimens will be found there in future.

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