

# New species of the genus *Thrissops* (Teleostei, Ichthyodectiformes) in the Upper Jurassic of the Solnhofen-Archipelago (Germany) and Kimmeridge Clay (England)

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## Abstract

Two new species of the poorly known genus *Thrissops* (Teleostei, Ichthyodectiformes) are described here in detail. *Thrissops ettlingensis* **sp. nov.** was recently found in the marine lower Tithonian Plattenkalk of Ettling (Bavaria, Germany), at the excavation site of the Jura-Museum Eichstätt, and *Thrissops kimmeridgensis* **sp. nov.** from the Kimmeridge Clay of the Dorset, England. Six adults and one juvenile of *Th. ettlingensis* in excellent preservation, some with stomach content and color pattern, were excavated in Ettling by the author. Of *Th. kimmeridgensis* more than 80 specimens were excavated and exceptionally prepared over the last years by Steve Etches. The characters of the skull, the positions and shape of the dorsal and anal fins and some features of the caudal skeleton strongly support the assignment of these fish to the order Ichthyodectiformes. The two new species belong to the genus *Thrissops* by morphological and skeletal features such as high body shape and short but high cranium. The genus *Thrissops* from the Upper Jurassic (Kimmeridgian/Tithonian) is among the first true Teleostei and belongs to the stratigraphically oldest Ichthyodectiformes (Middle Jurassic to Upper Cretaceous). It is the genus with the first larger predatory fish among the Teleostei; *Th. ettlingensis* still possessing some primitive features such as a comparably low number of abdominal vertebrae and low number of anal pterygiophores. *Thrissops ettlingensis* and *Thrissops kimmeridgensis* are here compared to the other known Upper Jurassic *Thrissops* species of the Solnhofen Archipelago (Germany), Cerin (France) and Dorset (England), and all other known Jurassic Ichthyodectiformes.

## Keywords

Basal Teleostei, diversity, kimmeridgian, morphology, neopterygii, new taxa, taxonomy, Tithonian

## Introduction

Today the Teleostei Müller, 1845 make up over 96% of all fish (with around 30,000 species alive) and around half of all described vertebrate species. The oldest known Teleostei come from the Triassic (approx. 250 million years old) of China (Tintori et al. 2015; Arratia 2017). The Upper Jurassic of Solnhofen Archipelago (Germany) and Cerin (France) are the world's oldest window into Earth history (approx. 150 million years old) for studying the evolution of teleosts with a higher diversity of species. The “true”

teleosts (sensu Arratia 2015) or (“Echte Teleosteer” sensu Arratia and Schultze 2015), which evolved in the Lower Jurassic, are Teleostei at the level of *Leptolepis coryphaenoides* (from Lyme Regis) and further derived Teleostei (e.g., Arratia 1997, 2015).

One of the earliest orders of Teleostei are the Ichthyodectiformes Bardack & Sprinkle, 1969 discovered mostly in marine but to a lesser extent also in freshwater deposits of all continents from the Mid-Jurassic (Bathonian) to Upper Cretaceous (Maastrichtian) (Patterson and Rosen 1977; Cavin et al. 2013; Cavin and Berrell 2019). The group

contains at least 20 genera and about twice that number of species. At present, eight valid families of Ichthyodectiformes are described: Allothrissopidae Patterson and Rosen, 1977; Cladocyclidae Maisey, 1991; Ichthyodectidae Crook, 1892; Saurodontidae Bonaparte, 1846; Unamichthyidae Alvarado-Ortega, 2004; Chuhsiungichthyidae Yabumoto, 1994; Saurocephalidae Zittel 1887; Luisiellidae Sferco, López-Arbarello and Báez, 2015.

Ichthyodectiformes are distinguished from all other Teleostei by the construction of the caudal fin skeleton and a special bone in the cranium, called ethmopalatin. All genera have an anterior-posteriorly elongated anal fin with 24 to 37 fin rays (and anal pterygiophores). The dorsal fin is small and located far back; in most genera the origin of the fin is even posterior to the anal fin origin. The Ichthyodectiformes were predatory fish, which in the Cretaceous (*Xiphactinus*) can reach over five meters in length (Shimada and Everhart 2004). In the Jurassic the Ichthyodectiformes are by far the largest Teleostei with up to 90 cm and the only predatory Teleostei with more than 30 cm length.

In the Jurassic, three genera of Ichthyodectiformes are accepted so far: *Occithrissops* Schaeffer & Patterson, 1984 from the Middle Jurassic of Hulett, Wyoming, USA; *Allothrissops* Nybelin, 1964; and *Thrissops* Agassiz, 1833 (the last two from the Upper Jurassic of England, France, and Germany). *Pachythrissops* Woodward, 1919 and *Ascalabothrissops* Arratia, 2000 are excluded from Ichthyodectiformes by Cavin et al. (2013).

More than 20 species of *Thrissops* have been mentioned in the literature (Bardack 1965; Cavin et al. 2013). In this article seven valid species of the genus *Thrissops* are accepted including the two new species described here. Already Nybelin (1964) pointed out that the number of vertebrae, the number of anal fin rays and the shape of the skull are the main distinguishing features of the different *Thrissops* species. Here we describe two new species of the genus *Thrissops* one from Ettling, Markt Pförring, Solnhofen Archipelago, Bavaria, Germany and a second from the Kimmeridge Clay of Dorset, England and compare them to the known *Thrissops* species, i.e., *Thrissops formosus* Agassiz, 1833 (from the Solnhofen Archipelago, Germany and Cerin, France), *Thrissops subovatus* Münster in Agassiz, 1843 (Solnhofen Archipelago), *Thrissops cirinensis* Nybelin, 1964 (Cerin, France), *Thrissops portlandicus* Woodward, 1895 (Isle of Portland, Dorset, England), *Thrissops curtus* Woodward, 1919 (Purbeck and Portland, Dorset, England) and some as yet undescribed *Thrissops* sp. from further localities. In addition, some problems with the species of the genus *Allothrissops* Nybelin, 1964 are pointed out.

The new *Thrissops* species described here, differ from the previously known *Thrissops* species mainly in body shape, the number of vertebrae, abdominal ribs, anal pterygiophores (anal fin rays) and dentition. Previously, the specimens of the new species *Thrissops ettlingensis* were considered to be juveniles of *Th. formosus* (Ebert and Kölbl-Ebert 2010b, fig. 5).

This is a further step in the comparison of fish fauna diversity in the Upper Jurassic of the opening Tethys of Southern England (Kimmeridge Clay), Southern France (Cerin), and Southern Germany (Nusplingen, Solnhofen Archipelago and Wattendorf).

## Materials, geological setting, and methods

A paleogeographic reconstruction of the carbonate platform of Central Europe shows the localities of the genus *Thrissops* in the Upper Jurassic (Fig. 1A). Together with the biostratigraphy, the distribution of the different *Thrissops* species in the Plattenkalk localities of the Solnhofen Archipelago, Bavaria, Germany, is shown (Fig. 1B, C).

The fossils were examined using a Zeiss 47 50 97 Stereo Zoom microscope, PZO 20138 microscope and a Leica M80 microscope. Drawings were made with Affinity Designer, from photos of the specimens, with direct comparison to the specimens under the microscope (apart from Fig. 15 where only photos were used).

Photos were taken with various digital cameras (Nikon D5100, SONY HX80, Canon EOS 200D, Canon EOS 60 D and Nikon D7000). Digital microscope system KEYENCE VHX-7000 Series 4K with a facility to take UV-photos was used to produce Fig. 10. Unless otherwise noted, all photos are by M. Ebert. Terminology used here for the fin rays is based on Arratia (2008). For the sake of consistency with most of the recent literature on Ichthyodectiformes, the terminology for cranial bones used by Cavin et al. (2013) is employed here. Standard Length (SL) is measured here as the distance from the anteriormost point of the snout to the posteriormost tip of the vertebra or uro-neurals of the caudal peduncle. The number of vertebrae is always without ural centra.

The fossil fish from Ettling come from the field site of the Jura-Museum Eichstätt, where they have been excavated since 2006 (Ebert et al. 2015; Kölbl-Ebert and Ebert 2020; Ebert 2024). The fossil fish from the Kimmeridge Clay described here come from the coast of the Isle of Purbeck near the village Kimmeridge, Dorset, England. All specimens were mechanically prepared under the microscope with the aid of air-pressure vibration tools, scalpels, and tiny soft paint-brushes. The fossils from Ettling in the Jura-Museum Eichstätt were excavated and prepared by the author, if not mentioned otherwise in the acknowledgements. The fossils from the Kimmeridge Clay were excavated and prepared by Steve Etches and the most exquisite specimens are on display in the Museum of Jurassic Marine Life – The Etches Collection, Kimmeridge, Dorset, England. The fish from Ettling are preserved in finely laminated, white Plattenkalk of nearly 100% CaCO<sub>3</sub>, whereas the fishes of Kimmeridge were preserved in the bituminous, grey to black Kimmeridge Clay.



Grenoble, Switzerland; **OSUG-COLLECTIONS** is a database of rocks, minerals, and fossils, <https://web.collections.osug.fr>, OSUG, UGA. doi:10.5072/OSUG-COLLECTIONS.all; **PIMUZ**, Paläontologisches Institut und Museum, Universität Zürich, Switzerland; **ROM**, Royal Ontario Museum, Toronto, Canada; **SDSM**, South Dakota School of Mines and Technology, Museum of Geology, Rapid City, USA; **SMF**, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt a. M., Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **SNSB**, Staatliche Naturwissenschaftliche Sammlungen Bayerns, Germany; **UCBL**, Université de Lyon, Université Claude Bernard Lyon 1, France; **TM**, Teylers Museum, Haarlem, Netherlands.

## Anatomical abbreviations

**a.cer**, anterior ceratohyal; **ang**, angular; **ao**, antorbital; **asph**, autosphenotic; **br**, branchiostegal rays; **bsc**, basal sclerotic bone; **cl**, cleithrum; **cor**, coracoid; **d**, dentary; **dpro**, dorsal procurrent rays; **E**, epural; **ect**, ectopterygoid; **enp**, endopterygoid; **ex**, extrascapular; **fr**, frontal; **H**, hypural; **hs**, haemal spine; **hy**, hyomandibula; **io**, infraorbitals; **iop**, interoperculum; **let**, lateral ethmoid; **mx**, maxilla; **na**, nasal, **na.pi**, nasal pit; **ns**, neural spine; **op**, operculum; **or**, orbit; **pa**, parietal; **pal**, palatine; **p.cer**, posterior ceratohyal; **pf**, pectoral fin; **PH**, parhypural; **pmx**, premaxilla; **pop**, preoperculum; **p.r**, pectoral ray; **PR**, principal ray; **pr.bpt**, basipterygoid process; **psp**, parasphenoid; **pto**, pterotic; **ptt**, posttemporal; **PU**, preural centrum; **qu**, quadratum; **r**, pleural rib; **rode**, rostrodermethmoid; **SC**, scute; **scl**, supracleithrum; **smx**, supramaxilla; **sn**, supraneurals; **sop**, suboperculum; **sr**, sclerotic ring; **sym**, symplectic; **U**, ural centrum; **UD**, urodermal; **UN**, uroneural; **vc**, vertebra centrum; **vpro**, ventral procurrent rays.

## Material examined

In addition to the specimens listed in Systematic Palaeontology below, a large number of Jurassic specimens of Ichthyodectiformes were examined for the purpose of comparison (see Suppl. material 1).

## Results

### Systematic palaeontology

#### Class Actinopterygii Cope, 1887

#### Subclass Neopterygii Regan, 1923

#### Subdivision Teleostei Müller, 1845 (sensu Arratia 1999)

#### Order Ichthyodectiformes Bardack and Sprinkle, 1969

#### Genus *Thrissops* Agassiz, 1833

**Type species.** *Thrissops formosus* Agassiz, 1833.

**Type horizon and locality.** Late Kimmeridgian; Kelheim, Bavaria, Germany.

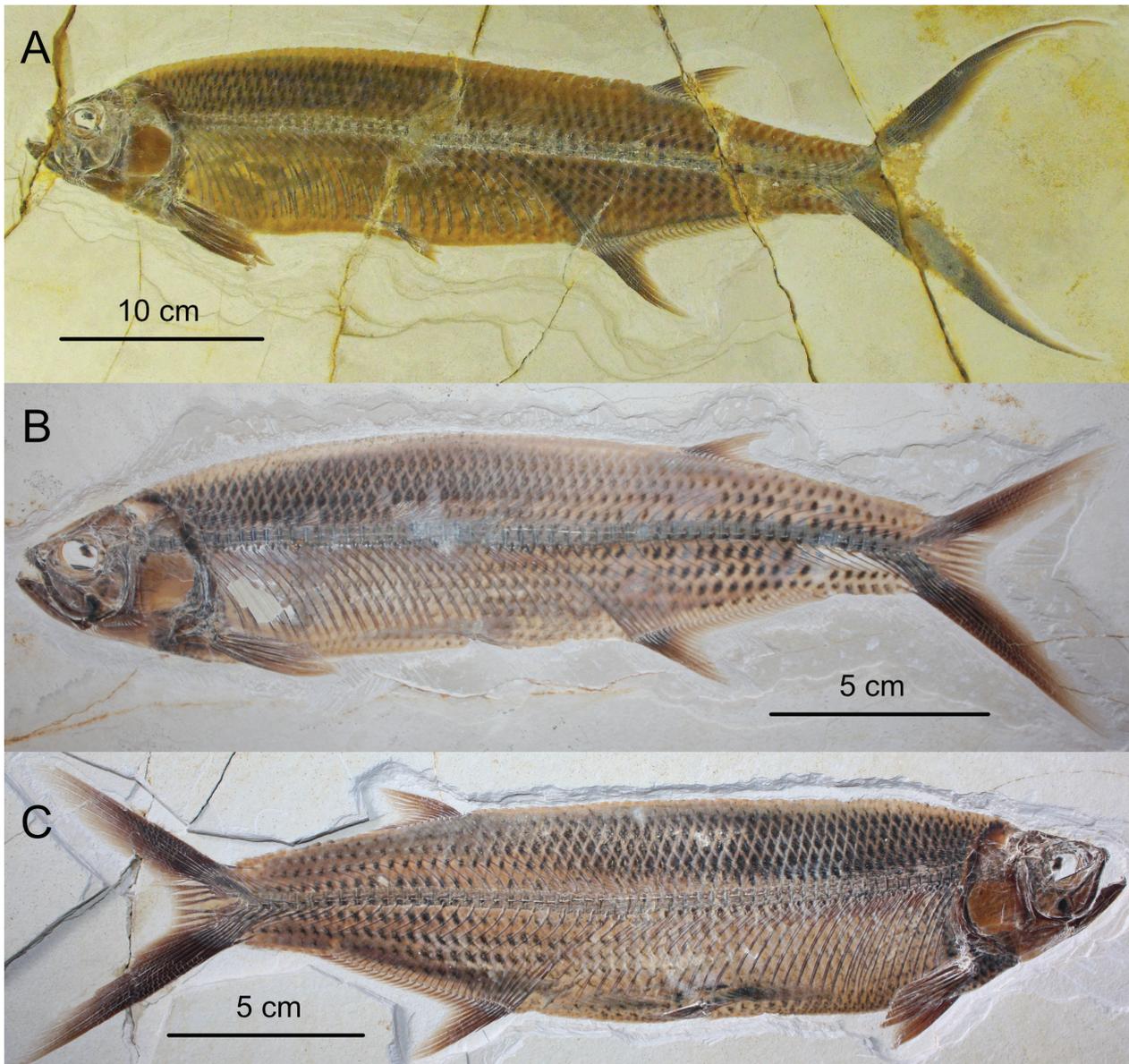
**Diagnosis of the genus** (amended from Nybelin 1964; Bardack 1965; Alvarado-Ortega and Brito 2010): Elongate, slender or fusiform fishes known to reach a standard length of up to 0.9 m; head length included 4–6.5 times in standard length; mouth cleft directed upward; premaxillary teeth longer than those of maxillary and stoutly conical; triangular lower jaw; mandible without enlarged coronoid process; vertical and horizontal arms of preoperculum form right angle at posteroventral corner; preopercle with well-developed posteroventral process; tubules of preopercular sensory canal confined to horizontal arm of preoperculum; parietals not fused; dorsal fin posterior to anal fin origin; 13–15 dorsal pterygiophores; 23–31 anal pterygiophores; six elongated uroneurals; one urodermal.

**Distribution.** In the late Kimmeridgian and early Tithonian of England, France, and Germany.

#### *Thrissops formosus* Agassiz, 1833

Figs 2–5, 18A, B, 20B, 21

- 1833 *Thrissops formosus* Agassiz: Vol. II, pt. 1, p. 12.  
 1843 *Thrissops formosus* Agassiz: Vol. II, pt. 2, p. 124, 293.  
 1843 *Thrissops formosus* Agassiz: Atlas, Vol. II, pl. 65a.  
 1852 *Thrissops formosus* Agassiz; Quenstedt: p. 219, pl. 17, fig. 19.  
 1854 *Thrissops Heckeli*; Thiollière: pl. 10, fig. 1.  
 1863 *Thrissops formosus* Agassiz; Wagner: p. 734.  
 1887 *Thrissops formosus* Agassiz; Zittel: p. 274, figs 280, 281.  
 1895 *Thrissops formosus* Agassiz; Woodward: p. 521 (partim only NHMUK PV OR 49139, 35013, P.913, P.3683, P.3684).  
 1914a *Thrissops formosus* Agassiz; Eastman: p. 387.  
 1914b *Thrissops formosus* Agassiz; Eastman: p. 423 (only CM 4702).  
 1949 *Thrissops formosus* Agassiz; Saint-Seine: p. 268 (partim), pl. 26A.  
 1958 *Thrissops formosus* Agassiz; Nybelin: p. 447, textfig. 1.  
 1964 *Thrissops formosus* Agassiz; Nybelin: p. 5–10, pl. 1, figs 1, 2; pl. 2, figs 1, 2.  
 1965 *Thrissops formosus* Agassiz; Bardack: p. 33, fig. 13F.  
 1977 *Thrissops formosus* Agassiz; Taverne: figs 1, 2, 5, 6, 9–12, 14–16.  
 1977 *Thrissops formosus* Agassiz; Patterson and Rosen: figs 12–14.  
 1984 *Thrissops formosus* Agassiz; Schaeffer and Petterson: p. 41; figs 24B, 26C, 27D, I.  
 1994 *Thrissops formosus* Agassiz; Frickhinger: fig. 493.  
 1998 *Thrissops formosus* Agassiz; Tischlinger: figs 3, 4; pls 1–3.  
 2008 *Thrissops cf. formosus* Agassiz; Ebert and Kölbl-Ebert: fig. 11.  
 2010a *Thrissops cf. formosus* Agassiz; Ebert and Kölbl-Ebert: fig. 3.  
 2011 *Thrissops cf. formosus* Agassiz; Ebert and Kölbl-Ebert: fig. 7.  
 2013 *Thrissops formosus* Agassiz; Cavin et al.; p. 155–156.  
 2013 *Thrissops cf. formosus* Agassiz; Ebert and Kölbl-Ebert: p. 44; figs 2a, 2b, 5; tab. 1.  
 2014 *Thrissops formosus* Agassiz; Berrell et al.: figs 7B, 8.  
 2015 *Thrissops cf. formosus* Agassiz; Ebert et al.: p. 20, figs 8a, b.  
 2018 *Thrissops formosus* Agassiz; Yabumoto et al.: fig. 7, 8.



**Figure 2.** *Thrissops formosus* from the lower Tithonian of Ettlting, Markt Pförring, Bavaria, Germany. **A.** JME-ETT75; **B.** JME-ETT74; **C.** JME-ETT3686.

2019 *Thrissops formosus* Agassiz; Cavin and Berrell: fig. 9.

2020 *Thrissops formosus* Agassiz; Kölbl-Ebert and Ebert: fig. 15a.

2021 *Thrissops formosus* Agassiz; Ebert: p. 38; figs 6a, 6b; tabs 1, 2.

2024 *Thrissops formosus* Agassiz; Alvarado-Ortega: fig. 16, tab. 2.

2024 *Thrissops formosus* Agassiz; Ebert: p. 355; figs 12.10A–C, 12.15, 13.8; tab. 12.1.

**Holotype.** SNSB-BSPG AS VII 2 (Ebert 2021, fig. 6A).

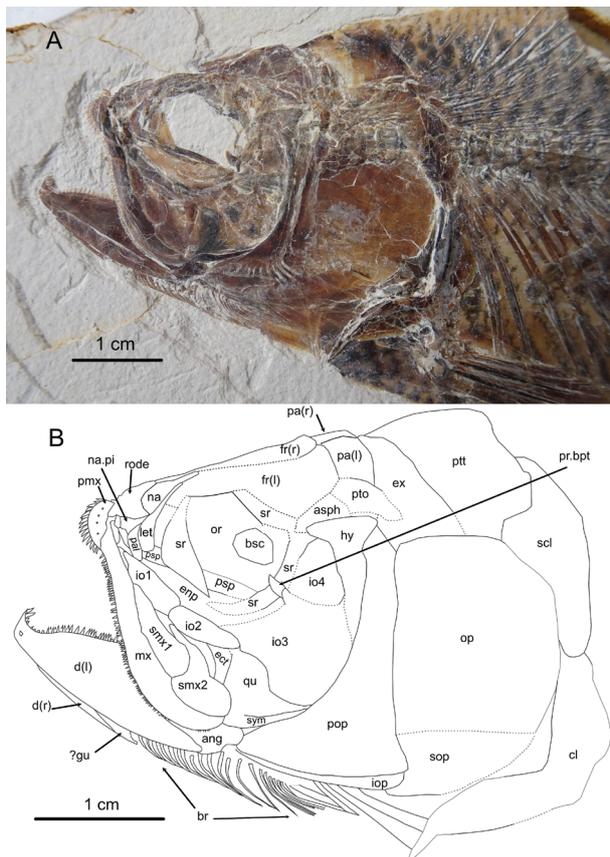
**Type locality.** Kelheim (most probably Kapfelberg), Bavaria, Germany.

**Type horizon.** Upper Kimmeridgian.

**Determination** (for measurements of specimens and counts of features see Suppl. material 1: table S1). Maximum length 75 cm; 37–40 supraneurals; 57–61 vertebrae (without ural centra); 29–32 ribs anterior of anal fin; 28–31 (maximum at 30) anal pterygiophores; small teeth on all jaws (Figs 3, 18A, B); dorsally curved hook at the anterior-

most tip of the dentary with two small, posteriorly directed teeth (Figs 3, 18A, B); curved maxilla (Figs 3, 18A, B, 20B).

**Additional material.** BMMS (Eichstätt without number); CAM SM F.11220 (Kelheim); CM4702 (Eichstätt or Solnhofen); CM4083, 4091 (both Cerin); Coll. Tischlinger 88/91 (Eichstätt), 09/2, 92/2 (both Ettlting); DMA (Painten without number); GPIT-PV-42046, 50597 (both Kelheim); JME-ETT 46, 47, 73, 74 (Fig. 2B), 75 (Fig. 2A), 76, 87a,b, 93, 103, 126, 139, 157, 209, 211, 245, 281, 283, 564, 869, 873, 879, 886, 887, 900a,b, 972, 1350, 1357, 1595, 1799, 1805a,b, 2076, 2079, 2166, 2171, 2550, 2750, 2872, 2941, 2942, 2966, 3108, 3109a,b, 3111, 3205, 3208, 3340, 3341, 3344, 3355, 3371, 3379, 3471, 3473, 3476, 3630, 3657, 3680, 3685, 3686 (Fig. 2C), 3909, 3914, 3917, 4094, 4108, 4315, 4379, 4413 (all Ettlting); JME-SOS 2516 (Eichstätt), 4254 (Schernfeld), 7849 (Ettlting); LF 1215 (Eichstätt), 2319 (Ettlting); MB.f.1375 (Kelheim), 1590 (?Solnhofen), 9756, 15864,



**Figure 3.** Cranium of *Thrissops formosus* (JME-ETT887) from the lower Tithonian of Ettlting, Markt Pförring, Bavaria, Germany. **A.** Photo; **B.** Drawing.

15874, 18259 (all Kelheim); MHNL 20015136, 20015137, 20015185, 20015188, 20015760, 20150031, 20150198, 20150525, 20150558, 20150799, 20150913, 20272030 (all Cerin); MMG-SNSD BaJ2120 (Kelheim); MNHN SLN2 (Kelheim), MNHN CRN9, 73, 82 (all Cerin); NHMW 1852.II.61 (Kelheim); NHMUK PV OR 35013 (Kelheim), P.913, P.913B (both Kelheim), P.917 (Solnhofen), P.918 (Cerin), P.3683, P.3684 (both Kelheim); NMP UC10, 103, 104 (all three Kelheim), NMS 1879.30.5, 1882.32.4 (both Kelheim); NMWIN 801821 counterpart 801822 (Kelheim); NRM P00002924 (Solnhofen), PIMUZ A/I 0389 (Kelheim); SMNS-P-86701 (Eichstätt); SNSB-BSPG AS VII 2 (holotype), AS VII 175 (both Kelheim), SNSB-BSPG 1997 XVIII 1514, 1515 (both from Brunn); TM14842 (Cerin); UCBL-FSL 93382, 502300, 503200 (all Cerin); YPM VPPU.003282 (Eichstätt).

**Distribution and frequency.** In the Upper Kimmeridgian and Lower Tithonian. Common in Ettlting and Kelheim (both Solnhofen Archipelago, Bavaria, Germany) and Cerin (Ain, France); rare in the following localities of the Solnhofen Archipelago: Brunn, Eichstätt, Painten and Solnhofen (for localities and exact numbers see Fig. 1 and Suppl. material 1: table S1).

**Features.** Due to space constraints, not all features of *Th. formosus* can be described in detail, as the new species described below have priority and features of *Th. formosus* have already been described before (see list of publications above). In this article, the features

of *Th. formosus* are presented mainly in detailed photos and corresponding drawings of specimens from Ettlting (for the cranium see Figs 3A, B, 4A–D, 18A, B, 20B and for the caudal fin and skeleton see Figs 5A–C, 21).

**Features not described before.** Thanks to the embedding of JME-ETT3371, it was possible for the first time to take a photo and a drawing of the skull of *Th. formosus* in dorsal view (Fig. 4C, D). Particularly interesting in this specimen is the parietal in dorsal view, as it seems that the parietal bones of both sides have fused together to form a median bone.

At the anteriormost tip of the dentary, all specimens of *Thrissops formosus* have a dorsally curved hook that carries two posteriorly directed teeth which have nearly the same size as the other dentary teeth (see Figs 3, 18A, B and comparison to the other species in the discussion section below).

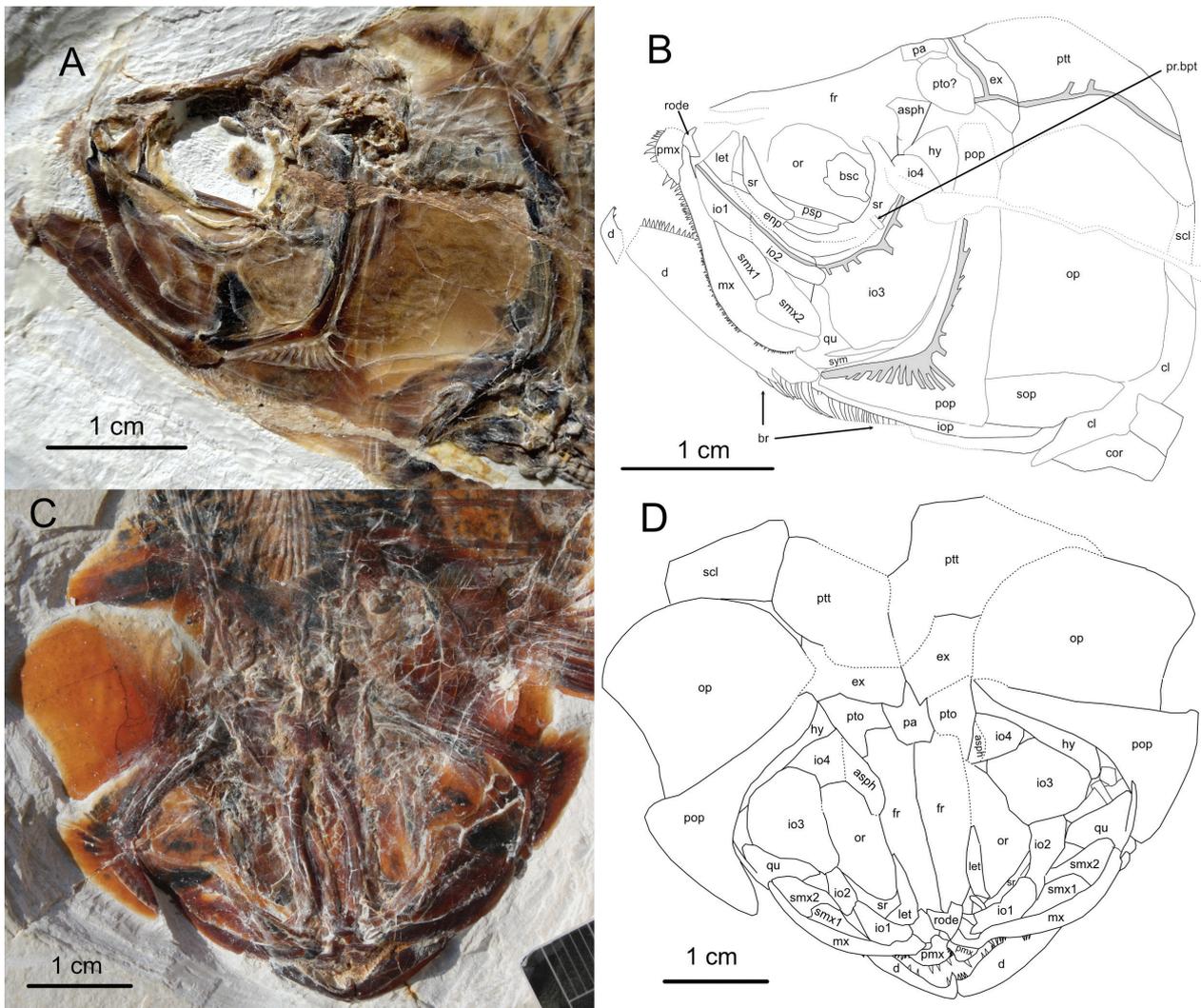
The caudal fin is deeply forked, but in some very well-preserved specimens (JME-ETT126, 173, 283, 564, 887, 2750 (Fig. 21A), 2941, 3111 (Fig. 5C), 3340, 3473, 4108) an elongation of parts of the principal rays seven and eight is visible. The extension is in ray seven only on the ventral side and in ray eight on the dorsal side, so that together they form an inner caudal tip (Figs 2C, 5C).

**History.** The holotype of *Thrissops formosus* (SNSB-BSPG AS VII 2) and type specimen of the genus, which survived the bombing of WWII were stolen from a display case in Munich in 1975 and found again in 1979 in the collection of an invertebrate collector in Munich who claimed to have bought the piece at a flea market (see document in old catalogue of the BSPG).

### *Thrissops subovatus* Münster in Agassiz, 1843

Figs 6, 18C, 20D

- 1843 *Thrissops subovatus* Münster in Agassiz: p. 128.  
 1863 *Thrissops subovatus* Münster in Agassiz; Wagner: p. 734.  
 1895 *Thrissops formosus* Agassiz; Woodward: p. 521 (partim NHMUK PV P.920, P.3678, P.3683a).  
 1914b *Thrissops formosus* Agassiz; Eastman: p. 423 (partim, CM 4030), pl. 72, fig. 2.  
 1964 *Thrissops subovatus* Münster in Agassiz; Nybelin: p. 10; pl. 3, fig. 1, 2, pl. 4, fig. 1; pl. 5, figs 1–3.  
 1965 *Thrissops subovatus* Münster in Agassiz; Bardack: p. 33.  
 1968 *Thrissops subovatus* Münster in Agassiz; Leich: fig. on p. 112.  
 1977 *Thrissops subovatus* Münster in Agassiz; Taverne: figs 3, 7.  
 1994 *Thrissops subovatus* Münster in Agassiz; Frickhinger: figs 495, 496.  
 2008 *Thrissops subovatus* Münster in Agassiz; Taverne: figs 1, 9.  
 2013 *Thrissops subovatus* Münster in Agassiz; Ebert and Kölbl-Ebert: p. 45; fig. 3, 5; tab. 1.  
 2020 *Thrissops subovatus* Münster in Agassiz; Kölbl-Ebert and Ebert: fig. 15b.  
 2021 *Thrissops subovatus* Münster in Agassiz; Ebert: p. 38; fig. 6C, tabs 1, 2.  
 2024 *Thrissops subovatus* Münster in Agassiz; Alvarado-Ortega: fig. 16.



**Figure 4.** Cranium of *Thriassops formosus* from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Photo of JME-ETT1350 in lateral view; **B.** Drawing of JME-ETT1350; **C.** Photo of JME-ETT3371 in dorsal view; **D.** Drawing of JME-ETT3371.

2024 *Thriassops subovatus* Münster in Agassiz; Ebert: p. 355; figs 12.12A–C, 12.15, 13.8; tab. 12.1.

**Holotype.** SNSB-BSPG AS VII 178 (Ebert 2021, fig. 6C).

**Type Locality.** Kelheim (most probably Kapfelberg), Bavaria, Germany.

**Type horizon.** Upper Kimmeridgian.

**Determination.** Standard length (SL) to body depth (BD) specimens 26–29% (average 28%); Maximum length 43 cm; 59–60 vertebrae (without ural centra); 38–40 supraneurals; 30–31 abdominal ribs; 30–31 anal pterygiophores; larger, bigger and less numerous teeth than other *Thriassops* species (except for *Th. cirinensis*); dentary teeth of irregular size; ventral margin of maxilla more straightened than in the other Ichthyodectiformes; vertebral axis in front of the caudal fin first bends slightly downwards before turning into the upper caudal lobe.

**Distribution and frequency.** Only known from the Solnhofen Archipelago, Bavaria, Germany, but rare in all localities (see Fig. 21 and Suppl. material 1: table S1).

**Additional specimens.** CM 4030 (“Solnhofen”); Coll. Leich Bochum (Eichstätt without number); Coll. Tischlinger 01/26 (Öchselberg), 98/23 (Eichstätt); DMA (Painten without number); JME-ETT2639, 3465 (both Ettling); JME-SOS2525 (Solnhofen), 4253 (Wintershof, Eichstätt Basin); LF 1469 (Eichstätt); MB.f.15887 (Kelheim); MBH20253251, 20253252 (both Blumenberg, Eichstätt Basin); MMG-SNSD BaJ 2115 (Eichstätt); NHMUK PV P. 920, P.3678, P.3683a (all three Kelheim); NMP UC2280 (Solnhofen); NMS 1905.83.12 (Kelheim); ROMVP 947 (Solnhofen); SMNS-P-86700 (Zandt).

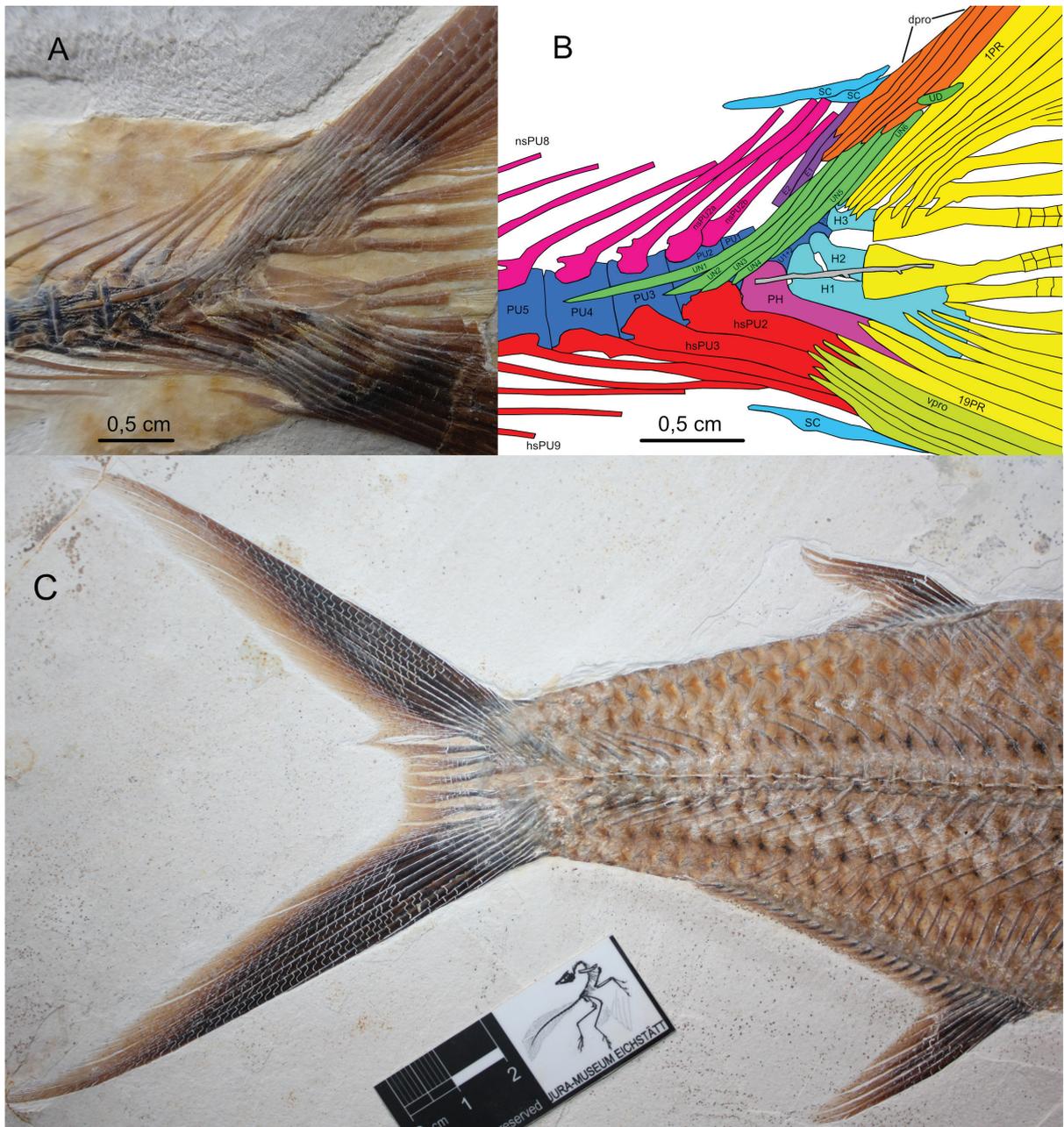
### *Thriassops cirinensis* Nybelin, 1964

1964 *Thriassops subovatus cirinensis* Nybelin: p. 14–16; pl. 4, fig. 2; pl. 5, fig. 4.

1977 *Thriassops cirinensis* Nybelin; Taverne: figs 4, 8.

2013 *Thriassops cirinensis* Nybelin; Ebert and Kölbl-Ebert: tab. 1; fig. 5.

2024 *Thriassops cirinensis* Nybelin; Ebert: fig. 13.8.



**Figure 5.** Caudal fin of *Thrissops formosus* from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Detail photo of JME-ETT1350; **B.** Drawing of JME-ETT1350; **C.** Complete caudal fin of ETT3111 with principal rays seven and eight slightly elongated.

**Holotype.** MNHN CRN 66 (Fig. 7), complete specimen in lateral view, 18.5 cm standard length (SL).

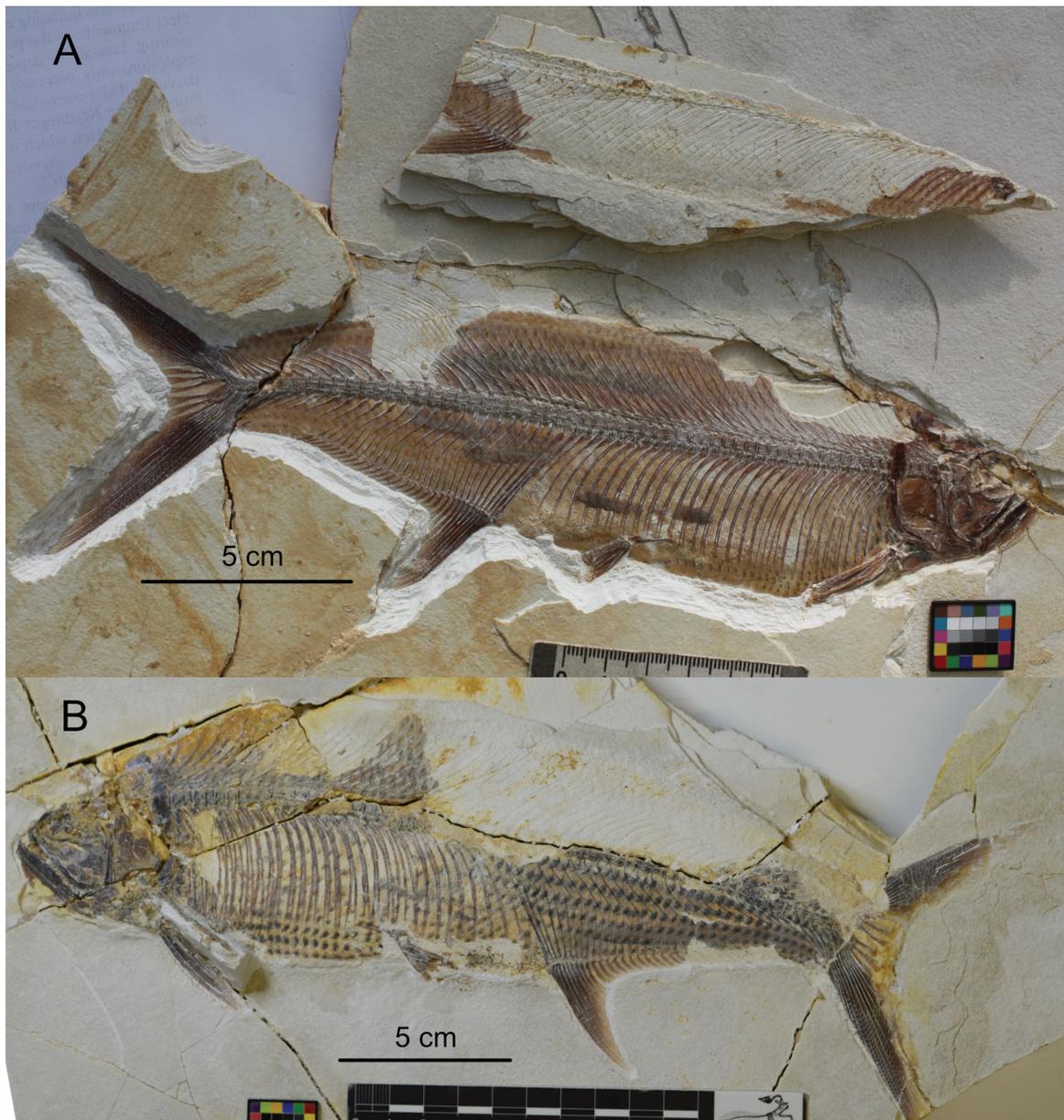
**Type locality.** Cerin, France. The location of Cerin is marked with a question mark on the rock slab of the holotype. The rock is also somewhat unusual for the Plattenkalk of Cerin. However, this problem must be left to future research.

**Diagnosis** (amended from Nybelin 1964 and Taverne 1977). teeth in premaxilla and dentary larger than in other *Thrissops* species; 32 supraneurals; 27 anal pterygiophores; 54 vertebrae (without ural centra); 24 ribs.

**Remark.** Nybelin (1964) was somewhat cautious about calling this taxon a new species, since there was only a single specimen and that could be pathological. Taverne (1977) finally determined the species name *Thrissops cirinensis*.

**Further specimens from Cerin** (probably belonging to the same species): MHNL20150008, 20150311, 20150312, 20150313 (counterpart of 20150311), 20150401, 20150661, 20150690, 20150736, 20150831; UCBL-FSL P371, 502407, 502412.

All these specimens are poorly preserved and it is impossible to say for sure if they are specimens of *Thrissops cirinensis*. More detailed examinations under optimal UV light may help. These specimens are similar to the holotype of *Th. cirinensis* mainly in the following features: short length of the body (compared to other Ichthyodectiformes); the body shape with SL/BD 27–33%; the number of 30–31 supraneurals; 23–26 anal pterygiophores; ~49–51 vertebra and 24–25 abdominal ribs (for measurements



**Figure 6.** *Thrissops subovatus* from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** JME-ETT3465a,b; **B.** JME-ETT2639.

of specimens see Suppl. material 1: table S1). In UCBL-FSL P371 some large teeth in the praemaxilla and in UCBL-FSL 502412 some larger teeth in the dentary, typical for *Th. cirinensis*, are visible.

### ***Thrissops ettlingensis* sp. nov.**

<https://zoobank.org/52E8F627-2181-4C7E-8166-D0B748080CEE>  
Figs 8–13, 18D, 20A

2010b *Thrissops* cf. *formosus* Agassiz, 1833; Ebert and Kölbl-Ebert: figs 5a, b.

2013 *Thrissops* n. sp. Ebert and Kölbl-Ebert: p. 46; figs 4a, 4b, 5; tab. 1.

2020 “unbenannte *Thrissops* Art” Kölbl-Ebert and Ebert: fig. 15e.

2024 *Thrissops* n. sp. Ebert: p. 357; figs 12.11A, B, 12.15, 13.8; tab. 12.1.

**Holotype.** JME-ETT3345 (Figs 8, 11, 13A, 18D), complete specimen in lateral view, 11.6 cm standard length (SL).

**Type locality.** Ettling, Markt Pförring, Bavaria, Germany.

**Type horizon.** From the *eigeltingense*  $\beta$  horizon of the lower Tithonian (see Tischlinger and Schweigert 2020).

**Additional material** (all from Ettling). Coll. Tischlinger 20/4, 20/8; JME-ETT166 (Figs 9A, 12), 220 (Fig. 9B), 1360 (Fig. 10A, B), 4104a, b (Figs 9C, 13C, D).

**Etymology.** The specific epithet in *Thrissops ettlingensis* refers to the village of Ettling, Markt Pförring, Bavaria, Germany where the specimens were found.

**Diagnosis.** *Thrissops* reaching 15.5 cm total length (13 cm SL), with the following unique combination of characters (for measurements of specimens and counts of features see Suppl. material 1: table S1): standard length (SL) to body depth (BD) 26–33% (average 31%); 30–31 supraneurals; 49–50 vertebrae (without ural centra); 24–25



**Figure 7.** *Thrissops cirinensis* Nybelin 1964 holotype (MNHN CRN66) from the Upper Jurassic of Cerin, France.



**Figure 8.** *Thrissops ettlingensis* sp. nov. holotype (JME-ETT3345a) from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Photo in normal light; **B.** UV-photo (A. Hecker); **C.** Fragment of anal fin in counterpart.

ribs anterior of anal fin; 23–25 anal pterygiophores; small teeth (Figs 11, 12, 18D); curved maxilla (Figs 11, 12, 18D, 20A); regular dentition in the lower jaw.

**Morphological description** (for measurements of specimens see Suppl. material 1: table S1).

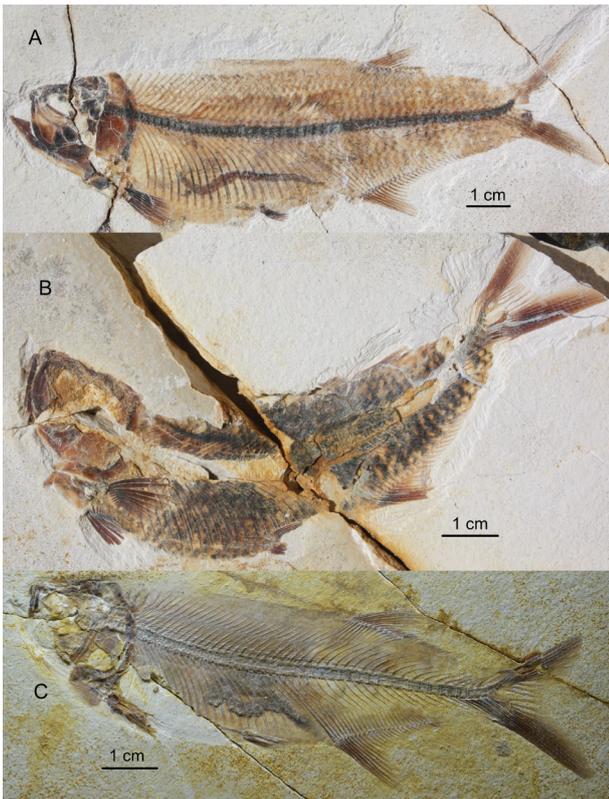
**General features.** In *Thrissops ettlingensis*, the maximum body depth (MD) is 26–33% (average 31%) of its standard length (SL), with up to 15.5 cm in total length (13 cm SL). One juvenile specimen of 3.5 cm SL (JME-ETT1360) is also known from Ettling. The dorsal and the anal fins are in the posterior half of the body, with the

dorsal fin origin slightly posterior to the anal fin origin, which is typical for *Thrissops* and *Allothrissops* (Nybelin 1964) (for differences to other species see Table 1).

**Skull and dentition.**

**Cranial morphology.** Cranial morphology of *Thrissops ettlingensis* is best visible in the holotype (JME-ETT3345a, Fig. 11) and JME-ETT166 (Fig. 12), both showing the left side of the cranium. None of the cranial bones shows ornamentation or have serrated posterior borders.

**Braincase and Ethmoid region.** Most bones of the braincase are covered by other bones of the cranium, only



**Figure 9.** *Thrissops ettlingensis* sp. nov. from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** JME-ETT166; **B.** JME-ETT220; **C.** JME-ETT4104a.

the rostrodermethmoid and parts of the palatine, the ethmoid complex and the parasphenoid are visible. A small part of the palatine is visible at the anteriordorsal border of the maxilla ventral to the nasal pit. The lateral ethmoid separates the orbita posteriorly from the nasal capsule anteriorly. The ethmoid complex in Ichthyodectiformes is described in detail in Cavin et al. (2013). A small part of the parasphenoid is visible at the ventral border of the orbita. The rostrodermethmoid is an unpaired bone, at the anterior part of the cranium posterior of the premaxilla. Posteriorly it extends between the paired frontals.

**Skull roof.** The elongated frontals are the largest bones of the skull roof, with the posterior part twice as wide as the anterior part. The anteriormost part of the frontals is covered by the rostrodermethmoid, posteriorly the frontals overlap slightly the parietals. It is unclear if the parietal in *Th. ettlingensis* is an unpaired ossification median on the skull roof, because only one side of the cranium is visible. The visible parietal at the posterioridorsal border of the frontal, are nearly quadrangular, only about half the size of the extrascapular and probably as large as the pterotics. The pterotic is smaller anteriorly and gradually widens posteriorly, but the exact shape is not clearly visible due to the incomplete preservation of the specimens. There is one large extrascapular and one posttemporal on each side of the cranium. The nasal is a short, tubular, nearly rectangular bone at the posterior border of the nasal pit, with a canal running in its center.

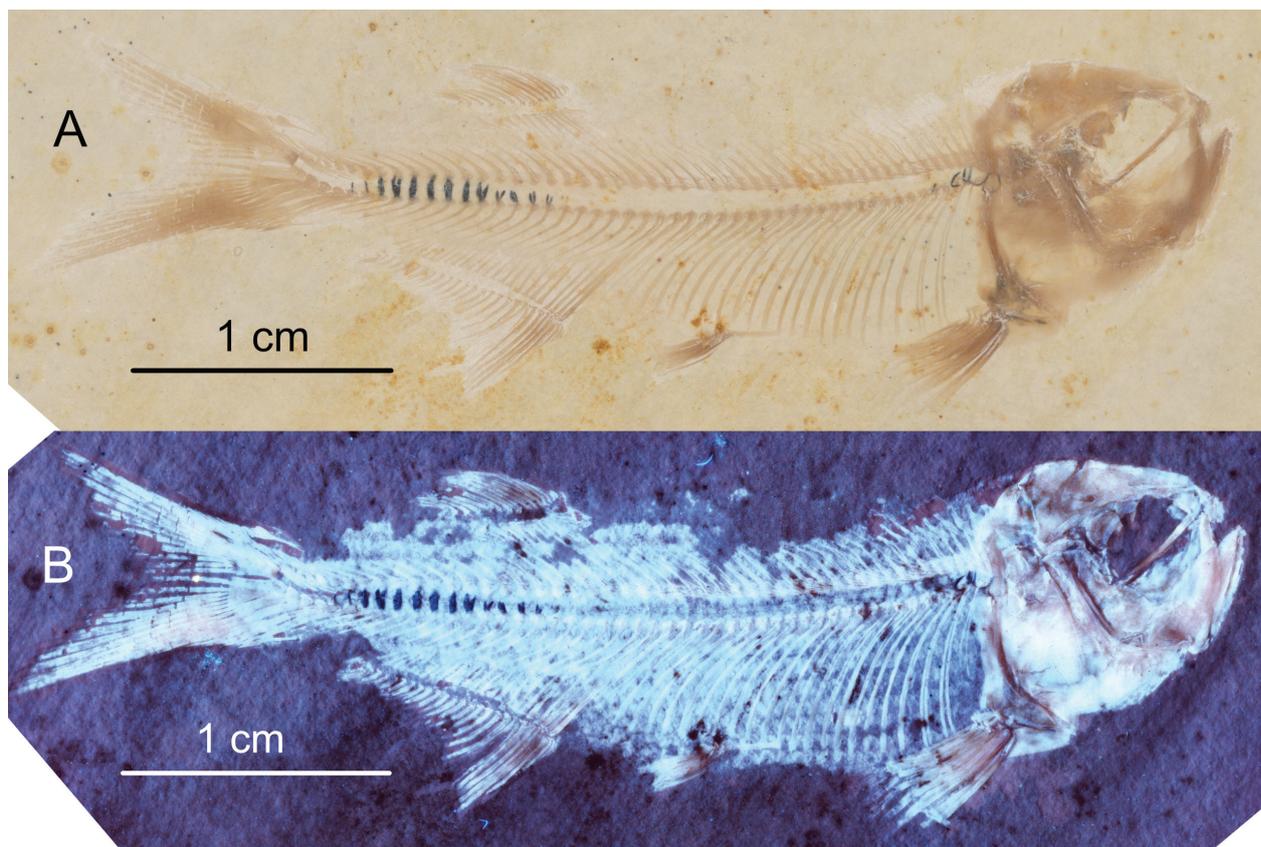
**Circumorbital series.** Antorbitals anterior of the frontals are not recognizable in any of the specimens. There is a total of four thin infraorbitals (io) ventral and posterior of the orbit. The anteriormost two infraorbitals (io1, io2) are slender and anteriorly posteriorly elongated. The lacrimal (io1) extends from the nasal pit to the level of the first third of the orbita. The second infraorbital (subinfraorbital, io2) nearly went to the posterior border of the orbita. The third infraorbital (io3 = ventral postinfraorbital), is the largest infraorbital, it is nearly as long as it is deep. This bone is recognizable by postero- and postero-ventrally directed branches of the infraorbital canal. The fourth and last infraorbital (io4 = dorsal postinfraorbital) is best visible in the holotype JME-ETT3345a (Fig. 11). This bone is higher than long and lies on the posterior border of the orbit posterior to the sclerotic ring. A gap in which parts of the hyomandibula are visible separates the two posterior infraorbitals from the preoperculum. The infraorbital sensory canal is well visible in the holotype and JME-ETT166 (Fig. 11, 12). The autosphenotic is a somehow triangular bone at the posteroventral border of the orbit, but its exact borders are not clearly visible in any of the specimens. Suborbitals and supraorbitals are not recognizable in any of the specimens and probably generally absent. At least two large, broad bones of the sclerotic ring surround the orbita, but these fragile bones are broken and its borders are not everywhere clearly visible. The basal sclerotic bone is a thin, rounded bone in the posterior dorsal part of the orbita.

**Opercular series.** The preopercle is large with a long and slender dorsal part and a broad ventral part which extends anteriorly and posteriorly. It has slightly concave posterior margin; ventrally it has a well-developed posteroventral process. In the ventral part the preopercular canal is well visible. Some extensions of this canal bend ventrally and end in small openings on the surface.

The opercle is twice as high as it is wide (antero-posteriorly). Its dorsal border to the posttemporal is convexly curved, whereas its posterior border to the supracleithrum and cleithrum, its ventral border to the subopercle and the anterior border to the preopercle is nearly straight. The subopercle is small, with its anteriormost part with the anteriordorsal process covered by the preopercle. An interopercle is not visible, probably totally overlapped by the preoperculum.

**Branchiostegal series and gular plate.** There are 16 branchiostegal rays on the holotype (Fig. 11). The rays in the anterior half of the series being fine and hair-like. The posterior five rays are wider with the posteriormost being about three times as wide as the ray anterior to it. The anterior hair-like rays end in a point whereas the posterior rays have rounded posterior margin. Anterior to the branchiostegals, between the two dentaries there is a part of a small, thin bone visible, which is interpreted here as a small gular plate.

**Jaws and suspensorium.** The upper jaw consists of maxilla, premaxilla and two supramaxillae. The premaxilla at the anteroventral edge of the upper jaw is broad. On its



**Figure 10.** Juvenile specimens of *Thrissops ettingensis* sp. nov. (JME-ETT1360) from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Photo in normal light; **B.** UV-photo.

convexly rounded anteroventral border there are eight to ten small teeth which are about twice as long and wide as the maxillary teeth (best visible in the holotype, Fig. 11). The posteriodorsal part of the premaxillae is covered by the maxilla and the rostrodermethmoid.

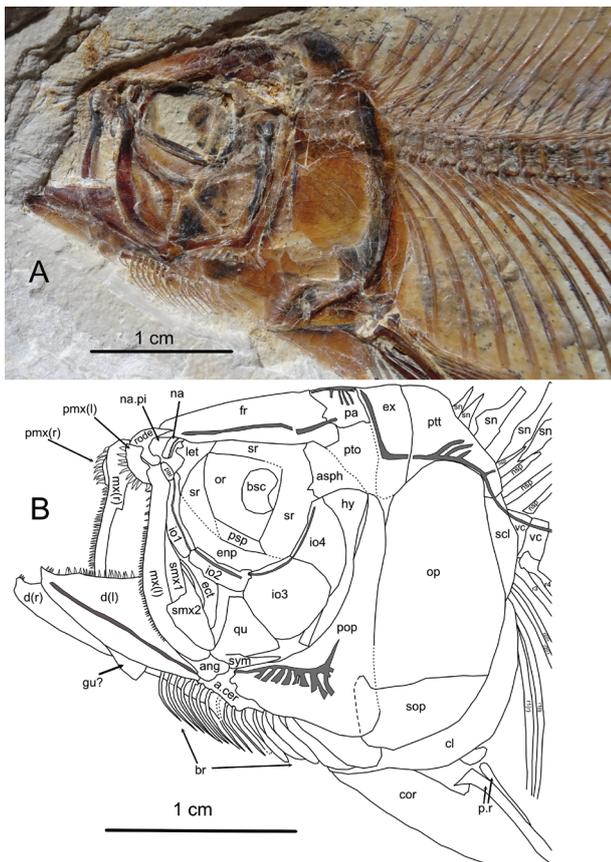
As in all Ichthyodectiformes the maxilla is long. In *Thrissops ettingensis* at least as long as the dentary but not reaching the posterior border of the orbita. Its posterior border to the angular is rounded, covering the anterior part of the quadrate. The anteriormost part of the maxilla, which is covered by the premaxilla and the rostrodermethmoid, bends ventrally, whereas the visible anterior part is nearly straight. The posterior half of the maxilla bends continuously dorsally. Only one row of teeth with 51 small, pointy teeth is visible on the ventral margin of the maxilla of the holotype (Fig. 11). Almost all teeth are of the same length only the posteriormost are slightly smaller.

There are two supramaxillae on both sides of the cranium which run along more than half of the posteriodorsal margin of the maxilla. The anterior supramaxilla is slender, half as large as the posterior one and tapers towards the front. The posterior supramaxilla is as long but twice as wide as the anterior one. The posterior supramaxilla has an anteriodorsal process that ends in a point and covers the posterior half of the dorsal margin of the anterior supramaxilla. The maximum height of the posterior supramaxilla, is a little higher than the maxilla at its highest point in the centre of the maxilla.

The mandible is moderately long, reaching the posterior edge of the orbita. There are 22 small, pointed teeth along the dorsal border of the dentary visible in the holotype (Fig. 11). The dentary teeth are slightly larger than the corresponding maxillary teeth. They are situated in one row and are of approximately the same size all along the whole length of the dentary. The mandibular sensory canal runs from anterior to posterior in the middle of the bone in a small groove. A border between the dentary and the angular is clearly visible at the dorsalmost part of the mandible. Dorsally the angular is covered by the posteriormost part of the maxilla.

The quadrate is large, but the articulation to the mandible is covered by the angular. The slender, elongated symplecticum branches off from the posteroventral part of the quadrate and extends posteriodorsally between the quadrate and the preoperculum.

**Pectoral girdle.** The large posttemporal borders the operculum dorsally. Along its ventralmost part, which is twice as broad as the dorsal part, the posttemporal sensory canal is well visible. This canal has at least four branches posteriorly, which ends in small pores. The supracleithrum, which lies on the posteriodorsal edge of the operculum, and covers some of the anteriormost vertebrae, is at most half as large as the posttemporal. In its dorsalmost part, the extension of the posttemporal canal runs to the lateral line. The cleithrum is, as usual, the largest bone in the shoulder girdle, but a large part of

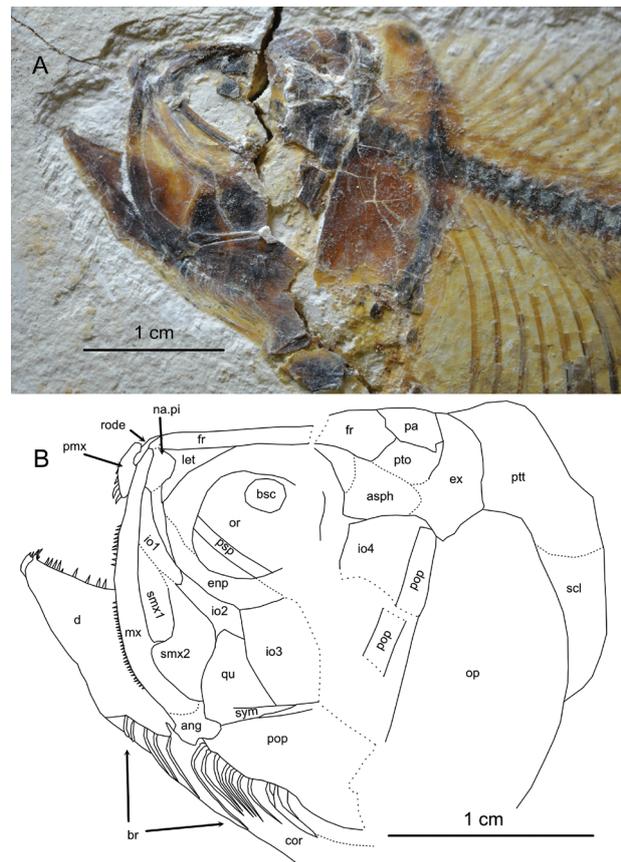


**Figure 11.** Cranium of *Thriassops ettlingensis* sp. nov. from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Photo of holotype (JME-ETT3345a); **B.** Drawing of holotype (The fine dashed lines in the drawings are uncertain bone boundaries or missing parts, the coarse dashed parts are bone boundaries that are visible behind other bones. The dark gray filled areas are sensory lines).

the cleithrum is covered by the operculum and suboperculum anteriorly. However, its approximate shape can be estimated through these transparent bones (Fig. 11A). As in all Ichthyodectiformes the coracoid is a large but thin bone ventral to the cleithrum.

**Axial skeleton.** The axial skeleton is clearly visible in nearly all specimens (Figs 8, 9), apart from the juvenile specimen JME-ETT1360 where most vertebra centra are not developed yet (Fig. 10). Only embryonal ring centra are visible on some parts of the vertebral axis of this juvenile specimen (JME-ETT1360); two behind the cranium and about 14 between the dorsal and anal fin. Embryonal ring centra are not fully ossified and without contact to each other. Interestingly they appear in black colour in normal-light (Fig. 10A) and UV-light (Fig. 10B), whereas all other bones are brown in normal light (Fig. 10A).

The vertebral column in adult specimens consists of 51 or 52 total centra, including 26 or 27 abdominal centra, 23 or 24 caudal centra including the parhypural, and two ural centra. The vertebrae are best visible in areas where the scales are absent. The centra in the anterior half of the body (best visible in JME-ETT4014a) have small anteriorly posteriorly aligned ridges and a few small pores. In the posterior half



**Figure 12.** Cranium of *Thriassops ettlingensis* sp. nov. from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Photo of JME-ETT166; **B.** Drawing of JME-ETT166 (The fine dashed lines in the drawings are uncertain bone boundaries or missing parts, the coarse dashed lines are broken bones).

of the body (best visible in JME-ETT3345a) only the ridges are present, with the middle one or two ridges being slightly more pronounced. The anterior vertebrae are deeper than long, from about the 36<sup>th</sup> to the 48<sup>th</sup> vertebra they have about the same length as high. All parapophyses, haemal arches and neural arches are autogenous from the centra. 24 or 25 long, paired pleural ribs cover the middle abdominal cavity. The anteriormost four vertebrae, which are covered by the operculum and the subcleithrum are without ribs.

The ribs are bow shaped, slightly curved anteriorly, only the posteriormost pair, which is the smallest, is straight.

There are 26 short paired neural spines in the abdominal part, with the two posteriormost, which are connected to the dorsal pterygiophores, being the longest. The epineural processes, which are connected to the ventral bases of the neural spines, are elongated, thread-like bones. Their anterior half runs dorsal to the neural arches, parallel to the body axis, but then bends dorsally to the tips of the neural spines. However, the posteriormost two or three epineural processes, ventral to the dorsal pterygiophors, hardly bend dorsally and therefore do not reach the ends of the neural spines. The epineural processes are as long as 8–9 centra. Epipleurals or epicentrals are absent. Small, unknown, ovoid structures are visible in JME-ETT3345a and JME-ETT4104a,

dorsal to the vertebrae 10–16, between the epineurals, which have two third the length of a vertebra.

In the preural region there are 18 unpaired neural spines with the anteriormost, connected to the dorsal pterygiophores being the longest. All unpaired neural spines have an anterior projection near the base to the neural arch which is most prominent in the anterior part dorsal to the anal fin.

Additionally, there are 22 or 23 unpaired haemal spines between the paired abdominal ribs and the parhypural.

Dorsal to the paired neural spines, between the cranium and the dorsal pterygiophores there are 30 or 31 supraneurals. The anteriormost three have broad bases which are partly covered by the posttemporal. The following four also have slightly widened bases but are less pronounced as the neural spines anterior to them. The penultimate supraneural is dorsally in contact with the anteriormost dorsal pterygiophore and the posteriormost supraneural is situated in JME-ETT4104a between dorsal pterygiophores two and three. The ventralmost part of the supraneurals insert between the dorsalmost parts of the neural spines. The supraneurals has nearly the same length as the neural spines in the same area, apart from the posteriormost, which is only half as long as the neural spines ventral to it.

#### Fins.

**Pectoral fins.** The shape of the pectoral fin is best preserved in JME-ETT220 (Fig. 9B). The anterior, unsegmented part of both pectoral fins in JME-ETT220 is visible from both sides of the body, with 13 rays each. The pectoral fin is larger and longer than the pelvic fin, with the anteriormost four rays being the largest and longest. The unsegmented proximal parts of the rays are long, approximately two third as long as the complete ray. In the juvenile specimen (JME-ETT1360) at least three pectoral radials are visible anterior of the pectoral fin (Fig. 10).

**Pelvic fins.** The pelvic fin is short, with approximately half the length of the pectoral fin. In JME-ETT220, the anterior part of both pelvic fins is visible from both sides of the body, with about nine rays each (Fig. 9B). Segmentation and branching are not well visible in any of the specimens. The pelvic bone is slender along the whole length; only the anteriormost and the posteriormost parts are slightly widened. It has the length of four vertebrae dorsal to it, but it is slightly shorter than the pelvic fin itself.

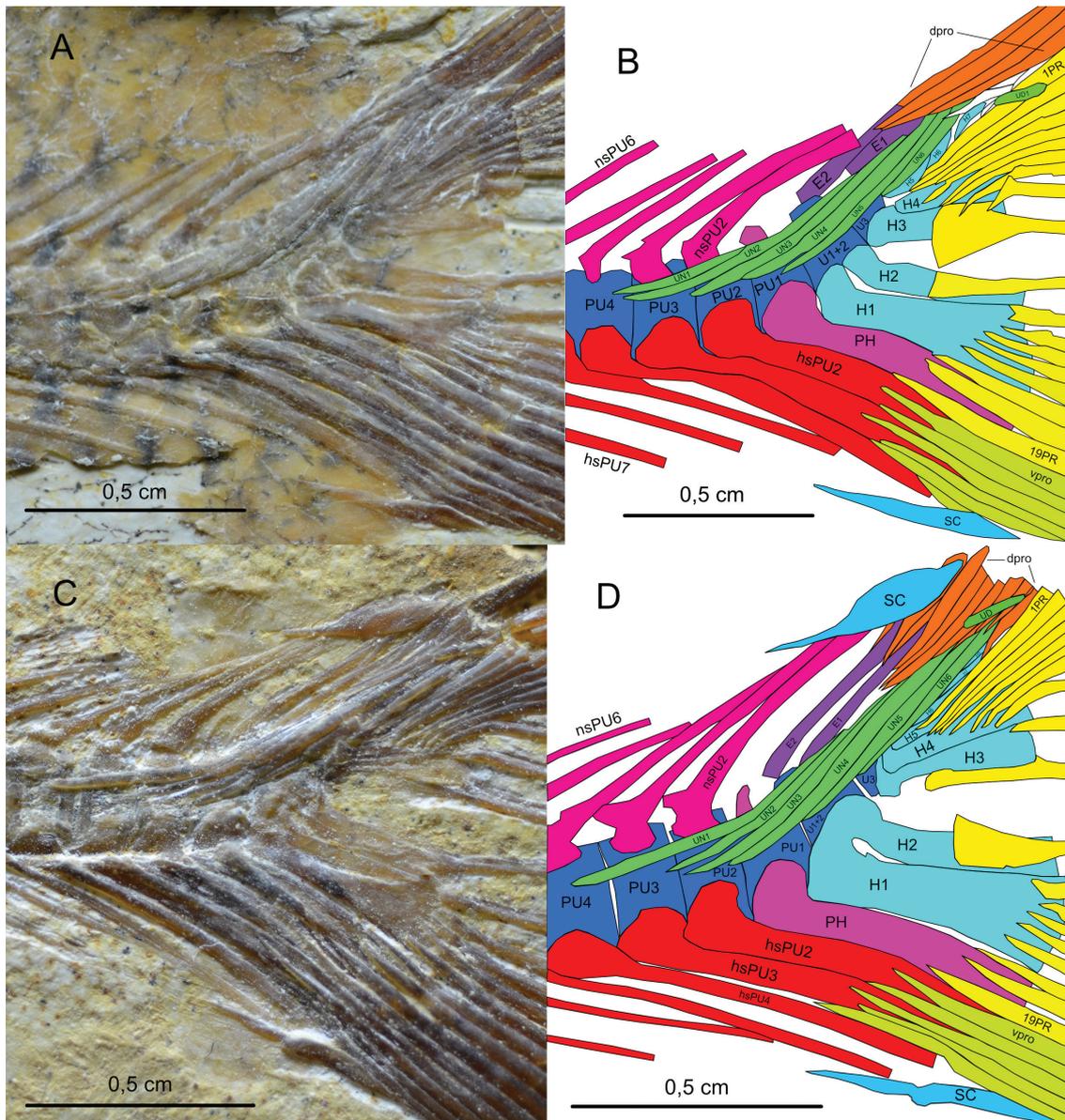
**Dorsal fin.** The dorsal fin is located far back on the trunk, posterior to the anal fin origin (Figs 8–10). The dorsal fin is slightly higher than long, forming a triangle. There are 14 (in one case possibly 13) dorsal pterygiophores supporting about the same number of distally segmented dorsal fin rays, plus anterior to the segmented rays three unsegmented procurrent rays. Each pterygiophore is composed of an elongated proximal radial and a middle radial. The middle radials are small and hardly visible. The first dorsal proximal pterygiophore is bifurcated at the dorsal base with a long anteriorventral directed process that corresponds to the posterior pterygiophores in position and length and a slightly shorter anterior process which is directed in the body axis. A thin bone membrane stretches between these

two extensions. The anterior dorsal radials are elongated and deeply overlap the neural spines. The posterior dorsal radials extend into the interneural spine spaces ventral to them. The first segmented ray is unbranched, posteriorly the rays branch at least once (in adult specimens).

**Anal fin.** As in all Ichthyodectiformes, the anal fin is anterior-posteriorly elongated but not as long as in other Ichthyodectiformes (Figs 8–10). 22–24 segmented anal fin rays are supported by 23–25 anal pterygiophores (Table 1). The first segmented ray is unbranched, posteriorly all rays are segmented and branched. The first segmented ray is the longest, then the length decreases rapidly up to the 10<sup>th</sup> ray. Behind the 10<sup>th</sup> ray the ray length is very short and decreases only slightly. The posteriormost anal ray is an exception; it is slightly widened and has several branches. The posteriormost branch is thin and elongated, so that this ray becomes twice as long as the rays immediately anterior to it (best visible in JME-ETT4104a and already hinted at the juvenile JME-ETT1360). Whether this is a characteristic of sexual dimorphism can only be decided when more well-preserved specimens are available. Cavin et al. (2013) described a similar long filament on the Ichthyodectiformes *Eubiodectes libanicus*, but here for the dorsal fin. Anterior to the first segmented ray, there are three or four unsegmented procurrent rays. The first anal pterygiophore is very elongated and rests along the anterior margin of the first haemal spine. All anal pterygiophores situated posterior to this first pterygiophore are long, extending into the interhaemal spine spaces dorsal to them. The anal pterygiophores supporting the posterior half of the fin are longer than the fin rays connected to them. Middle radials are small and mostly covered by the bases of the fin rays in the anterior part of the fin. In the posterior part of the fin the middle radials are visible in JME-ETT4104a which are rectangular in shape.

**Caudal fin and skeleton** (Fig. 13A, B). The caudal fin is deeply forked with two triangular lobes of the same length. The caudal formula (see Alvarado-Ortega 2024 p. 20) is  $iv+i+9-8+i+v$ . Four dorsal procurrent rays are visible in JME-ETT3345a in JME-ETT4104a the number of dorsal procurrents seems to be higher, but these are probably disarticulated lepidotrichia from both sides of the body. The dorsalmost procurrent in JME-ETT3345a is the shortest, which is unsegmented. The following procurrents are segmented but unbranched, with the number of segments from one up to at least 13, increasing with length of the rays.

Ventrally, we have five ventral procurrents in JME-ETT4104a and apparently six in JME-ETT3345a where the smallest can also be a part of the procurrent of the other side of the body. As in all modern Teleostei (since *Leptolepis cyprinoides* of the Lower Jurassic) there are 19 principal rays with the dorsal and ventralmost being the largest rays, which are unbranched but multiple segmented (Arratia 2008). The rays between these two rays are branched up to six times. The segmentation of the innermost principal rays and the procurrent rays are straight, whereas the segmentation of the principal rays close to the leading edges (dorsal and ventral) is step-like or Z-shaped (comparable to *Thrissops*



**Figure 13.** Caudal fin of *Thrissops ettingensis* sp. nov. from the lower Tithonian of Ettling, Markt Pförring, Bavaria, Germany. **A.** Photo of holotype JME-ETT3345a; **B.** Drawing of holotype JME-ETT3345a; **C.** Photo of JME-ETT4104a; **D.** Drawing of JME-ETT4104a.

*formosus* Ebert and Kölbl-Ebert 2010a, fig. 3). The proximal base of the ventralmost dorsal ray (ray 10) bears a small dorsal process, while the proximal bases of the dorsal rays five to nine are bent ventrally. The bases of the innermost two rays (rays 10, 11) are broadened. The unsegmented ray bases of the median rays are entirely covered by scales, whereas the unsegmented bases of the marginal rays are covered by scales only in their anterior two thirds.

There is one dorsal and one ventral caudal scute (best visible in JME-ETT4104a).

The skeleton supporting the caudal fin rays is composed of six vertebrae with two ural centra being involved in supporting the fin rays. The first ural centrum consists of the fused centra U1+U2 on which hypurals H1 and H2 are attached posteroventrally. The posteriormost ural centrum is the smallest centrum nearly completely covered by the uroneurals and the process of dorsal hypurals.

There are at least seven hypurals (H1–7) visible in JME-ETT3354a (Fig. 13A) and eight hypurals (H1–8) in JME-ETT4104a (Fig. 13B). The ventralmost three hypurals have well-developed articular heads which rest on U1–U3, and are developed as a thickening along its anteroventral edge. The heads of these hypurals are so broad that they are in contact with each other and enclose parts of the corresponding ural. The anteriormost two hypurals (H1, H2) attach the fused ural centra 1+2 (U1+2). Whereby in the holotype (JME-ETT3345a) the anterior bases of these two hypurals are separated with two separate heads (Fig. 13A), in JME-ETT4104a the anterior bases of H1 and H2 have grown together to form a joint head (Fig. 13B). The anteriormost two hypurals project posteroventrally, whereas the hypurals H3–8 joint the ural centrum (U3) and project posterodorsally, so there is a narrow and deep caudal diastema between the H2 and H3. The dorsalmost

hypurals (H5–8) are nearly completely covered by uroneurals and fin rays. In addition, there is a very thin layer of scales on all elements of the caudal skeleton, so that the boundaries of these small bones can hardly be seen.

All haemal spines, the parhypural and the hypurals are clearly separated from the centra. Hypurals H1 and H2, the parhypural and the posteriormost three haemal spines are close together with almost no gap between them.

The parhypural is located at the preural centrum one, with the associated neural spine being significantly shortened.

All hypurals, the parhypural and the posteriormost three haemal spines are wider than the haemal spines more anteriorly. The hypural H1 is particularly wide and becomes twice as wide posteriorly where the anterior bases of six lepidotrichia rest.

There are six elongated uroneurals covering the dorsal surface of the urals and preurals PU1–4. These six uroneurals have approximately the same diameter, with the middle ones (U3, U4) being the longest. The anteriormost uroneural extends with its anterior end to preural centrum PU4.

One short urodermal lies on the surface of the first principal ray in JME-ETT3345a or slightly anterior to it on the posterior procurrent rays in JME-ETT4104a. The urodermal is the only element in the area of the caudal skeleton that is not covered by scales.

Dorsal to the uroneurals there are two elongated epurals which are dorsally covered by procurrent rays.

On preural centrum PU1, only a part of the neural arch is visible. A neural spine is absent. PU2 has a long neural spine, as have all vertebrae anterior to it.

**Squamation.** The cycloid scales of the body are thin, deeper than long and comparably large. The number of scales in the body axes is not countable exactly, but it corresponds approximately the number of vertebrae. The highest number of scales in a single transverse scale row from dorsal to ventral is about 15 between skull and dorsal fin, whereas there are only ten scales per transverse scale row in the area between the dorsal, anal and caudal fin. The anteroventral body scales are smooth, whereas most body scales have up to nine thin, elongated furrows that originate from an anterior point of a scale and radiate posteriorly, most prominently between the dorsal and anal fins (Fig. 8). Each scale of the body has a dark spot in the center, which is interpreted as “melanophores (chromatophores containing the dark pigment melanin)” (Tischlinger 1998: 1) and was probably a color pattern visible along the body axis with 10–15 lines with dots (in *Thrissops ettlingensis* best visible in JME-ETT3345a (Fig. 8) and JME-ETT220 (Fig. 9B). This color pattern of Ettlingle fishes was already described for *Thrissops formosus* by Tischlinger (1998) and Ebert et al. (2015).

**Sensory canals and lateral line.** The supraorbital sensory canal runs along the lateral margin of the frontal. The parietal branch of the supraorbital sensory canal is well developed and clearly visible in the holotype (Fig. 11), ending in the anteroventral part of the parietal. The preopercular sensory canal is with nine or ten ventral branches very well visible in the horizontal limb of the preoperculum in the holotype, whereas the sensory canal in the dorsal limb

is less visible. The mandibular sensory canal runs anterior-posteriorly within a groove nearly within the middle of the dentary. It is clearly visible along its entire length in the transparent bone, and in some places pores open to the surface. The infraorbital sensory canal runs alongside the posterior and ventral orbital edges within the infraorbital bones. Branches, probably present in infraorbital 3 are hardly visible. A connection between the infraorbital and supraorbital canals is not visible.

The main lateral line along the body comes from the parietal, runs through the extrascapular, posttemporal, and the subcleithrum and is then visible as an indentation in the scales directly above the vertebrae on to the caudal fin (Figs 8, 11).

**Prey.** There is one single, quite large prey fish of *Orthognikleithrus hoelli* in each of the stomachs of two specimens of *Th. ettlingensis*. In JME-ETT166 this single prey fish is well visible (Fig. 9A; Ebert and Kölbl-Ebert 2013, fig. 4b). In JME-ETT3345 the prey fish is already half digested, but here too there appears to be only one single prey fish in the stomach (see comparison with *Th. formosus* in discussion section below). In addition, the intestines in both fishes are filled with almost completely digested fish remains.

### *Thrissops kimmeridgensis* sp. nov.

<https://zoobank.org/15DD4296-8A51-49C7-A1EB-F4E12ABBB9FE>  
Figs 14A–C, 15A–D, 19A, B, D, 20C, 22A, B

1895 *Thrissops* sp.; Woodward: p. 527–528.

1977 undetermined specimen of *Thrissops*; Patterson and Rosen: p. 100 (NHMUK PV P.54597).

1984 *Thrissops* sp.; Schaeffer and Petterson: fig. 27J.

2013 *Thrissops* sp.; Cavin, Forey and Giersch: p. 156, figs 32, 33.

2018 “*Thrissops*” from Kimmeridge; Yabumoto et al.: figs 7, 8.

2019 *Thrissops* from Kimmeridge; Cavin and Berrell: p. 12, fig. 9.

2020 *Thrissops* sp.; Martill and Brito: text fig. 3.26C.

2024 *Thrissops* “Kimmeridgian”; Alvarado-Ortega: p. 27, fig. 16.

**Holotype.** MJML K2295.

**Type locality.** Kimmeridge, Isle of Purbeck, Dorset, England.

**Type horizon.** Upper Kimmeridgian.

**Formation.** Kimmeridge Clay, Dorset, England.

**Determination** (for comparison of taxa see Table 1; for measurements of specimens and counts of features see Suppl. material 1: table S1). Maximum length 75.5 cm standard length (~90 cm total length); ~55–57 vertebrae (without ural centra); ~25–28 ribs anterior to anal fin; 29–30 anal pterygiophores; dentary with anterior hook armed with one large fang-like, posteriorly directed tooth; dentary teeth of irregular size, with the most anterior tooth and the teeth in the middle of the dentition being twice the size of the other dentary teeth (Figs 15A–D, 19A, B, D); curved maxilla with small teeth all in the same size (Figs 15A–D, 19A, B, 20C).

**Etymology.** The specific epithet in *Thrissops kimmeridgensis* refers to the village of Kimmeridge, Dorset, England where most of the specimens were found.



**Figure 14.** *Thrissops kimmeridgensis* sp. nov. from Kimmeridge, Dorset, England. **A.** MJML K2295 (holotype); **B.** MJML K2138; **C.** MJML K1653.

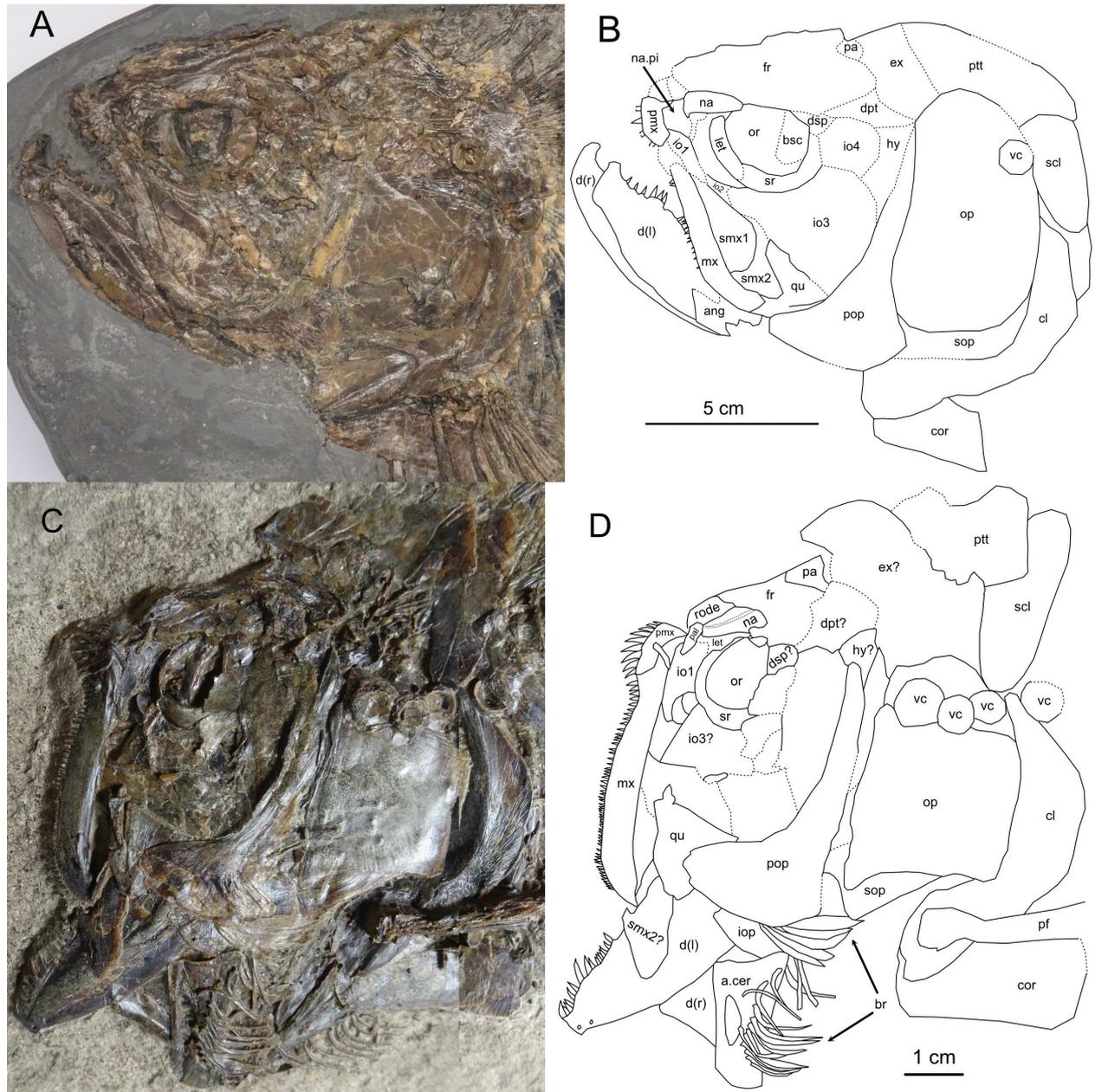
**Additional material.** MJML K26, 276, 306, 379, 452, 454, 518A, 518B, 525, 531C, 535, 547, 574, 575, 944, 949, 969, 998, 1001, 1002, 1015, 1069, 1085, 1129, 1142, 1155, 1159, 1167, 1173, 1194, 1196, 1230, 1282, 1283, 1290, 1301, 1304, 1313, 1316, 1338, 1373, 1378, 1379, 1395, 1407, 1419, 1439, 1440, 1456, 1506, 1520, 1521, 1534, 1550, 1590, 1653, 1669, 1672, 1676, 1677, 1690, 1714, 1745, 1786, 1792, 1804, 1839, 1925, 1934, 1946, 1981, 2003, 2022, 2063, 2079, 2119, 2138, 2167, 2294, 2333, 2399, 2491, 2700, 2770; NHMUK PV P.922, P.3686, P.3686a, P.54596, P.54597, P.54598, P.54599, NHMUK PV OR 40336, 40720.

**Features.** The features of *Th. kimmeridgensis* are very similar to the other Upper Jurassic *Thrissops* species described above (for the most distinguishing features see Table 1). The cranial features of *Th. kimmeridgensis* are described and figured in detail in Cavin et al. (2013), especially the ethmoid region.

Here, I add two drawings of the cranium of *Th. kimmeridgensis*; one of the holotype (MJML K2295; Fig. 15A, B), the other of the slightly disarticulated cranium of MJML K1456 (Fig. 15C, D). Additionally, I figure the jaws and dentition of three specimens (MJML K1129, Fig. 19A; MJML K2119, Fig. 19B; MJML K1313, Fig. 19D), and the shape of the maxilla (Fig. 20C). In the following, I only describe features characteristic for *Th. kimmeridgensis* or which are not visible in the other above-described species.

**Irregular size of dentary teeth.** The irregular size of the dentary teeth, the most striking feature to distinguish *Th. kimmeridgensis* from *Th. formosus* and *Th. ettingensis*, was already recognised in Schaeffer and Petterson (1984, fig. 27J) and Cavin et al. (2013, fig. 33C) (see discussion in chapter discussion of features below).

**Anterior ceratohyal.** The anterior ceratohyal is visible in some of the partially disarticulated craniums of



**Figure 15.** Cranium of *Thrissops kimmeridgensis* sp. nov. from Kimmeridge, Dorset, England. **A.** Photo of holotype (MJML K2295); **B.** Drawing of holotype; **C.** Photo of MJML K1456; drawing of MJML K1456.

*Th. kimmeridgensis* (MJML K1173, 1205, 1283, 1313, 1456, 1786, 1946, 2119). It is a rectangular bone, nearly two times longer than high, and has an ovoid foramen near the center (Fig. 15C, D). In MJML K1456 a series of at least 13 elongated and dorsally bent branchiostegal rays are articulated proximally to the lateral surfaces of the anterior ceratohyal (Fig. 15C, D).

**Posterior ceratohyal.** The posterior ceratohyal or parts of it are visible in MJML K1173, 1313, 1456 (Fig. 15C, D), and 1946 (best visible in MJML K1173, 1946). It is a nearly reniform bone, which is broader than the anterior ceratohyal. At least the posteriormost five branchiostegals, which are twice as broad as the branchiostegals anterior to it, are articulated to the lateral surface of this bone.

**Gill arch.** Remains of the gill arch are visible in two specimens represented by rod-like elements of different length (MJML K1313, Fig. 19C; MJML K1407) probably epibranchials, hypobranchials and ceratobranchials). In MJML 1407 the ceratobranchials bear gill filaments.

**Preservation.** Of *Th. kimmeridgensis* only few are preserved as complete fish (Fig. 14), most of the specimens listed under additional material are preserved as isolated crania or caudal fins. It seems reasonable to assume that these are the remains left by larger predators, which are well known from the same sites in the Kimmeridge Clay (for example crocodiles, ichthyosaurs, plesiosaurs, pliosaurs and sharks; Martill and Etches 2000).

**Table 1.** Features to distinguish the different taxa of Upper Jurassic Ichthyodectiformes (updated from Ebert and Kölbl-Ebert 2013; individual specimens see Suppl. material 1: table S1).

Species name	Locality	max. SL cm	SL/BD %	SN	AP	TV	AV	CV	UD	Ribs	Teeth
<i>Thrissops formosus</i>	Br, Ei, Et, Ke, Pa, So	43	20-26	37-40	28-31	57-60	32-34	25-26	1	28-31	small
<i>Th. formosus</i>	Cerin	~67	16-25	39-40	30-31	59-61	32-36	25-26	?	31-32	small
<i>Th. cf. formosus</i>	Wattendorf	~50	24	41	30	59	35	24	?	32	small
<i>Th. subovatus</i>	Ei, Et, Ke, Pa, So, Za	35	26-29	38-40	29-32	59-60	33-34	26-27	1	30-31	large
<i>Th. ettlingensis</i>	Ettling	13	26-33	30-31	23-25	49-50	26-27	23-24	1	24-25	small
<i>Th. cirinensis</i>	Cerin	18.5	36	32	27	52	28	24	?	24	large
<i>Th. curtus</i>	Isle of Portland	13	29	?	26	52 or 53	28 or 29	~24	?	22	small
<i>Th. kimmeridgensis</i>	Kimmeridge	~75.5	22-27	?	29-30	~55-57	?	?	?	~25-28	small
<i>Allothrissops mesogaster</i>	Ei, So	25	15-23	?	24-26	58-59	33-34	25-26	1	28-30	small
					max 25						
<i>A. salmoneus</i>	Ei, So	31.5	17-18	?	27-30	59-60	33	26-27	?	30-31	small
<i>A. regleyi</i>	Cerin	23	19-27	~32	29-31	52-54	28-30	23-25	2?	24-25	small
<i>Allothrissops</i> sp.	Kelheim	19.5	18-23	?	25-27	56-57	31-32	25	?	26-29	small
<i>Allothrissops</i> sp.	Zandt	28	15-19	?	27-28	59-60	33-35	26	?	31	small
<i>Allothrissops</i> sp.	Ettling	23	17-19	~32	27-28	57-58	32	25-26	2	29	small
<i>Occithrissops willsoni</i>	Wyoming USA	~20	22-23		18-20	56	33-34	22-23			small

**Abbreviation of features:** AP, number of anal pterygiophores; AV, number of abdominal vertebrae; CV, number of caudal vertebrae; max. SL, maximal standard length (cm); Ribs, number of abdominal ribs; SL/BD, standard length in relationship to body depth; SN, number of supraneurals; Teeth, size of teeth; TV, number of total vertebrae (without ural centra); UD, number of urodermals. **Abbreviation of localities:** Br, Brunn; Ei, Eichstätt; Et, Ettling; Ke, Kelheim; Pa, Painten; So, Solnhofen; Za, Zandt.

**Thrissops specimens from further Upper Jurassic localities.** The following *Thrissops* specimens are probably independent species. However, since only a few specimens from these localities are known and mostly in poor preservation, they are still awaiting revision.

***Thrissops cf. formosus*** (late Kimmeridgian, **Wattendorf**, Bavaria Germany): NKMB (Wattendorf specimen, see Mäuser 2015, fig. 1014).

***Thrissops? curtus* Woodward, 1919** (Tithonian, Purbeck and Portland, Dorset, England): NHMUK PV P.417a (holotype of *Thrissops molossus* Woodward, 1919; Fig. 16D), P.8381, P.10612 (holotype; Fig. 16A).

***Thrissops portlandicus* Woodward, 1895** (Tithonian, Isle of Portland, Dorset, England): NHMUK PV P.5538a (holotype; Figs 16B, C).

***Thrissops* sp.** (early Tithonian, **Creys**, France): OSUG (UJF-ID. 16053\*).

***Thrissops* sp.** (early Tithonian, **Daiting**, Bavaria, Germany): coll. Tischlinger 76/72, 88/91; SNSB-BSPG 1964 XXIII 508.

***Thrissops* sp.** (Tithonian, **Purbeck**, Dorset, England): NHMUK PV P.12643.

### ***Allothrissops* Nybelin, 1964**

Figs 17A, B

**Type species.** *Allothrissops salmoneus* (Blainville, 1818b)

**Remarks.** The Upper Jurassic genus *Allothrissops* Nybelin, 1964, is problematic and needs to be revised. The existing literature has probably caused more confusion than clarity, because some important authors on

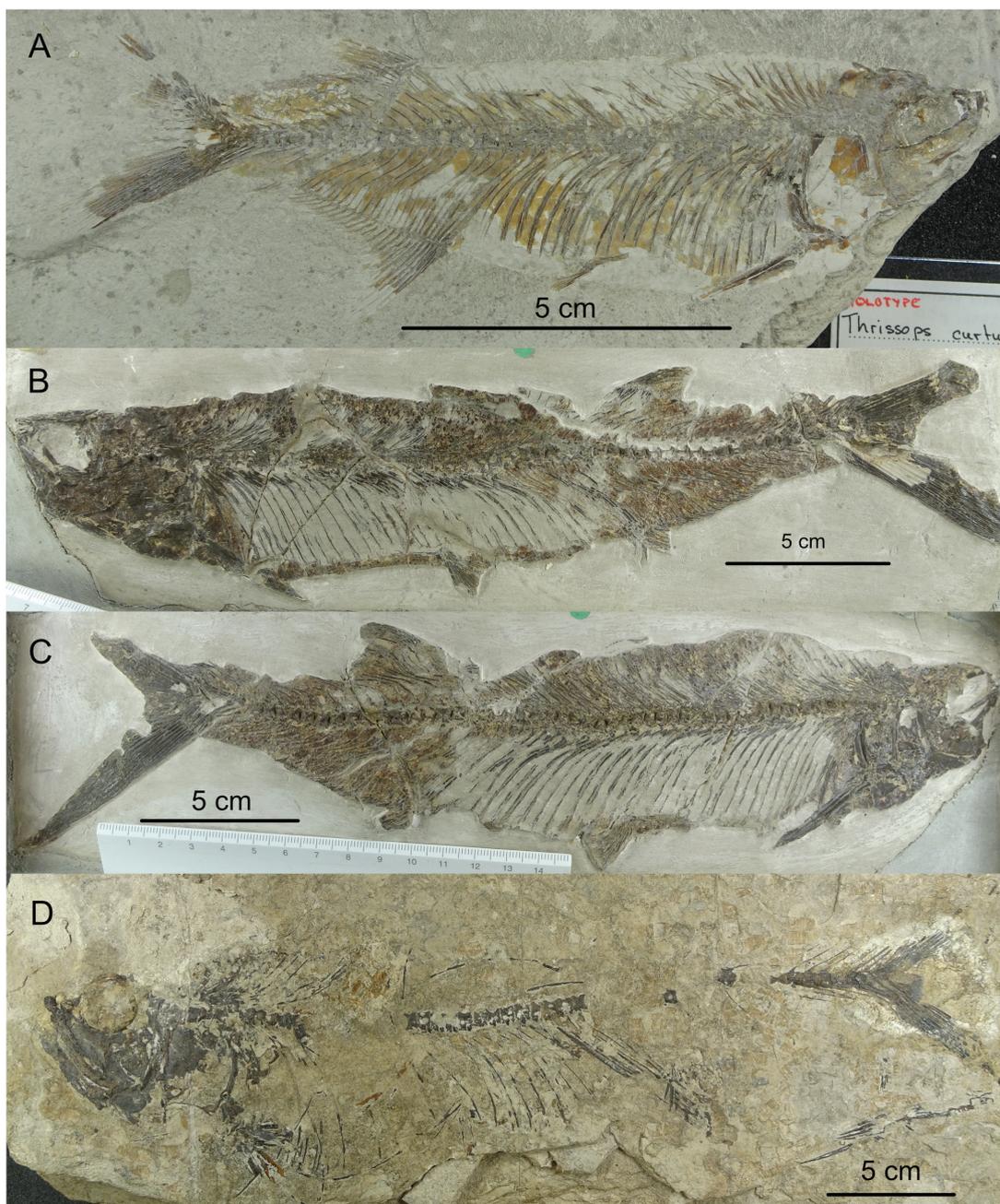
this taxon (Blainville 1818a,b; Agassiz 1833–43 and Nybelin 1964) described fish from different species under the name of the type species *Allothrissops salmoneus* (Blainville, 1818b).

The holotype of the type species *Allothrissops salmoneus* (Blainville, 1818b) which is figured in Knorr (1755, pl. 31, fig. 1) is lost. Unfortunately, the illustration in Knorr (1755) does not show any diagnostic feature on species level. The specimen was most likely from Zandt (Zandt Basin, Solnhofen Archipelago, for localities see Fig. 1) due to the Liesegang rings typical for the Plattenkalk of Zandt depicted in Knorr (1755). The neotype (NHMUK PV OR 37078), proposed by Nybelin (1964), however, came from the Solnhofen Basin of the Solnhofen Archipelago (Fig. 1).

Blainville (1818a, p. 331) first names this species "*Clupea elongata*". But since the species *Clupea elongata* Sesueur, 1818 (later recognized as synonymous with *Clupea harengus* Linneus, 1758) was described in the same year, Blainville (1818b, p. 27) renamed his species *Clupea salmonea*.

Nybelin (1964) split the genus *Allothrissops* from *Thrissops* Agassiz, 1833 with the species *Allothrissops salmoneus*, *A. mesogaster* both from Southern Germany and *A. regleyi* from Cerin, France.

However, the species *Thrissops salmoneus* described by Agassiz (1833) is not identical to the species *Allothrissops salmoneus* described by Nybelin (1964). All *Th. salmoneus* specimens, which Nybelin (1964) mentioned in his investigations originate from Eichstätt or Solnhofen, whereas those figured in the unpublished drawings intended for Agassiz's work LDGSL/614/2/167, LDGSL/614/2/168 come from Kelheim (except for a specimen in Prague LDGSL/614/2/166



**Figure 16.** *Thrissops* species from Purbeck and Portland of Dorset, England. **A.** *Thrissops? curtus* Woodward, 1919 holotype (NHMUK PV P.10612); **B.** *Thrissops portlandicus* Woodward, 1895 holotype (NHMUK PV P.5538a-1); **C.** *Thrissops portlandicus* Woodward, 1895 counterpart (NHMUK PV P.5538a-2); **D.** *Thrissops molossus* holotype (NHMUK PV P.417a).

(NMP Uc64, missing today, see Ebert et al. 2022, fig. 18) which comes from Solnhofen, but cannot be determined more precisely due to its poor preservation. The unpublished drawings to Agassiz (1833–43) work are today in the Geological Society of London’s collection and online available (refs: LDGSL/613–616).

Evidence for the different interpretations of the species *A. salmoneus* may also be that Agassiz (1843, p. 128) says *Allothrissops mesogaster* is more elongated than *A. salmoneus* (“*Thrissops mesogaster* ... une espèce très-voisine du *Th. salmoneus*, mais un peu plus allongée...”), whereas Nybelin (1964) described it the other way around.

#### ***Allothrissops mesogaster* (Agassiz, 1834)**

**Note.** Agassiz (1834) erected the nominal species *Thrissops mesogaster* with a brief description indicating its distribution in the Solnhofen limestones but without reference or illustration to a particular specimen. The first reviewer of this taxon, Nybelin (1964) refer the species to the genus *Allothrissops* and fixed the specimen NHMUK PV P.3679 as its lectotype.

Further specimens probably belonging to the type series of *Allothrissops mesogaster* are recognised in Ebert et al. (2022).

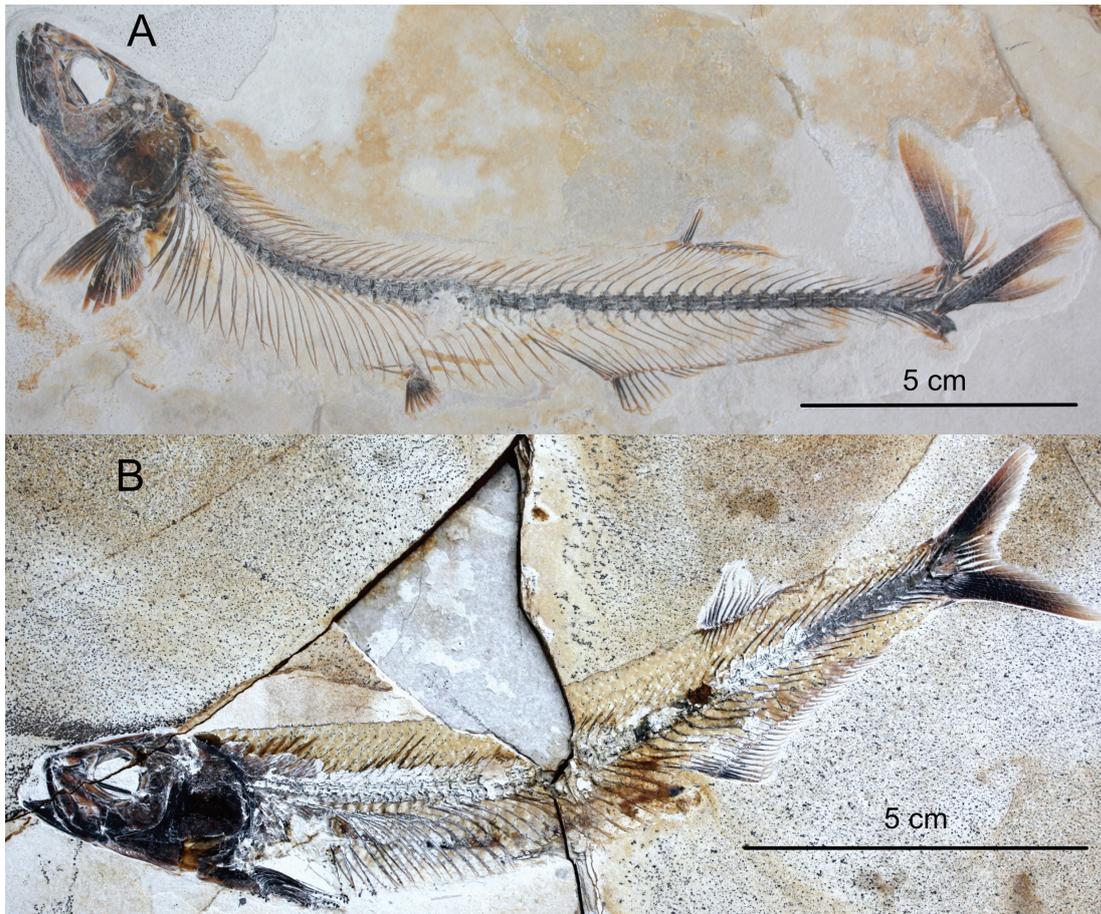


Figure 17. *Allothrissops* sp. from Ettling, Bavaria, Germany. A. JME-ETT874; B. JME-ETT253.

## Comparison and discussion

### Comparison of Jurassic Ichthyodectiformes

For overview see Table 1.

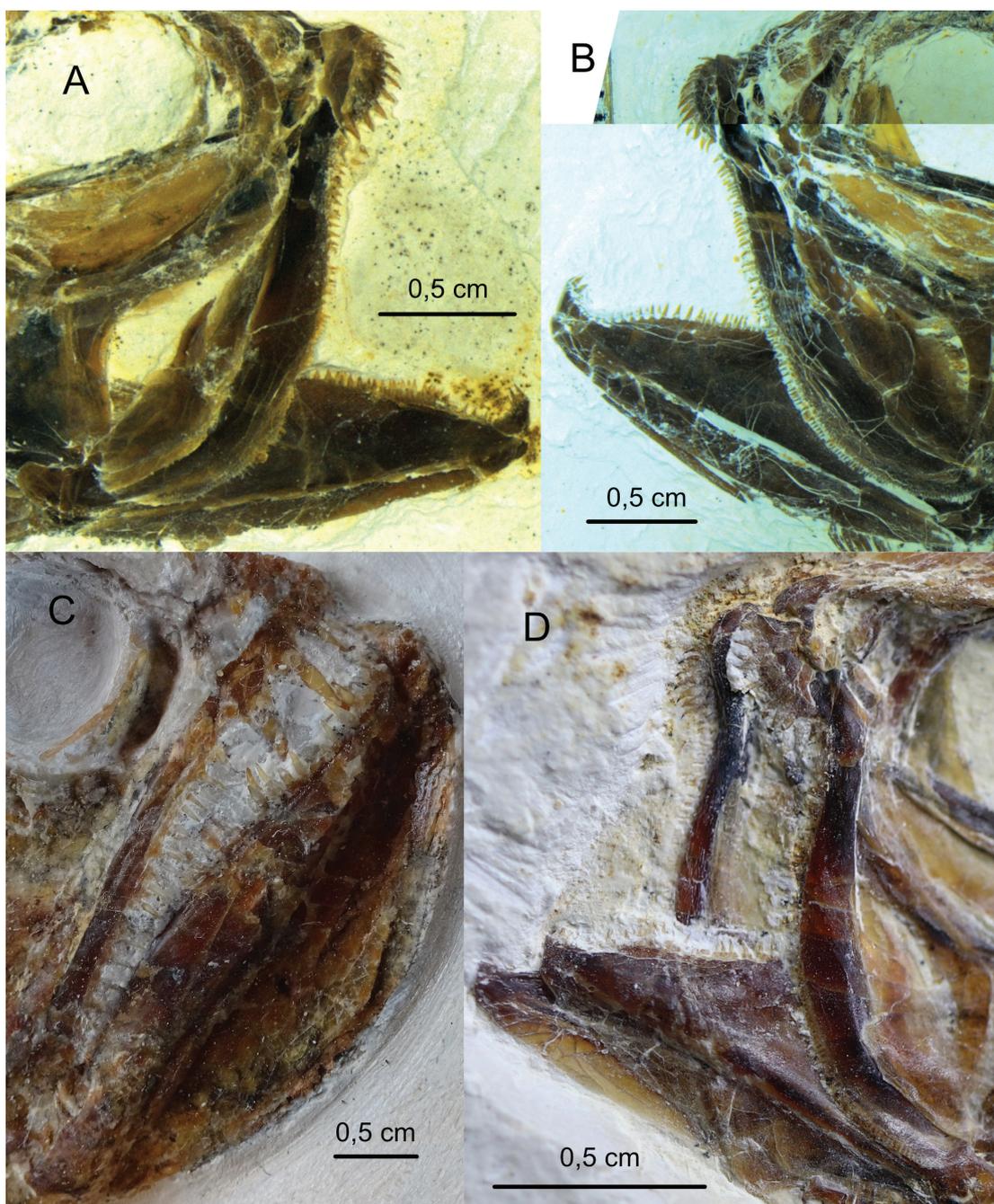
*Thrissops ettlingensis* sp. nov. and *Thrissops kimmeridgensis* sp. nov. are Ichthyodectiformes because they show all the important features of Ichthyodectiformes reported in Alvarado-Ortega (2024, p. 28–29) “features of Ichthyodectiformes previously documented by now classical researchers of the order (Bardack 1965; Bardack and Sprinkle 1969; Patterson and Rosen 1977; Schaeffer and Petterson 1984; Maisey 1991), such as an elongated and uniformly high body with a relatively small head, jaws with a single tooth row, the deeply bifurcated caudal fin, and unpaired fins placed far back on the trunk and opposed to each other ..., a pair of ethmopalatine bones forming the floor of the nasal capsule and ... broad or saber-like shape of the first rays in the pectoral and pelvic fins.” Only the elongated body shape and the shape of the first rays in the pectoral and pelvic fins are not expressed in the small new species *Thrissops ettlingensis*.

Both new species belongs to the genus *Thrissops* because they share with the genus the features described above in the diagnosis of the genus *Thrissops*.

*Thrissops ettlingensis* differs from other *Thrissops* species mainly in the size and shape of the body; a smaller number of vertebrae centra (49–50), particularly a smaller number of vertebrae between skull and anal fin and the associated abdominal ribs (24–25); and a smaller number of anal fin rays or the associated anal pterygiophores (23–25).

*Thrissops kimmeridgensis* sp. nov. is very similar in proportions and body shape to *Th. formosus*, but this new species differs from *Th. formosus* especially in a notably irregular dentition in the lower jaw with one large fang tooth anteriorly and larger teeth in the middle of the dentary (see description of new species above and discussion of irregular dentition below). From *Thrissops subovatus* it differs in the maxilla shape (Figs 18, 19; which is straighter in *Th. subovatus*, Figs 18C, 20D), a hook developed on the anterior tip of the dentary (which is not developed in *Th. subovatus* and *Th. ettlingensis*) and the teeth of the maxilla which are in *Th. kimmeridgensis* smaller and more numerous than in *Th. subovatus*.

*Occithrissops willsoni* Schaeffer & Patterson, 1984 from the Middle Jurassic of the Sundance Formation, near Hulett, Wyoming, USA is the stratigraphically oldest known Ichthyodectiformes. *Occithrissops* has with 18–20 the lowest number of anal pterygiophores within Ichthyodectiformes (see Schaeffer and Petterson 1984).



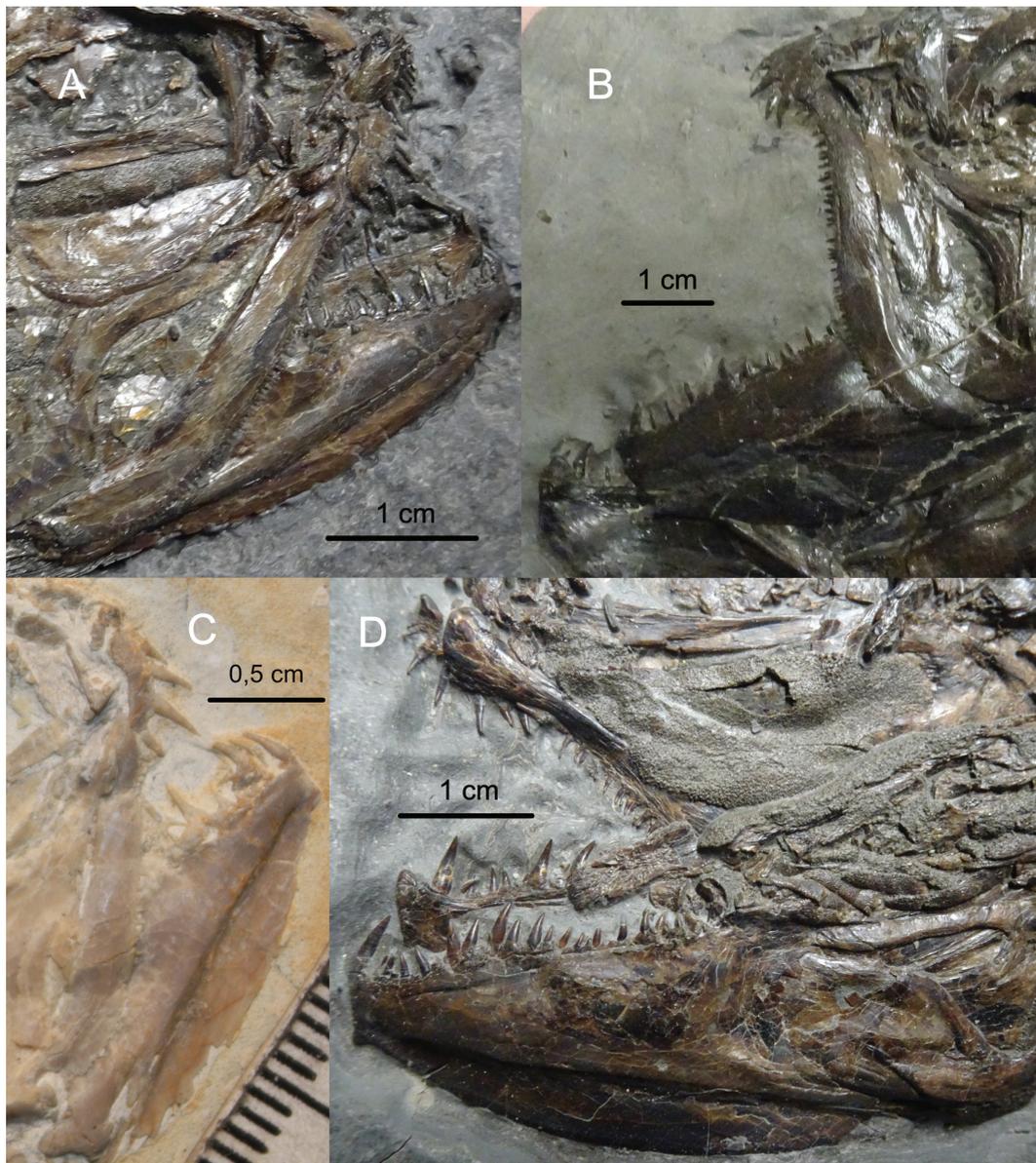
**Figure 18.** Jaws and dentition of *Thrissops* from the Solnhofen Archipelago, Bavaria, Germany. **A.** *Th. formosus* (JME-ETT1805) from Ettling; **B.** *Th. formosus* (JME-ETT887) from Ettling; **C.** *Th. subovatus* (LF 1469) from Eichstätt; **D.** *Th. ettlingensis* (JME-ETT3345a) from Ettling.

Next in line is the new species *Thrissops ettlingensis* described here, with 23–25 (see Table 1). The number of anal pterygiophores in the Upper Jurassic reaches 32 and increases in the Cretaceous to a maximum of 42 (Cavin et al. 2013, table 2).

***Thrissops formosus*** has a regular dentition with small teeth (Fig. 18A, B) and a bow-shaped maxilla (Fig. 20B) comparable to *Th. ettlingensis*, but it differs from *Th. ettlingensis* in a higher number of vertebrae centra and anal pterygiophores.

***Thrissops subovatus***. The main distinguishing features between *Th. subovatus* and the other species of the

genus is a nearly straight dorsal and ventral border of the maxilla (Fig. 20D) with comparably large teeth (Fig. 18C), only the posteriormost part of the maxilla bents dorsally. The differences in maxilla shape and size of the teeth of *Th. subovatus* was already figured in Nybelin (1964, pl. 5, fig. 3) and Taverne (2008, fig. 9). The teeth on the premaxilla and dentary are likewise larger and less numerous than in other *Thrissops* species (except *Th. cirinensis*). The skull is a little shorter (anterior posteriorly) in *Th. subovatus*, especially the opercular apparatus; and the vertebrae column first bends slightly downwards before turning into the upper caudal lobe (Fig. 6A).



**Figure 19.** Jaws and dentition of *Thrissops* from Kimmeridge, Dorset, England and Cerin, France. **A.** *Th. kimmeridgensis* sp. nov. (MJML K1129) from Kimmeridge; **B.** *Th. kimmeridgensis* (MJML K2119) from Kimmeridge; **C.** *Th. cirinensis* (MNHN CRN66) from Cerin; **D.** *Th. kimmeridgensis* MJML K1313 from Kimmeridge.

*Thrissops cirinensis* differs from the other *Thrissops* species mainly in the shape of the body (Fig. 7), the standard length to body depth is 36% (Table 1); a small number of vertebrae, abdominal ribs and anal pterigophores (only *Th. ettlingensis* has fewer, see Table 1); and the largest teeth in the premaxilla and dentary of this genus (Fig. 19C), whereas the maxillary teeth are small.

### Comments to the *Thrissops* species mentioned in table 2 in Alvarado-Ortega (2024)

Alvarado-Ortega (2024, table 2) mentioned in his table 11 nominal valid *Thrissops* species, but I can confirm only four of them without doubt to the genus *Thrissops*.

*“Thrissops cephalus* Agassiz, 1843 Oxfordian. England”:

This taxon is from the Tithonian of Eichstätt and Solnhofen and I agree with Wagner (1863) and Nybelin (1964) that it is a juvenile of *Allothrissops mesogaster*.

*“Thrissops cirinensis* Nybelin, 1964 (see Taverne, 1977) Kimmeridgian. Germany”:

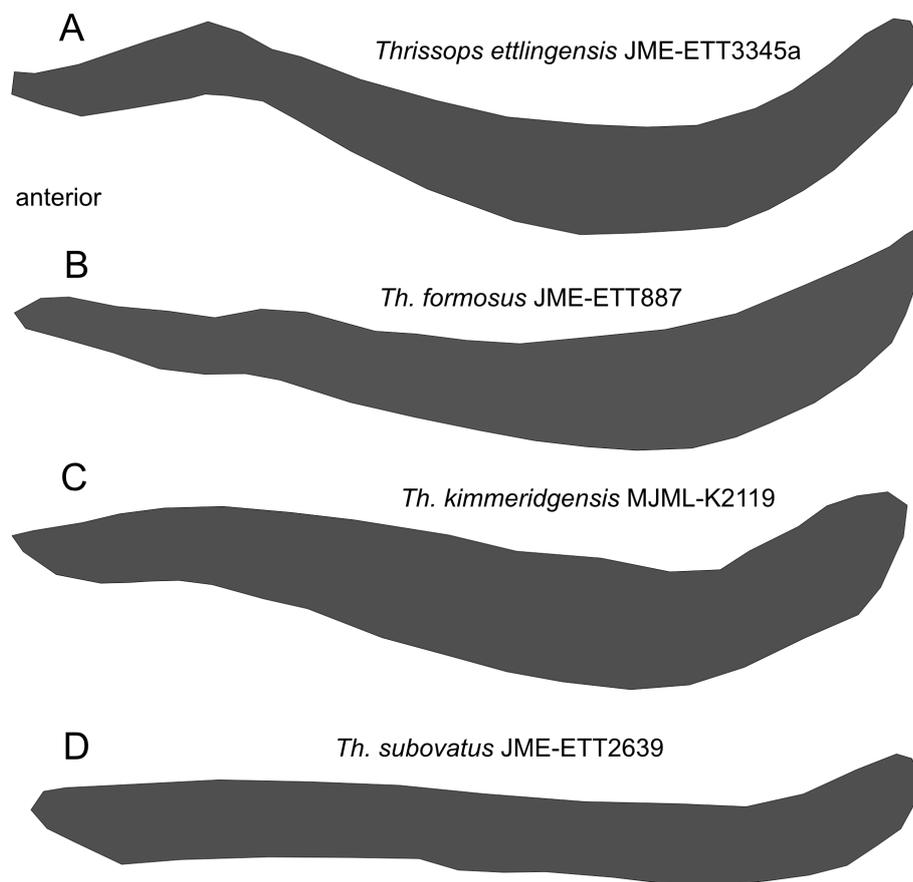
This valid species is from Cerin (France).

*“Thrissops costalis* Egerton, 1845 Oxfordian. England”:

The holotype (NHMUK PV P.3676), first described as *Lep-tolepis costalis* Egerton, 1845 from the Oxford Clay of Christian Malford, Wiltshire, England, is an indeterminate, elongated Teleostei with the jaws and fins missing. In my opinion this fish does not belong to the genus *Thrissops*.

*“Thrissops curtus* Woodward, 1919 Portlandian. England”

sensu Cavin et al. (2013): Its inclusion within the genus *Thrissops* cannot be justified.



**Figure 20.** Maxilla shape of different Upper Jurassic *Thrissops* species. **A.** *Th. formosus* (JME-ETT1805) from Ettling; **B.** *Th. formosus* (JME-ETT887) from Ettling; **C.** *Th. subovatus* (LF 1469) from Eichstätt; **D.** *Th. ettingensis* (JME-ETT3345a) from Ettling.

"*Thrissops exiguus* Bassani, 1879 Cenomanian. Slovenia" belongs most probably to the genus *Chirocentrites* Heckel, 1849.

"*Thrissops formosus* Agassiz, 1833 (see Taverne, 1977) Kimmeridgian. Germany": This species is from Kimmeridgian and Tithonian of Germany and France.

"*Thrissops gracilis* Heckel, 1849 Cenomanian. Slovenia" sensu Cavin et al. (2013): This species is synonymous to *Chirocentrites coroninii* Heckel, 1850 and belongs to the genus *Chirocentrites*.

"*Thrissops portlandicus* Woodward, 1895 Portlandian. England": Tithonian of the Isle of Portland, England.

"*Thrissops rochei* Sauvage, 1893 Kimmeridgian. France" sensu Bardack (1965, p. 33) from the "Kimmeridgian at Orbagnoux, Ain, France; Present location of holotype and sole specimen unknown; validity of this species uncertain.": In my opinion the holotype of *Th. rochei*, which is in the Muséum d'Histoire Naturelle Jacques de la Comble, Autun, France (MHNA.PAL.2019.0.39), belongs to the genus *Allothrissops* and is very similar to *Allothrissops regleyi* from Cerin, Ain, France.

"*Thrissops subovatus* Münster (in Agassiz, 1843) (see Taverne, 1977) Kimmeridgian. Germany": This species is known from the Kimmeridgian and Tithonian of the Solnhofen Archipelago.

"*Thrissops volganensis* Koslov, 1928 Portlandian. Russia": Bardack (1965, p. 33) noted concerning this taxon

"Lower Volgian (=Portlandian) near Gorodische, Government of Ulyanovsk, USSR; (5) if actually a *Thrissops*, this is the easternmost representative of the genus; only the holotype, an incomplete and poorly preserved specimen is known."

## Discussion of some features and peculiarities of *Thrissops*

**Dentary with anterior hook** (Figs 3, 15, 18A, B, 19B, D). The anteriormost tip of the dentary is slightly hook-shaped in all specimens of *Thrissops formosus* and *Th. kimmeridgensis*, where this part of the cranium is preserved. On this dorsally curved hook there are one or two posteriorly directed teeth. In *Th. formosus* there are two teeth which have approximately the same size as the other dentary teeth (Figs 3, 18A, B). On *Th. kimmeridgensis* this hook has one large, fanglike, posteriorly curved tooth (Figs 19A, B, D). Cavin et al. (2013, p. 159) already mentioned these "fanglike, posteriorly curved teeth" in *Th. kimmeridgensis* (there *Thrissops* sp.) on the dentary of NHMUK PV P.54598. In *Th. subovatus* and *Th. ettingensis* this hook is barely developed. In salmonids this hook-like structure is called kype. It develops at the distal tip of the lower jaw in some male salmonids prior to the spawning season. The structure usually develops in the weeks prior to, and

during, migration to the spawning grounds (Witten and Hall 2003). The hook is not as pronounced in *Thrissops* as in salmonids, and it cannot be said whether or not it served the same purpose of attracting females. In *Th. ettingensis* it may simply be advantageous for grabbing prey.

**Regular or irregular dentition in the lower jaw.** *Thrissops kimmeridgensis* (best visible in MJML K276, K379, K547, K1001, K1069, K1129 (Fig. 19A), K1155, K1167, K1194, K1196, K1283, K1283, K1290, K1313 (Fig. 19D), K1419, K1440, K1456 (Fig. 15C, D), K1534, K1669, K1786, K1797, K1925, K1946, K2063, K2119 (Fig. 19B), K2138, K2295 (Fig. 15A, B), K2399; NHMUK PV P.54597, 54598, 54599), *Th. subovatus* (NMS 1905.83.12, CM 4030, MMG-SNSD BaJ 2115), and *Th. cirinensis* (holotype) have a notably irregular dentition in the lower jaw (character 14 in Alvarado-Ortega and Brito 2010) with the anteriormost one or two teeth and one to four teeth in the middle of the dentary being two times larger than the other dentary teeth. The Ichthyodectiformes *Ogunichthys triangularis* Alvarado-Ortega & Brito, 2010 from the Cretaceous of Brazil, *Eubiodectes libanicus* (Pictet & Humbert, 1866) from the Cretaceous of Lebanon (see Cavin et al. 2024) and *Cladocyclus* sp. (AMNH 9981; Patterson and Rosen 1977, fig. 8), have a notably irregular dentition in the lower jaw as well. Already Nybelin (1964) described the irregular dentition in *Th. subovatus* and *Th. cirinensis*. In *Thrissops formosus* (Figs 3, 4, 18A, B), *Th. ettingensis* (Figs 11, 12), *Occithrissops willsoni* (Schaeffer and Petterson 1984, fig. 27C), and the *Allothrissops* species (Schaeffer and Petterson 1984, fig. 27K, L), these teeth are almost regular in size, only the anteriormost teeth and the teeth in the middle might be slightly larger (Figs 3, 18B).

**Parietal.** According to Patterson and Rosen (1977) *Thrissops* and *Allothrissops* show paired parietals. Cavin et al. (2013, fig. 41A) as well shows “clearly separated parietals in NHMUK PV OR 36050 (now *Thrissops kimmeridgensis*). Other Ichthyodectiformes from the Cretaceous have an unpaired parietal median on the scull roof (see discussion of character and individual species in Cavin et al. 2013). In this article the specimen of *Thrissops formosus* (JME-ETT3371) with the cranium in dorsal view shows an unpaired parietal (Figs 4C, D). On the other hand, there may also be specimens of *Th. formosus* with paired parietals (Fig. 3B). Hopefully we find more specimens in dorsal view to show this feature more clearly. In *Amia calva*, Grande and Bemis (1998, figs 12, 13) also show specimens with paired and unpaired parietal.

**Gular plate.** A gular plate has not been described in Ichthyodectiformes before (Patterson and Rosen 1977; Arratia 1999). However, I think there is a small gular plate in *Thrissops formosus* (JME-ETT887, Fig. 3 and JME-ETT2942) and in *Thrissops ettingensis* (JME-ETT3345a, Fig. 11). This has to be confirmed by further specimens where this bone might be visible more clearly.

**Suborbital.** According to Patterson and Rosen (1977, p. 100), another difference between *Allothrissops* and *Thrissops* is that there is a suborbital in the latter but none in the former. A large suborbital is mentioned in *Thrissops*

sp. of the Kimmeridge Clay by Cavin et al. (2013, fig. 33C) and Patterson and Rosen (1977, p. 100). I agree with Taverner (1977) there is no suborbital in *Thrissops formosus* or *Th. subovatus* and I was not able to see a suborbital in any of the specimens of *Thrissops kimmeridgensis* sp. nov. of the Kimmeridge Clay with certainty.

**Supraorbitals.** One large suborbital was reported in Ichthyodectiformes by Alvarado-Ortega (2024) and Cavin et al. (2013). I was not able to observe suborbitals in any of the *Thrissops* species.

**Number of total vertebrae.** The number of vertebrae is an important feature to compare Ichthyodectiformes (see Table 1 and Cavin et al. 2013, table 2). *Thrissops ettingensis* is with 49–50 vertebrae the Ichthyodectiformes with the lowest number of vertebrae. All other *Thrissops* and *Allothrissops* species have with 52–61 the highest number of vertebrae among the Teleostei in the Upper Jurassic (see Table 1 and Ebert 2021). In the Cretaceous there are Ichthyodectiformes with more than 100 vertebrae (Cavin et al. 2013, table 2).

**Feature “body elongated and laterally compressed”** described as synapomorphy of Ichthyodectiformes in Yabamoto et al. (2018) is absent in *Thrissops cirinensis* Nybelin, 1974 with standard length (SL) to body depth (BD) of 36% and *Thrissops ettingensis* sp. nov. with 26–33% SL/BD (for comparison see Table 1). Probably this feature is not developed in some more basal Ichthyodectiformes. Alvarado-Ortega (2024) mentioned this feature as “non-exclusive body features of Ichthyodectiformes previously documented by now classical researchers of the order (Bardack 1965; Bardack and Sprinkle 1969; Patterson and Rosen 1977; Schaeffer and Petterson 1984; Maisey 1991, such as an elongated and uniformly high body...)”.

**Large specimens with strongly elongated caudal fin lobes.** There are some very large specimens of *Thrissops formosus* with strongly elongated caudal fin lobes. For example: In Ettlign JME-ETT75 (Fig. 2A) with 53 cm total length (TL); JME-ETT3340 (50 cm TL) and Cerin MHNL20015185 (80 cm TL, ~67 cm SL; holotype of *Thrissops heckeli* Thiollière 1854, pl. 10, fig. 1); MHNL20015760 (~52 cm SL, 66 cm TL); and UCBL-FSL 503200 (72.2 cm TL, 50.8 cm SL; Bernier et al. 2014, fig. 10a).

**Ventral lobe of caudal fin longer than dorsal lobe.** In some Ichthyodectiformes (*Thrissops formosus*, *Th. kimmeridgensis*, *Th. subovatus*, *Eubiodectes libanicus* (Pictet & Humbert, 1866)) the ventral lobe of the caudal fin is longer than the dorsal lobe (see overview in Cavin et al. 2013). In *Th. ettingensis* both lobes have the same length. However, in the other taxa the difference in the length of the lobes of the caudal fin is only pronounced in larger specimens.

**Neural spine of PU2.** Patterson and Rosen (1977, fig. 14) figured a short neural spine of preural centrum PU2 for *Th. formosus*. But this neural spine is probably broken off in their specimen NHMUK PV P.3684 and therefore only an artefact of preservation. I found neural spines of normal length in all Ettlign specimens of *Thrissops formosus* (for example Fig. 5A, B) and *Th. ettingensis* (Fig. 13A–D) where this area is preserved.

**Colour pattern.** A colour pattern of Ettlting fishes was already described for *Thrissops formosus* by Tischlinger (1998) and Ebert et al. (2015, fig. 7) and is also visible in *Th. ettlingensis* (best visible in JME-ETT3345a (Fig. 8) and JME-ETT220 (Fig. 9B) described above) and *Th. subovatus* (Fig. 6B). A single scale of *Thrissops* sp. from Ettlting with the dark pigment melanin in the center is figured in Ebert (2021, fig. 4). This color pattern can also be seen in a less pronounced way in *Allothrissops* (Fig. 17B).

***Thrissops* with prey fish.** Two specimens of *Thrissops ettlingensis* each with a single, quite large prey fish of *Orthogonikleithrus hoelli* Arratia, 1997 in their stomach are known to the author. In JME-ETT166 this single prey fish is well preserved (Fig. 9A; Ebert and Kölbl-Ebert 2013, fig. 4b). In JME-ETT3345 the prey fish is already half digested. In addition, the intestine in both fishes is filled with almost completely digested fish remains.

Some specimens of *Thrissops formosus* are known to have prey fish in their stomach: Neumayer (1929) described a *Thrissops formosus* (BSPG AS VII 175) from the Solnhofen Archipelago of Kelheim with several fish in its abdomen. He suspected that these were embryos of this fish and that *Thrissops formosus* was viviparous. Nybelin (1958) contradicted this view. In his opinion, the ten small fish in the abdominal cavity of SNSB-BSPG AS VII 175 were juvenile *Leptolepides sprattiformis* (Blainville, 1818a) and thus prey. Zittel (1887: 274) had already written: "Bei Kelheim und Eichstätt findet man öfters grosse Exemplare von *Th. formosus* Ag. mit zahlreichen kleinen *Leptolepis* im Bauch." Other *Thrissops* specimens from Kelheim with similar prey fish are in the National History Museum in London (NHMUK P.913, NHMUK P.3678). Through his knowledge of extant fish, Nybelin (1958) was able to document the shape of the alimentary canal of *Thrissops formosus* (SNSB-BSPG AS VII 175). He explained: „dass *Thrissops formosus* einen nach hinten sich erstreckenden Magenblindsack besass, der sich bei gefülltem Magen bis in den hintersten Teil der Bauchhöhle erstreckte.“

From Ettlting two approximately 40 cm long specimens of *Thrissops formosus* (JME-ETT2750, JME-ETT3111) were found with many prey fish (estimated around 30–50 specimens) in their stomachs (Ebert and Kölbl-Ebert 2013, figs 2a, b). The prey fish are juvenile fish of the species *Orthogonikleithrus hoelli* Arratia, 1997. The location of the prey fish in the two Ettlting specimens (JME-ETT2750, JME-ETT3111) confirms Nybelin's view of a gastric blind sack that extends long backwards (Ebert and Kölbl-Ebert 2013, figs 2a, b). Nybelin (1858) further concluded that the feeding behaviour of *Thrissops formosus* was similar to mackerel and herring, which continue to eat until the stomach is full of food, after which they rest from hunting for digestion. In the two Ettlting specimens, the vertebrae of all prey fish are still connected. According to Maisey (1994), this indicates that all these prey fish were eaten in a very short period of a few hours. If it has been a while since the meal, the prey fish should be digested more and then soon are transported into the intestinal canal. The individual prey

fish are then no longer articulated but usually only visible as individual, disjointed vertebrae (e.g. JME-ETT3371).

In contrast to *Thrissops ettlingensis* with only one comparably large prey fish in the stomach, *Thrissops formosus* has several small Orthogonikleithridae in the stomach (Ebert and Kölbl-Ebert 2013, fig. 2a,b; Neumayer 1929; Nybelin 1958; Zittel 1887). This is most likely because *Thrissops ettlingensis* is relatively small in relation to the prey fish (*Orthogonikleithrus* or *Leptolepides*).

**Fishes who preyed on *Thrissops*.** In the Solnhofen Museum there is a large Caturidae from Brunn, Bavaria, Germany (SNSB-BSPG 1997 XVIII 1507) which swallowed a *Thrissops* specimen of approximately 35 cm total length. This prey fish is visible in the gastrointestinal tract with the anteriormost part of the skull anterior of the anal fin of the predator and the posterior part of the caudal fin still protruding from the mouth of the caturid.

**Pathologies in *Th. formosus*.** On the well-preserved material from Ettlting some rare pathologies of the axial skeleton and the caudal fin are observable.

In JME-ETT2750 there is a pathology of the two ventralmost principal rays 18 and 19 of the caudal fin (Fig. 21A). The unsegmented parts of the lepidotrichia 18 and 19 are clearly separated as normal, but posterior to about the ninth ray segment, these two rays grow together into one ray. As a replacement, an additional ray formed slightly anterior to the first ray segments between the 17<sup>th</sup> and 18<sup>th</sup> ray. This additional ray is smaller than the rays dorsal and ventral to it. It is segmented, but unbranched. The 16<sup>th</sup> ray also still has slight irregularities in the segmentation.

In JME-ETT1350 there are two neural spines on preural centrum PU2 (Fig. 5A, B).

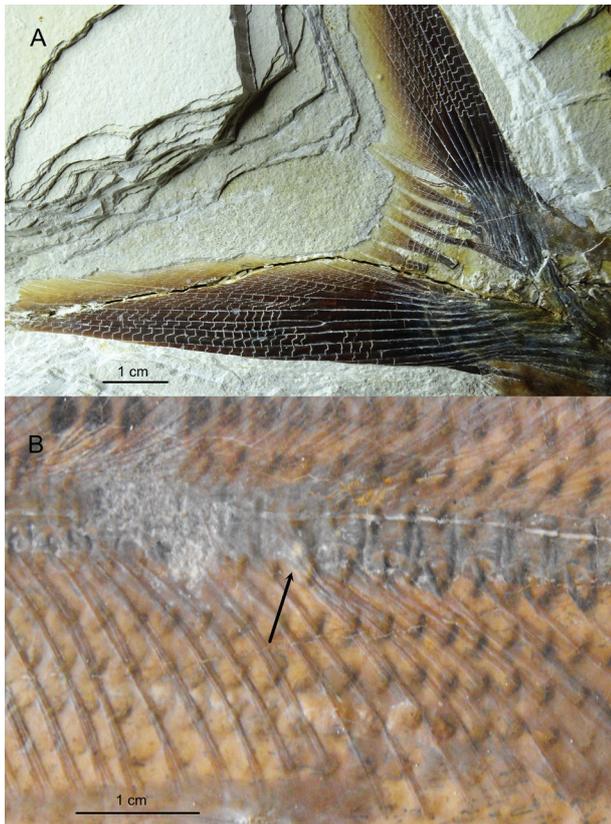
In JME-ETT74 two pairs of ribs were connected to the 25<sup>th</sup> vertebra centra (Figs 2B, 21B). Additionally, this vertebra centra is slightly enlarged compared to the vertebrae anterior and posterior to it. JME-ETT74 is also the specimen with the pathologically lowest number of 56 vertebrae (see number of vertebrae in Suppl. material 1), since in this specimen two vertebrae are probably fused.

In *Thrissops kimmeridgensis* (MJML K1797) from the Kimmeridge Clay of Dorset, England there is an additional ray between the ventralmost principal caudal fin ray and the first procurvent ray (Fig. 22A). This additional ray develops slightly posterior to the first ray segments of the rays dorsal and ventral to it.

There are also fragmentary *Thrissops* specimens (MJML K2003, K2285, K2770) in the Kimmeridge Clay which have caudal rays that are nearly twice as narrowly segmented than normal *Th. kimmeridgensis*, which is probably also pathological (Fig. 22B).

**Distribution of Upper Jurassic Ichthyodectiformes** (for localities see Fig. 1; for number of specimens see Fig. 23).

In general, the genus *Thrissops* is quite common in the Kimmeridge Clay (Dorset, England); in Cerin (Ain, France); and in Ettlting and Kelheim Kapfelberg (both Solnhofen Archipelago, Bavaria, Germany). But *Thrissops* is very rare at other localities of the Solnhofen Archipelago, particularly in



**Figure 21.** Pathologies in *Thrissops formosus* von Ettlting, Bavaria, Germany. **A.** Pathological caudal fin of JME-ETT2750; **B.** Two pairs of ribs on one vertebra in JME-ETT74.

the Eichstätt and Solnhofen Basins, the Zandt Basin, Brunn, Painten, and Wattendorf. In Nusplingen (Baden-Württemberg, Germany), *Thrissops* seems to be absent.

*Thrissops formosus* is common in Ettlting (110 specimens thus far), Kelheim Kapfelberg (32 specimens), and Cerin (29 specimens), but rather rare in the Eichstätt and Solnhofen Basins with together 16 specimens; two specimens from Painten and Brunn and one from Wattendorf.

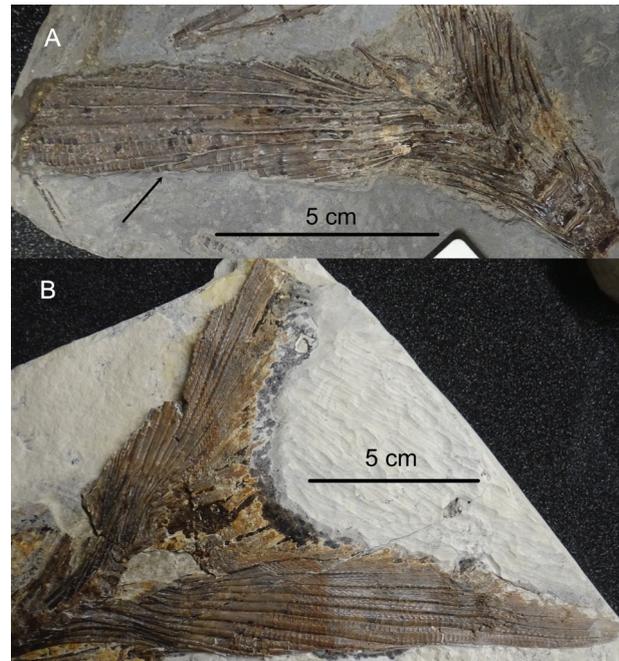
*Th. subovatus* is only known from the Solnhofen Archipelago, Bavaria, Germany, but rare in all localities. Five specimens are known from the Kelheim Basin (probably all from Kelheim Kapfelberg, five from the Eichstätt Basin, four from Ettlting, three from the Solnhofen Basin, two from the Zandt Basin and one from Painten.

*Th. ettlingsensis* is only known from Ettlting but with seven known specimens rather rare.

*Th. cirinensis* is only known from Cerin and with 16 specimens rather rare, even if we include the not exactly identified, poorly preserved specimens.

*Th. kimmeridgensis* is known only from the Kimmeridge Clay in Dorset. With 94 known specimens, it is one of the most common fish species there. But it should be noted that smaller teleost species are often overlooked due to the poorly splitting of the Kimmeridge Clay and additionally, it is very difficult to prepare small fishes in this material.

Of *Th. portlandicus* and *Th? curtus* of the Purbeck and Portland, Dorset, England only single specimens are known.



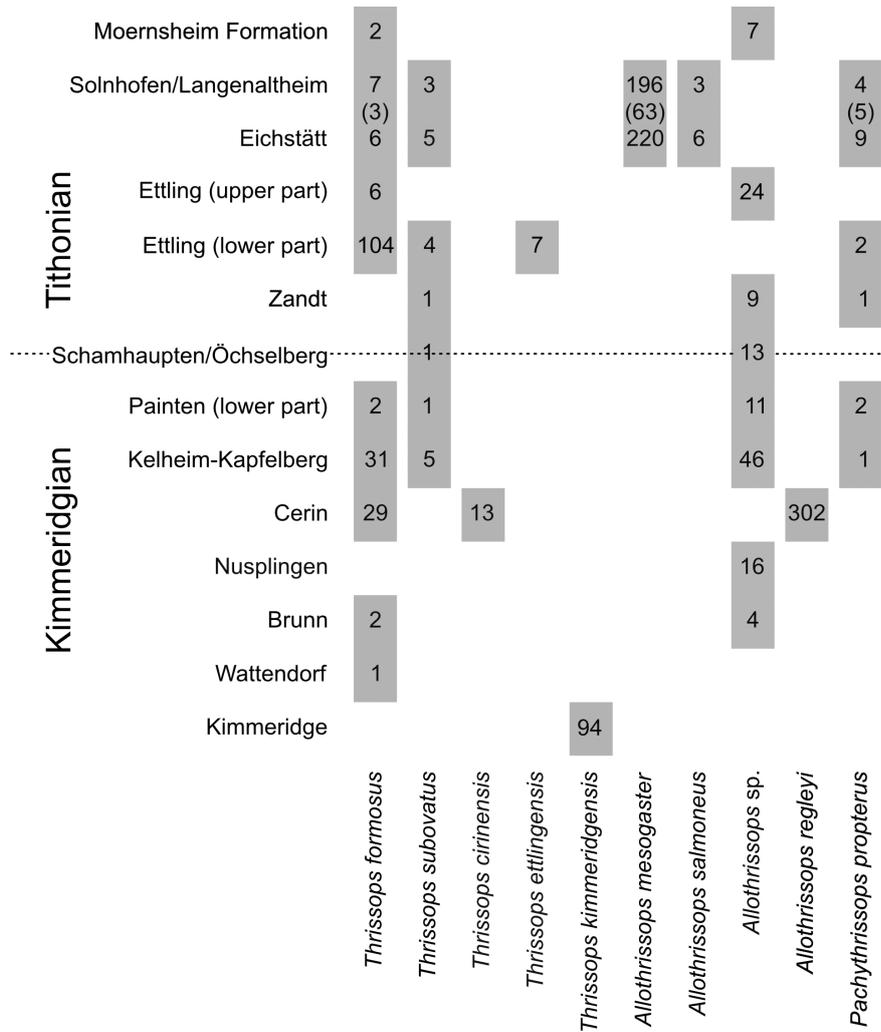
**Figure 22.** Caudal fins of *Thrissops kimmeridgensis* from the Kimmeridge Clay of Dorset, England with pathologies. **A.** Pathological additional ray between the ventralmost principal caudal fin ray and the first procurrent ray in MJML K1797; **B.** MJML K2003 with caudal rays that are nearly twice as narrowly segmented than normal.

*Allothrissops* Nybelin, 1964, is one of the most common fish in Eichstätt, Solnhofen and Cerin with many juvenile specimens. In Ettlting *Allothrissops* is rather rare, and in the lower part of the quarry, Plattenkalk I–III (Ebert et al. 2015, fig. 2), it is completely absent.

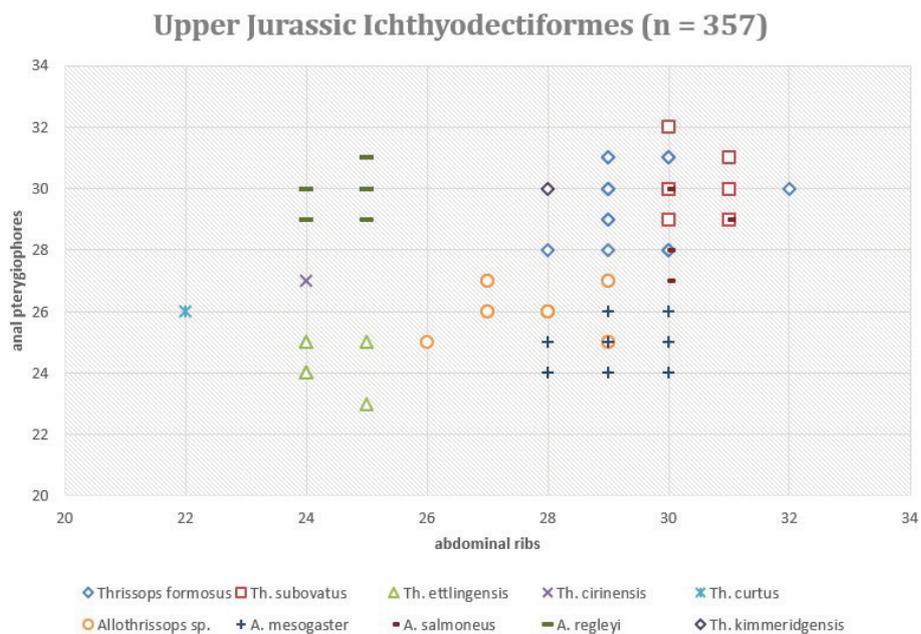
**Size of specimens.** Nybelin (1964) reports a maximum standard length (SL) of 390 mm for the genus *Thrissops*. Now specimens of *Thrissops* measuring ~75.5 cm SL (~90 cm total length TL) are known (see Suppl. material 1: table S1).

The largest known specimen in the genus *Thrissops* is *Thrissops kimmeridgensis* (MJML K2295, Fig. 14A) from the Kimmeridge Clay of Dorset, England with ~75.5 cm SL (~90 cm TL), followed by *Thrissops formosus* from Cerin (MHNL20015185 (~67 cm SL, 80 cm TL; holotype of *Thrissops heckeli* Thiollière 1854, pl. 10, fig. 1); MHNL20015760 (~52 cm SL, 66 cm TL); and UCBL-FSL 503200 (50.8 cm SL, 72.2 cm TL; Bernier et al. 2014, fig. 10a)); *Thrissops* cf. *formosus* from Wattendorf, Bavaria Germany (NKMB Wattendorf specimen; see Mäuser 2015, fig. 1014) with ~50 cm SL, ~60 cm TL and *Thrissops formosus* from Ettlting (JME-ETT75 (Fig. 2A) with 53 cm TL; and JME-ETT3340 with 50 cm TL).

**Juvenile to subadult status.** There is only one juvenile specimen of the genus *Thrissops* known to the author in any locality (see *Thrissops ettlingsensis* JME-ETT1360 described above). This juvenile specimen has 3.5 cm standard length (SL) whereas the other probably adult specimens of *Th. ettlingsensis* have 9–13 cm SL (for length of specimens see Suppl. material 1: table S1).



**Figure 23.** Stratigraphic range and abundance of Upper Jurassic Ichthyodectiformes in southern Germany, Cerin France and Cerin, France (updated from Ebert 2024 fig. 13.8).



**Figure 24.** Number of abdominal ribs plotted against the number of anal pterygiophores in Upper Jurassic Ichthyodectiformes (n = number of measured specimens; updated from Ebert 2024, fig. 12.15).

In *Thrissops formosus*, *Th. kimmeridgensis*, and *Th. subovatus* there are no juvenile specimens known, but there are probably some subadult specimens in *Th. formosus*. For example, in JME-ETT76, a specimen of 25 cm SL, the posteriormost vertebra in the caudal peduncle are not fully ossified with small transparent areas between them (probably filled with cartilage), additionally, the caudal fin rays are comparably short. A similar development is present in JME-ETT87 with 25 cm SL as well. All other specimens of *Th. formosus* of around 25 cm SL have fully ossified vertebrae, without gaps and normally developed caudal fin rays.

Juvenile specimens are quite common in Teleostei in the Upper Jurassic of the Solnhofen Archipelago in most taxa, e.g. in the closely related Ichthyodectiform genus *Allothrissops*. This suggests that juvenile *Thrissops* lived in other, yet unknown, locations.

*Thrissops cephalus* Agassiz, 1834 was mentioned as juvenile specimens of *Thrissops* by Wagner (1863), but I agree with Wagner (1863) that *Thrissops cephalus* are juvenile specimens of "*Thrissops salmoneus*" which since Nybelin (1964) belong to the genus *Allothrissops*. Nybelin (1964) described *Thrissops cephalus* as juvenile specimens of *Allothrissops mesogaster* Agassiz, 1834.

## Conclusions

By comparing the different *Thrissops* specimens, I was able to identify two new *Thrissops* species *Thrissops ettingensis* (Figs 8–13, 18D, 20A) and *Thrissops kimmeridgensis* (Figs 14, 15, 19A, B, D, 20C). All specimens of *Thrissops ettingensis* sp. nov. are from the locality Ettling, Markt Pförring, Solnhofen Archipelago, Bavaria, Germany and are only up to a maximum of 15.5 cm total length. *Thrissops kimmeridgensis* sp. nov. were found in the Kimmeridge Clay of Dorset, England.

The main characteristic feature to distinguish *Thrissops ettingensis* sp. nov. from the other known *Thrissops* species is a smaller number of vertebrae, in particular a smaller number of vertebrae between the skull and the anal fin and a smaller number of ribs associated to these abdominal vertebrae. Additionally, *Th. ettingensis* has a smaller number of anal fin rays and the associated anal pterygiophores (which are easier to count).

The total number of vertebrae in *Thrissops ettingensis* is 49–50 in contrast to 57–61 in *Th. formosus*; 59–60 in *Th. subovatus*; ~55–57 in *Th. kimmeridgensis*; 52 in *Th. cirinensis*; 52 or 53 in *Th. curtus*; 58–59 in *Allothrissops mesogaster*; 59–60 in *A. salmoneus*; 52–54 in *A. regleyi* (for comparison see Table 1).

The number of anal pterygiophores in *Thrissops ettingensis* is 23–25 in contrast to 28–31 in *Th. formosus*; 29–32 in *Th. subovatus*; 29–30 in *Th. kimmeridgensis*; 27 in *Th. cirinensis*; 26 in *Th. curtus*; 24–26 in *Allothrissops mesogaster*; 27–30 in *A. salmoneus*; and 29–31 in *A. regleyi* (for comparison see Fig. 24, Table 1).

*Thrissops kimmeridgensis* is very similar in proportions and body shape to *Th. formosus*, but this new species differs from *Th. formosus* especially in a notably irregular dentition in the lower jaw with one large fang tooth anteriorly and larger teeth in the middle of the dentary. From *Thrissops subovatus* it differs in the maxilla shape (which is more straight in *Th. subovatus*, Fig. 20D); a hook developed on the anterior tip of the dentary (which is not developed in *Th. subovatus* and *Th. ettingensis*) and the teeth of the maxilla which are in *Th. kimmeridgensis* smaller and more numerous than in *Th. subovatus*.

The greatest similarity of *Thrissops ettingensis* is to *Th. cirinensis* or *Th. curtus*. *Th. cirinensis* of Cerin, France, of which only a single specimen is known (MNHN CRN 66), differs from *Th. ettingensis* especially due to its noticeably larger teeth in the premaxilla and dentary (Fig. 7; Taverne 1977: fig. 8). Of *Th. curtus* from the lower Purbeck layers of the Isle of Portland (UK) only a few specimens are known (NHMUK P.10612 holotype (Fig. 16A); P.8381), which are unfortunately poorly preserved. I agree with Cavin et al. (2013) that it had to be justified if this species belongs to the genus *Thrissops*.

Table 1 shows the most important features that distinguish the new species from the other *Thrissops* species and the other known Upper Jurassic Ichthyodectiformes.

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## Supplementary material 1

### Specimens of Ichthyodectiformes of the Jurassic examined for comparative purposes

Authors: Martin Ebert

Data type: docx

Explanation note: Features, collection numbers and localities of studied Upper Jurassic *Thrissops* specimens.

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