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The Problematic Genus *Liodesmus* Wagner and a New Genus of Caturoidea (Halecomorphi, Neopterygii) from the Upper Jurassic Solnhofen-Archipelago †

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Abstract: Our revision of the type material of *Liodesmus* led to significant adjustments in our understanding of the taxon when the original type specimen of *Pholidophorus gracilis*, which was later determined as the type species of the genus *Liodesmus*, was recently found in the collection in Berlin. It had been confused with a specimen that was described as the type specimen of the species *Liodesmus gracilis* in the collection in Munich. Moreover, the Munich specimen was mistakenly considered by all authors who have studied *Liodesmus* as a type specimen for the genus *Liodesmus*. However, the original holotype of *Pholidophorus gracilis* and this Munich specimen of *Liodesmus gracilis* belong to two different families. *Caturus brevicostatus*, whose holotype was recently found in Berlin as well, is described in detail here for the first time. *Liodesmus sprattiformis* is now described under the new genus *Nasrinsotoudehichthys* outside Caturidae but within the Caturoidea. Since all specimens that have been described so far under *Liodesmus* either belong to other, previously described genera, belong to new genera clearly outside the description of the genus *Liodesmus*, or are nomina dubia (including the type species *Pholidophorus gracilis*), the genus *Liodesmus* and the Liodesmidae are nomina dubia as well.

Keywords: Amiiformes; *Caturus*; Caturoidea; Liodesmidae; Jurassic; Solnhofen Plattenkalk

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1. Introduction

The generic name *Liodesmus* is mentioned for the first time in Wagner [1], but without a description or illustration. It was not until 1863 that Wagner gave a short description of the genus, thus determining the authorship and date of *Liodesmus* [2]. It originally included two species, *Liodesmus gracilis* [3] and *Liodesmus sprattiformis*, which Wagner newly proposed in [2]. Woodward [4] assigned *Liodesmus gracilis* [3] as the type species of the genus *Liodesmus*.

Wagner [2] also considered two older taxa (*Megalurus parvus* [5] and *Megalurus intermedius* [6]) to be younger synonyms of *Liodesmus gracilis* [3]. Additionally, he introduced the new species name *Liodesmus sprattiformis* [2], and he thought that the taxon *Coccolepis bucklandi* [7] was probably also a member of the genus *Liodesmus*.

Wagner's [2] description of the genus is primarily based on his *Liodesmus gracilis*, which included four specimens, three of which, however, represented different nominal species: the holotype descriptions of *Pholidophorus gracilis* [3], *Megalurus parvus* Münster in [5], and *Megalurus intermedius* Münster in [6]. Additionally, Wagner [2] mistook a specimen from the Münster collection in Munich (today SNSB-BSPG AS VII 1122; Figure 2C) for the holotype of *Pholidophorus gracilis* [3]. Thus, SNSB-BSPG AS VII 1122 became the fourth specimen

included in *Liodesmus gracilis*, and, due to Wagner's error, it has been taken for the holotype of this species by all subsequent authors who worked on the genus *Liodesmus*, e.g., [4,8,9]. The specimen was figured as a holotype of *Liodesmus gracilis* for the first time in Grande and Bemis [9] (fig. 406a).

The senior author (ME) recently discovered the specimen MB.f.15598 (Figure 2A) in the collection of the Berlin Natural History Museum and recognized this specimen to be the type specimen for *Pholidophorus gracilis* [3], which is described in Agassiz [7] and figured in Agassiz [3] (Atlas of Tome II, pl. 42, fig. 2; see Figure 2B). Both specimens (SNSB-BSPG AS VII 1122 and MB.f.15598) were originally part of the Münster collection and were originally labeled *Pholidophorus gracilis* in the same handwriting (probably by Münster).

A further specimen from the Münster collection that was recently discovered by the senior author (ME) in the collection in Berlin is the holotype of *Caturus brevicostatus* [10] (MB.f.3849; Figures 4–9). Specimens of this taxon were described under *Liodesmus* as well (see list of references below), and most probably the Munich specimen of *Liodesmus gracilis* [2] (SNSB-BSPG AS VII 1122) belongs to this taxon *Caturus brevicostatus* as well.

After close examination of the holotype of *Pholidophorus gracilis* [3], the holotype of *Caturus brevicostatus* [10], and the other specimens originally included in *Liodesmus gracilis* by Wagner [2], we have been able to recognize a mixture of four different taxa under this nominal species. This contribution includes the description and discussion of the taxonomic status of each of those specimens as well as the species *Liodesmus sprattiformis* [2], which is transferred to a new genus. Concerning the taxonomic status of the non-neopterygians actinopterygian *Coccolepis bucklandi* [7], we refer the readers to López-Arbarello and Ebert [11] and the literature cited therein.

2. Materials and Methods

All described specimens have been collected in the Upper Jurassic lithographic limestones of the Solnhofen Plattenkalk region of Bavaria (Figure 1). The Bavarian Plattenkalk basins are diverse, differing in ecology and slightly in age [12]. The Bavarian Plattenkalk basins range in age from late Kimmeridgian to early Tithonian [13].

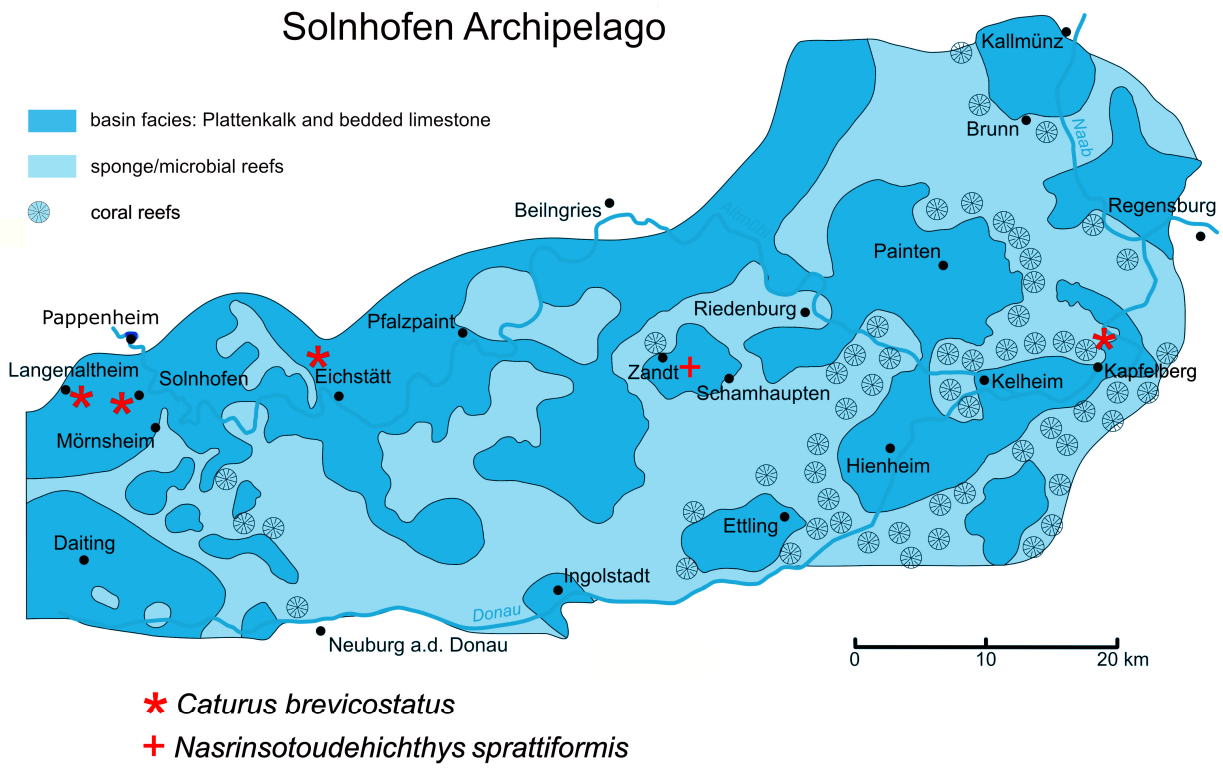

Figure 1. Palaeogeographic reconstruction of the Solnhofen Archipelago (modified from [11]).

The fossils were examined using a Zeiss 47 50 57 Stereo Zoom microscope (ZEISS, Jena, Germany), a PZO 20138 microscope (PZO, Warszawa, Poland), and a Leica M80 microscope (Leica Microsystems, Wetzlar, Germany). Photographs were taken with a Sony DSC-HX80 (Sony, Tokyo, Japan), Nikon D 7000 digital camera (Nikon, Tokyo, Japan), and digital microscope system KEYENCE VHX-7000 Series 4K with a facility to take UV-photos. Unless otherwise noted, all photos are by M. Ebert.

Drawings were made with Affinity Designer from photographs of the specimens, with direct comparison to the specimens under the microscope. The pterygial formula is according to Westoll [14], with scale rows from postcleithra to insertion of: D = dorsal fin; P = pelvic fin; A = anal fin; C = caudal fin. T is normally the total number of scale rows from postcleithra to hinge line. However, this cannot be countable in Caturidae because there is no hinge line. Therefore, we propose to count the number of rows of scales at T from the poscleithra to the base of the caudal fin at the level of the first scute or basal fulcra of the ventral lobe. Standard Length (SL) is measured here as the distance from the anteriormost point of the snout to the posteriormost tip of the scales of the caudal peduncle.

2.1. Institutional Abbreviations

AMNH, American Museum of Natural History, New York, U.S.A.; **BMMS**, Solnhofen Museum; Germany; **CM**, Carnegie Museum of Natural History, Pittsburgh, U.S.A.; **ETHZ**, Eidgenössische Technische Hochschule Zürich, Switzerland; **FMNH**: Museum of Natural History, Chicago, U.S.A.; **GLAHM**, The Hunterian Museum and Art Gallery, University of Glasgow (Hunterian Museum Geology Collections), U.K; **GPIBO**, Geologisch-Paläontologisches Institut Bonn, Goldfuß Museum, Germany; **GPIT**, Geologisches und Paläontologisches Institut, University of Tübingen, Germany; **JME**, Jura-Museum Eichstätt, Germany (ETT Ettling collection, SOS Solnhofen Archipelago collection); **LF**, Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, U.S.A.; **LfU**, Bayrisches Landesamt für Umwelt, Munich, Germany; **MB**, Museum für Naturkunde, Berlin; **MBH**, Museum Bergér, Harthof, Eichstätt, Germany; **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.; **MfNC**, Museum für Naturkunde Chemnitz, Germany; **MGB**, Museo de Geología de Barcelona, Barcelona, Spain; **MHH**, Urwelt-Museum Hauff, Holzmaden, Germany; **MHNL**, Muséum d'Histoire Naturelle de Lyon, France; **MHNN**, Musée d'Histoire Naturelle in Neuchâtel, Switzerland; **MMG–SNSD**, Museum für Mineralogie und Geologie–Senckenberg Naturkundliche Sammlungen Dresden, Germany; **MNHN**, Musée d'Histoire Naturelle, Paris, France; **MOZ**, Museo Provincial Dr Prof. Juan Augusto Olsacher, Zapala, Neuquén, Argentina; **NHMUK**, The Natural History Museum, London, U.K.; **NMBE**, Naturhistorisches Museum Bern, Switzerland; **USNM**, Smithonian Institution, Washington, U.S.A.; **NMP**, National Museum Prague, Department of Palaeontology, Czech Republic; **NMS**, National Museums of Scotland, U.K.; **OUMNH**, Oxford University Museum of Natural History, U.K.; **PIMUZ**, Palaeontologisches Institut der Universität Zürich, Switzerland; **RE**, Ruhr Museum, Essen, Germany; **ROM**, Royal Ontario Museum, Toronto, Canada; **SMF**, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt a. M., Germany; **SMNK,** Staatliches Museum für Naturkunde Karlsruhe, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns–Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **TLM,** Sammlungs- und Forschungszentrum der Tiroler Landesmuseen, 133 Hall in Tirol, Austria; **TM**, Teylers Museum, Haarlem, Netherlands; **UCBL**, Université de Lyon, Université Claude Bernard Lyon 1, France; **YPMPU**, Yale Peabody Museum, Princeton, Dep. of Geology, U.S.A.

2.2. Anatomical Abbreviations

ao, antorbitals; **ang**, angular; **br**, branchiostegal rays; **ch**, cheratohyal; **cl**, cleithrum; **d (l)**, dentary (left); **d (r)**, dentary (right); **dpt**, dermopterotic; **ds**, dermosphenotic; **ex** extrascapular; **fr**, frontal; **gu**, gular plate; **hy**, hyomandibular; **io**, infraorbitals; **iop**, interoperculum; **mx**, maxilla; **na**, nasals; **op**, operculum; **or**, orbit; **pa**, parietal; **pcl**, postcleithrum;

pmx, premaxilla; **pop**, preoperculum; **psp**, parasphenoid; **ptt**, posttemporal; **qu**, quadrat; **ro**, rostral; **scl**, supracleithrum; **smx**, supramaxilla; **so**, supraorbitals; **sop**, suboperculum; **sr**, sclerotic ring; **suo**, suborbital.

2.3. Material Examined

In addition to the taxa described in the Results and Systematic Paleontologie section below, the following specimens of Caturidae were examined for the purpose of comparison: (All specimens were examined by the authors; however, the specimens marked with an asterisk were examined from photographs only). ***Amblysemius bellicianus*** [15], Kimmeridgian/Tithonian, Cerin, France: MHNL20015164 (holotype), 20015172, 20150730; ***Amblysemius granulatus*** [10], Tithonian, Solnhofen Archipelago, Germany: GLAHMV3482; JME-ETT3369, 3243, 3381, 4607a,b; LF 1971, 1978, 6010; LfU München (without number); MB.f. 15622; MBH (two specimens without number); MfNC F10365; MNHN 1900-16-1; NHMUK PV OR 37027, OR 37076, P.4380, P.44900; NMBE D3380; NMS 1875. 14. 31A,B; SNSB-BSPG AS VII 1139 (holotype), AS I 1249, 1957 I 352, 1960 XVII 50, 1991 I 121; ***Caturus agassizi*** [16], Lower Jurassic, Lyme Regis, U.K.: NHMUK PV P.567 (holotype), NHMUK PV OR 41856; ***Caturus chirotes*** [5], Lower Jurassic, Lyme Regis, U.K.: NHMUK PV P.3643 (holotype); ***Caturus dartoni*** [17], Bathonian, Hot Springs, South Dakota, U.S.A.: USNM 4792* (holotype); ***Caturus deani*** [18], Oxfordian, Sheet La Palma, Cuba: AMNH FF 6371* (7930*) (holotype); ***Caturus furcatus*** [19], Upper Jurassic, (Southern Germany; Cerin, France): CM 872, 4721, 4725, 4726, 4727, 4728, 4770, 4790, 4808, 4861, 5020, 34431; FMNH P 15457; GPIBO P-1889, 1954, 1956, 1966; JME-ETT3366, ETT3927, SOS553, SOS3041, SOS3049, SOS3072, SOS3233, SOS3269a, SOS3397, SOS3402, SOS4011a, SOS4076, SOS7961; LF 306, 1423, 3524; MMG-SNSD-BaJ1706, 1721, 1731, 1739, 1760, 2349, 2355; NHMUK PV 37026, 37038, 37812, P.3726, P.6941; NMP Uc9 holotype, Uc83 counterpart of holotype; SMF P8743; SMNK-PAL 29706; SMNS-P-9532, 9623, 56056, 59767; PIMUZ A/I 0387*, 0540*; private coll. Eller 303, 304, 635; private coll. Tischlinger 01/20; SNSB-BSPG AS I 1250, AS I 1251, 1950 XXXV 21, 1954 I 367, 1955 I 545, 1960 XVIII 49, 1962 I 295, 1963 I 270, 1964 XXIII 571, 1964 XXIII 578, 1964 XXIII 603, 1990 XVIII 2, 1990 XVIII 31, 1993 VXIII—VFKO 320; UCBL 93137; USNM PAL 323035_1*; ***Caturus heterurus*** [5], Lower Jurassic, Lyme Regis, U.K.: NHMUK PV P.897, P.898a, P.3696b, P.3696c, OR 38121; OUMNH P853343* (holotype); ***'Caturus' insignis*** [20], Upper Triassic, Seefeld, Austria: TLM F.117 (holotype); ***'Caturus' latipennis*** [7], Lower Jurassic, Lyme Regis, U.K.: NHMUK PV P.568 (holotype); ***Caturus latus*** [21], Upper Jurassic, (Southern Germany; Cerin, France): AMNH FF 8002*; CM 868, 869, 871, 4019, 4028, 4713, 4769, 4771, 4778, 4788, 4848, 4857, 5000, 30881, 31398; FMNH UC 2038; JME-ETT4133, SOS536a,b, 538, 3034, 3039, 3047, 3050, 3053, 3064, 3067, 3231, 3234, 3237, 3241, 3242, 3244, 3248, 3631, 3685, 4302, 4307=2720, 4608, 4623, 4624, 4625, 4628, 4631; LF 1938, 1973, 1977, 2085, 2188a, 5294; MCZ 6262* (holotype of *Uraeus pachyurus* [22]), 10457*, 16450*; MHNN FOS378*; MMG-SNSD BaJ1707, 1716, 1718, 1720, 2551; NHMUK PV 37028, 37035, 37095, 37097, 37808, 37811, 75939, P.3724, P.3725, P.3729, P.7566; RE A 0209*, 0222*, 0558*; private coll. Eller 615, 788, 831; private coll. Tischlinger 70/236, 73/99; SMF P4239, 7182, 8284; SMNK-PAL 29703, 29704; SMNS-P-6005, 7186, 53652, 56072; SNSB-BSPG AS I 1247 (holotype of *Caturus gracilis* [2]), AS V 514 (holotype of *Caturus cyprinoides* [2]), AS VII 263 (holotype of *C. latus*), 1960 I 150, 1960 I 195, 1961 I 48, 1961 I 215, 1964 XXIII 159, 1964 XXIII 555, 1964 XXIII 557, 1964 XXIII 562, 1964 XXIII 587, 1984 I 85, 1986 XV 111; UCBL 93059, 93065, 93083, 93448; TM6901, 10247; USNM V 11165_2*, 21059*; YPM PU003233*; ***Caturus macrurus*** [19], Upper Jurassic, Solnhofen Archipelago, Bavaria, Germany: MB.f.12850 (holotype of *Caturus obovatus* [10]); NMP Uc74 (holotype); ***Caturus porteri*** [23], Callovian-Oxfordian, Callovian of Christian Malford, U.K.: NHMUK PV P.6902*, P.29049 (holotype); ***Caturus purbeckensis*** [24], Berriasian, Swanage, Dorset, U.K.: NHMUK P PV OR 46911 (holotype); ***Caturus smithwoodwardi*** [25], Toarcian, Holzmaden, Germany, MHH (without number); NHMUK PV P.11127 (holotype); ***Caturus tarraconensis*** [26], Berriasian-lower Valanginian, El Montsec, Lérida, Spain: MGB 514* (holotype); ***Caturus tenuidens*** [4], Berriasian, Swanage, Dorset, U.K.: NHMUK PV OR 40656, 40657*, P.442a* (type specimens),

P.29389, ***Catutoichthys olsacheri*** [27], Tithonian, Los Catutos, Neuquén, Argentina: MOZ-Pv 3645* (holotype); ***Strobilodus cliftoni*** [4], Tithonian, Isle of Portland, U.K.: NHMUK PV P.6034 (type), P.6034a (type), P.6035 (type), OR 40719; ***Strobilodus giganteus*** [6], upper Kimmeridgian to lower Tithonian, Solnhofen Archipelago and Nusplingen, Germany: ETHZ 10707*; GPIT-PV-31392 ([28]/T.24); JME-SOS573a,b, 3997, 4055, 8316; LF 3473; NHMUK PV P.5544; SMF P9989; SMNS 96393/1; SNSB-BSPG 1953 1 579 neotype, 1960 XVIII 54; BMMS without number; ***Strobilodus impar*** [29], Kimmeridgian, Oxfordshire, U.K: NHMUK PV OR 46318 (type); ***Strobilodus suchoides*** [30], Kimmeridgian, Norfolk, U.K.: NHMUK PV OR 41386 (holotype).

3. Results

Several nominal species revised in this work are considered nomina dubia. The corresponding material is described and discussed in this section. The valid taxa are included in the Systematic Paleontology section.

Figure 2. Specimens described as holotypes of *Pholidophorus gracilis* [3]. (**A**) holotype of *Pholidophorus gracilis* [3] (MB.f.15598) from Kelheim, Solnhofen Archipelago, Bavaria, Germany, from the collection of

Georg Graf von Münster, now in the collection in Berlin. This is the specimen figured in [3] (Atlas Tome II, pl. 42, fig. 2; to be able to compare it better with the drawing, the photo is mirrored); (**B**) original drawing of *Pholidophorus gracilis* by Sixtus Heinrich Jarwart, [1836–1838], later this drawing was figured in [3] (Atlas Tome II, pl. 42, fig. 2); (**C**) specimen (SNSB-BSPG AS VII 1122) in Munich, from Kelheim, Solnhofen Archipelago, Bavaria, Germany, from the collection Münster, incorrectly described as holotype of *Pholidophorus gracilis* [3] by [2]. (Photos: M. Ebert).

3.1. Pholidophorus gracilis [3], Nomen dubium (Figures 2A,B and 3A,B)

Holotype: MB.f.15598 from Kelheim, Bavaria, Germany (Figures 2A,B and 3A,B).

Remarks: The genus *Pholidophorus* is restricted to the Triassic since Arratia [31]. The holotype of *Pholidophorus gracilis* (MB.f.15598) has diamond-shaped ganoid scales (Figure 3B), which Agassiz already figured [3] (Atlas of Tome II, pl. 42, fig. 2) using a drawing that he received from Münster (Figure 2B). Most of these scales are visible from the interior side of the body. Only some scales posterior to the dorsal fin are visible from outside, and these scales have serrated posterior borders (Figure 3B).

Diamond-shaped scales are unknown in Caturoidea, 'Liodesmidae' or modern teleosts sensu Arratia [32].

Amongst the Late Jurassic fishes, similar massive diamond-shaped ganoid scales with smooth surfaces and intensely serrated posterior borders as the scales in MB.f.15598 are typical of the Ophipsiformes [33] or the Ankylophoridae (all Late Jurassic 'Pholidophorids' with ganoid scales are currently classified in the Ankylophoridae; see [34]). For the following reasons, we think MB.f.15598 belongs to the Ophiopsiformes and not the Ankylophoridae: The pelvic bone in Amiiformes (except Vidalamiidae) and Ophiopsiformes (where this feature is known) has a deep constriction distinguishing a long proximal portion and a short distal portion. In Pholidophoriformes and Ankylophoridae, the pelvic bone is uniformly rectangular. The relatively large and massive ganoid scales extend far into the axial lobe and cover a large part of the anteroventral bases of the basal fulcra. In Ankylophoridae, the scales of the caudal area are smaller, and the area of the axial lobe covered with ganoid scales is smaller. The scales in the center of the body in MB.f.15598 and in Ophiopsiformes are approximately as long as high. In Ankylophoridae, the scales in this area are at least two times higher than long. The scales in MB.f.15598 have few and relatively large serrations. In Ankylophoridae, the serrations are usually smaller and more numerous. MB.f.15598 has no large caudal scutes. Most Ankylophoridae have distinctly large caudal scutes. The teeth in MB.f.15598 are relatively large and not small and numerous as in Ankylophoridae.

Due to incomplete preservation, it is not possible to identify the specimen at the generic level, nor is it possible to diagnose a species. Therefore, *Pholidophorus gracilis* [3] should be treated as a *Nomen dubium*.

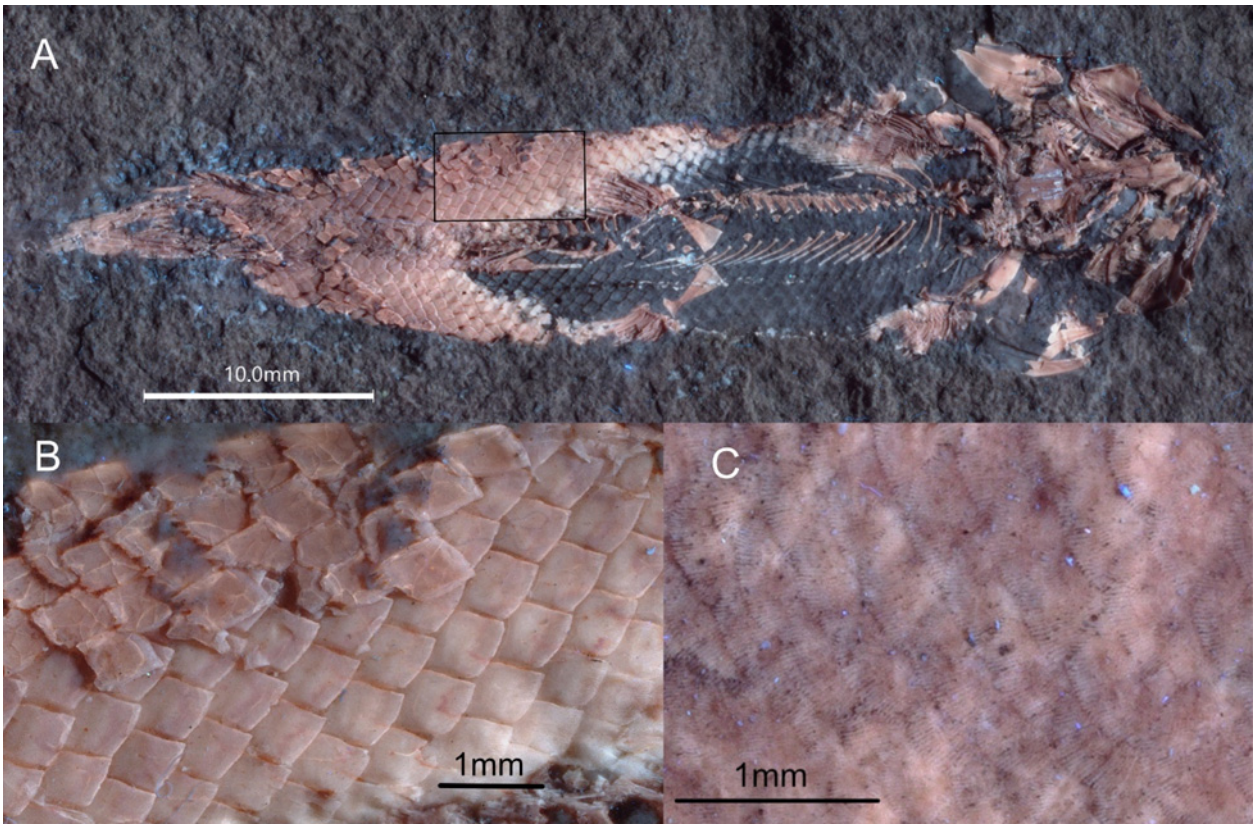

Figure 3. UV photographs. (**A**) *Pholidophorus gracilis* [3] (MB.f.15598, holotype) from Kelheim, Solnhofen Archipelago, Bavaria, Germany; (**B**) detail of Figure 3A (see black box), with ganoid scales of *Pholidophorus gracilis* Agassiz, 1838 (MB.f.15598). Most scales are visible from their interior side; only the scales top left with serrations at the posterior border are visible from the outside (cranium to the right); (**C**) amioid scales of *Liodesmus gracilis* [2] with striations on the surface, visible from the interior side (cranium to the left). (Photos: M. Ebert).

3.2. Megalurus parvus Münster in [5] Nomen dubium

Holotype: Missing specimen from Kelheim, Bavaria, Germany, figured [5] (Ag. II, pl. 51, fig. 4).

Remarks: The genus *Megalurus* [19], whose name was preoccupied and replaced by *Urocles* [35], with the type species *Megalurus lepidotus* [19], is currently a subjective junior synonym of *Amiopsis* [36] (see details in [9]). According to the illustration in Agassiz [5], with the posterior margin of the caudal fin rounded and the short dorsal fin, the holotype of *Megalurus parvus* [5], probably represents a specimen of *Amiopsis* [36]. Already Agassiz [7] and Wagner [6] suggested that *M. parvus* could be a junior synonym of *Amiopsis lepidota*: "*M. lepidotus* [today *Amiopsis lepidota*] and *M. parvus* nur Altersverschiedenheiten voneinander seyn dürften" [6] (p. 70).

The type specimen from Kelheim, which was originally in the collection Münster, is missing today, and the drawing in [5] (Figure 3, Ag. II, pl. 51, fig. 4) and the description are not informative enough to decide which taxon this specimen belongs to. Therefore, we consider *Megalurus parvus* Münster as a *Nomen dubium*.

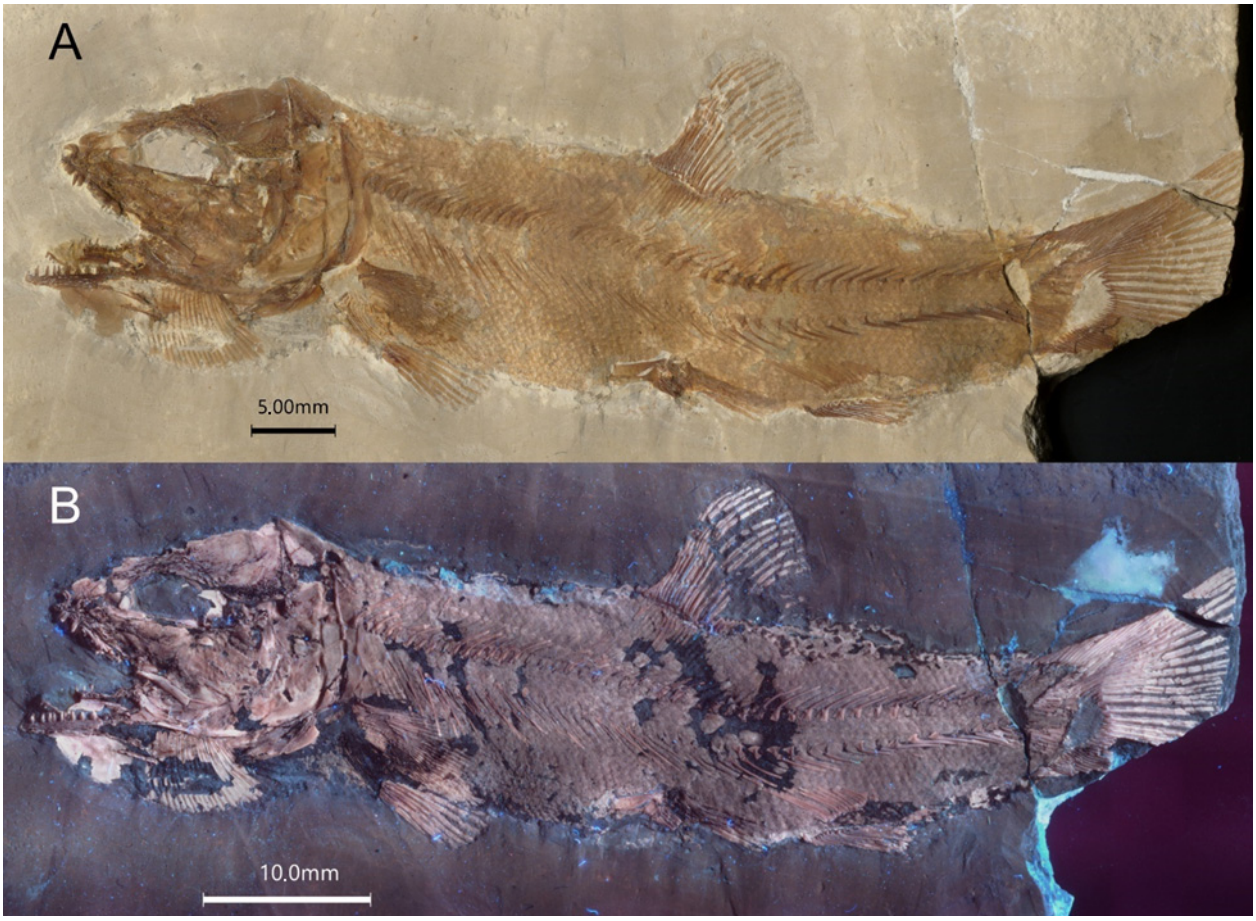

Figure 4. "*Liodesmus intermedius*" (SNSB-BSPG AS VII 1123) from Kelheim, Bavaria, Germany, labeled with the name "*Megalurus intermedius*" by Münster and mentioned in [3,6]. (**A**) original photograph; (**B**) UV photograph. (Photos: M. Ebert).

3.3. Megalurus intermedius Münster in [6] Nomen dubium (Figure 4)

Holotype: SNSB-BSPG AS VII 1123 from Kelheim, Bavaria, Germany (Figure 4).

Remarks: Although the name is available because it fulfills the requirements of the ICZN, neither Münster nor Wagner [2,6] ever figured out or properly described the species *Megalurus intermedius*. There is only one specimen (SNSB-BSPG AS VII 1123) labeled "*Megalurus intermedius*" in the collection in Munich, but the old label is lost, and we have not been able to find any useful historical information. However, this specimen, SNSB-BSPG AS VII 1123 (Figure 4), matches roughly the measurements given by Wagner [6] for the specimen to which he referred the species, and, thus, it is accepted as the holotype specimen. Grande and Bemis [9] (fig. 406B) figured this specimen under the name *Liodesmus intermedius*, and Martin-Abad [37] (fig. 1.8) figured this specimen under the name *Liodesmus gracilis*.

Specimen SNSB-BSPG AS VII 1123 refers to the genus *Caturus* based on the following features: the thin and rod-like maxilla, the posteriorly inclined haemal spines, the high number of branchiostegals (~24), 23 supraneuralia, the high number of caudal fin rays (>30), the massive basal fulcra on the dorsal lobe of the caudal fin, the posteriorly forked caudal fin, and the large urodermal-like scales covering the posterior part of the notochord. SNSB-BSPG AS VII 1123 differs from the other caturid taxon *Amblysemius*, which has 57–61 transverse scale rows between postcleithra and the dorsal fin origin and 26–27 supraneuralia. Based on the number of scale rows (approximately 29 transverse scale rows between postcleithra and dorsal fin origin), SNSB-BSPG AS VII 1123 might be a juvenile specimen of *Caturus latus* (for number of scale rows, see Figure 20).

4. Systematic Palaeontology

Subclass Actinopterygii [38]
Series Neopterygii [39]
Superdivision Holostei [40]
Division Halecomorphi [41]
Order Amiiformes [42]
Superfamily Caturoidea [43]

Diagnosis (emended from [9,44]): The superfamily Caturoidea is defined by the following combination of features: Amiiformes without solid perichordally ossified centra; high number of supraneurals (19–27); preural haemal and neural spines near the caudal peduncle region strongly inclined to a nearly horizontal orientation; presence of sharply carinate acrodin tooth caps on the larger jaw teeth.

Family Caturidae [42]

Diagnosis (emended from [9]): Caturoidea with an extremely slender rod-like maxilla; a relatively high number of branchiostegal rays (22 or more on each side); and haemal spines broadly spatulate in the transverse plane.

Genus *Caturus* [45]

Diagnosis: caturid fishes with the following unique combination of features (possible apomorphies are indicated with an asterisk): long, slender, rod-like maxilla with more than 20 teeth; dentition with large, elongated, sharp teeth with laterally compressed ganoin caps; two to three suborbitals; multiple supraorbitals, at least the posterior ones thin and elongated and arranged in many rows*; four infraorbitals; subinfraorbital small and slender (at least four times longer than broad); preopercle ventrally expanded*; one paired of extrascapulars with smooth posterior borders; more than 20 branchiostegals; vertebral centra formed by dorsal and ventral hemicentra; 18–23 dorsal pterygiophores; dorsal fin origin anterior to pelvic fin origin; large, forked caudal fin with a high number of segmented caudal fin rays (24–34) and amioid type of scales with 24–51 transverse scale rows between postcleithra and dorsal fin origin, and 50–97 transverse scale rows from postcleithra to caudal fin origin.

4.1. Caturus brevicostatus [10] (Figures 5–10)

v* 1842 *Caturus brevicostatus* [10]: p. 44.
1848 *Caturus brevicostatus* [10]; [46].
v. 1863 *Liodesmus gracilis* [2]: p. 711.
1895 *Caturus brevicostatus* [10]; [4]: p. 350.
v. 1895 *Liodesmus gracilis* [2]; [4]: p. 361.
v. 1895 *Liodesmus sprattiformis* [2]; [4]: p. 362.
1904 *Liodesmus gracilis* [2]; [47]: p. 180.
1905 *Liodesmus gracilis* [2]; [48], name only.
pv. 1998 *Liodesmus gracilis* [2]; [9]: pp. 10, 575, 580, 584, 611, figs. 243, 244, 406a.
1998 *Liodesmus sprattiformis* [9]: pp. 10, 575, 580, 584, 611. 618.
1999 *Liodesmus gracilis* [2]; [8]: pp. 216, 220.
2013 *Liodesmus gracilis* [2]; [49]: fig. 6.
2013 *Liodesmus gracilis* [2]; [50]: fig. 2.
2013 *Liodesmus gracilis* [2]; [51]: p. 193, figs. 5, 6.
2015 *Liodesmus gracilis* [2]; [52]: p. 569 (name only).
2018 *Liodesmus gracilis* [2]; [53]: fig. 9.
2019 *Liodesmus gracilis* [2]; [54]: fig. 14.
2020 *Liodesmus gracilis* [2]; [55]: fig. 7.

Holotype: MB.f.3849 (Figures 5A,B, 6, 8A, 9A and 10)

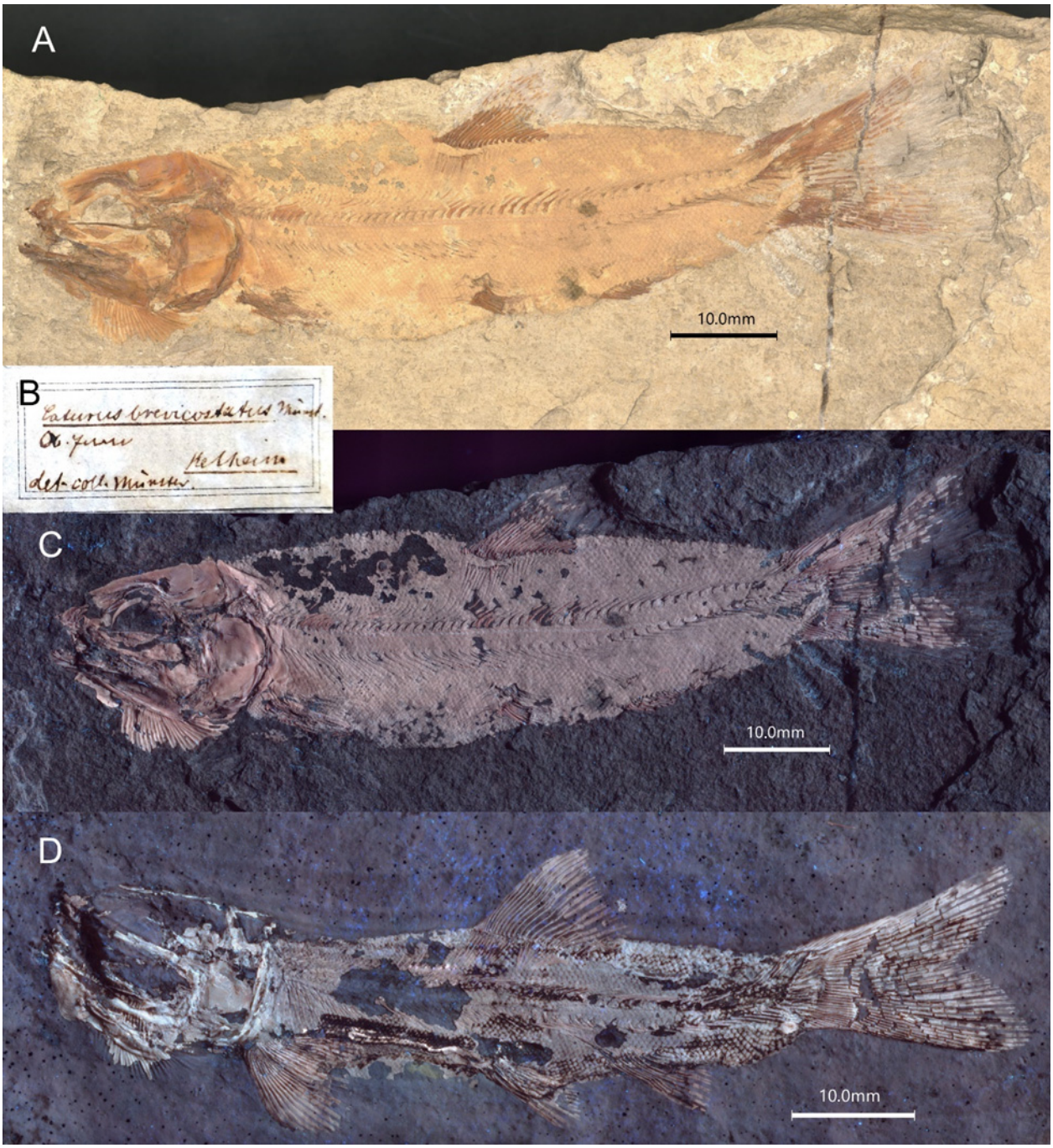

Figure 5. *Caturus brevicostatus* [10] from the Solnhofen Archipelago, Bavaria, Germany. (**A**) MB.f.3849 from Kelheim original photograph; (**B**) MB.f.3849 old label; (**C**) MB.f.3849 UV-photo; (**D**) SNSB-BSPG 1986 XV 136 from Eichstätt (UV-photo). (Photos M. Ebert).

Additional material: JME-SOS4308 (from Langenaltheimer Hardt), JME-SOS4787a,b (Wintershof), LF 578 (Eichstätt), NHMUK PV OR 37931 (Figures 7 and 8B; Solnhofen), NHMUK PV P.912 (Solnhofen), NHMUK PV P.3659 Kelheim, NMS 1891. 42. 1 (Kelheim), NMS 1905. 62. 5 (Solnhofen), SNSB-BSPG 1986 XV 136 (Figures 5D and 9B; Eichstätt); and most probably SNSB-BSPG AS VII 1122 (Figure 2C; Kelheim).

Type locality: Kelheim (most probably Kapfelberg), Solnhofen Archipelago, Bavaria, Germany.

Type horizon: Upper Kimmeridgian (*Ulmense* subzone).

Other localities and stratigraphy: Eichstätt and Wintershof, both Eichstätt basin (lower Tithonian, *eigeltingense* β horizon); Solnhofen (lower Tithonian, *rueppellianus* subzone).

Species diagnosis: Small Caturidae with the following unique combination of features; possible apomorphies are identified with an asterisk *: maximum body depth in proportion to SL is 17–25%; four infraorbitals; lacrimal (first infraorbital) longer than deep; subinfraorbital (infraorbital two) subrectangular, deeper than long; one posteriorly unserrated extrascapular; sclerotic ring present; anterior part of the lower jaw straight; maxilla narrow (rod-like), with small postmaxillary notch; teeth on maxilla and dentary large; 23–25 branchiostegals; 25–26 supraneurals; 50–51 neural spines; 20–21 dorsal pterygiophores; 11–12 anal pterygiophores; caudal fin only slightly forked with long median fin rays and 30–31 segmented caudal fin rays; both lobes of the caudal fin posteriorly rounded*; ventral caudal scute present; small and numerous amioid scales, with 49–51 transverse scale rows between postcleithra and dorsal fin origin*, 95–97 transverse scale rows from postcleithra to caudal fin origin, and a maximum of ~21 scales in one transverse scale row dorsal to the lateral line.

$$\textbf{Pterygial formula}: \frac{D49\text{–}51}{P37\text{–}40 \quad A60\text{–}63 \quad C95\text{–}97}\, T?$$

Morphological Description

General features: *Caturus brevicostatus* is a small, slender Halecomorphi, with 10.1 cm total length (standard length SL = 8.3 cm) in the largest specimen (JME-SOS4787). The maximum body depth is 17–25% SL. The fins are relatively short. The deepest part of the body is slightly anterior to the dorsal fin. The head, including the opercular series, measures approximately 27% of SL The description is mainly based on the holotype (MB.f.3849) (for measurements of different species see Table 1).

Skull roof: The skull roof is well preserved in the holotype (MB.f.3849, Figure 6), where the left side of the skull is visible, and in NHMUK PV OR 37931 (Figure 7), the skull is split in the middle and parts can be seen from both sides. The skull, roof bones, and the operculum are smooth, without ridges or tubercles. The nasals are large triangular bones anterior to the frontals and dorsally to the premaxilla. The rostral at the anterior tip between the nasal and premaxilla is small, tubular, and slightly curved in a U-shape (visible in NHMUK PV OR 37931, Figure 7). The antorbital is not preserved in any of the specimens.

The elongated frontals are the largest bones of the skull roof, as usual in Halecomorphi. The supraorbital sensory canal is visible on the posterior-ventral part of the frontal, passing above the dorsal border of the eye and then curving ventrally through the dermosphenotic into the dermopterotic. Another branch of the supraorbital sensory canal runs directly into the parietal.

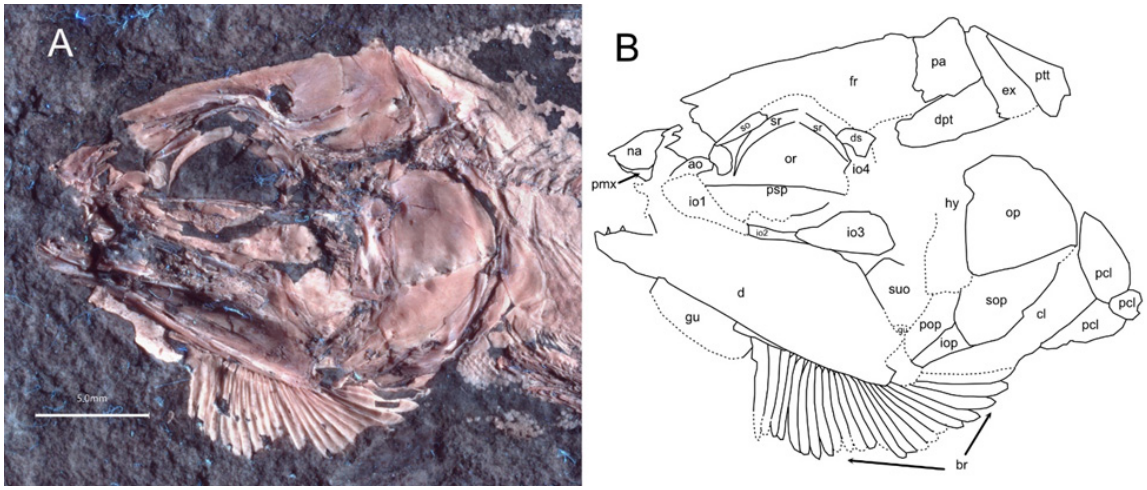

Figure 6. Cranium of *Caturus brevicostatus* [10] holotype (MB.f.3849) from Kelheim, Bavaria, Germany. (**A**) UV photograph. (Photo: M. Ebert); (**B**) drawing.

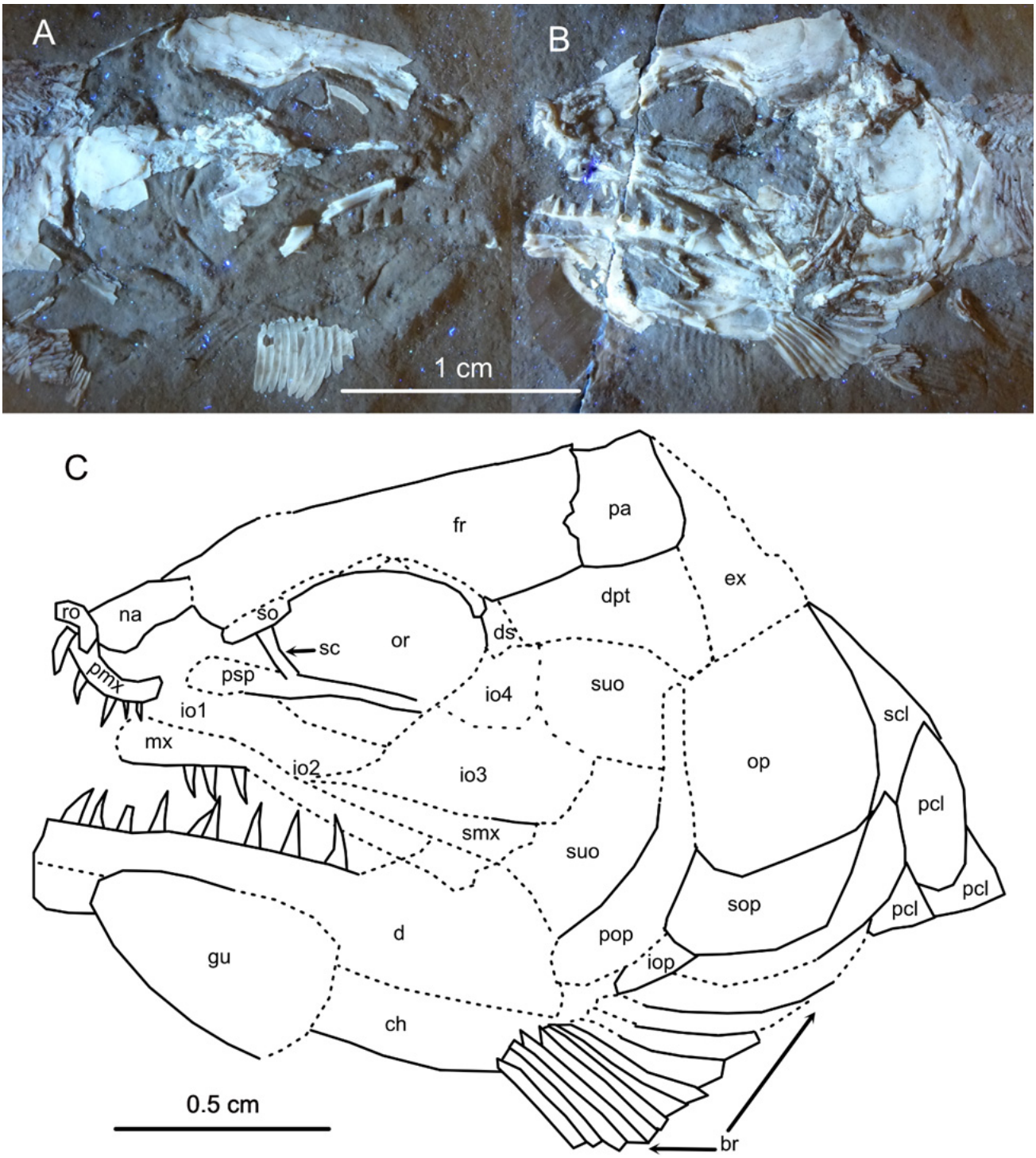

Figure 7. Cranium of *Caturus brevicostatus* [10] (NHMUK PV OR 37931) from Solnhofen, Bavaria, Germany. (**A**,**B**) UV photo of part and counterpart. (Photos: M. Ebert); (**C**) drawing of counterpart.

The parietal is nearly quadrangular and has some pores on the surface. It has an indentation for the sensory canal at the anterior ventral border.

There is a single, triangular extrascapular on each side, which reaches the dorsal midline of the skull. The extrascapulae completely enclose the occipital sensory canal (=supratemporal commissural canal), which is visible as a groove along the midline of the bone. The supratemporal sensory canal is only weakly visible along the ventral border of the extrascapular.

The posttemporal has nearly the same shape as the extrascapular. Posttemporal and extrascapular are not serrated posteriorly. The posterior ventral border of the posttemporal is overlapped by scales.

The dermosphenotic is fully incorporated into the skull roof. The visible part is ventrally smaller than dorsally. Ventrally, where the dermosphenotic contacts the dorsalmost infraorbital, this bone tapers to a point for the opening of the infraorbital canal. The dorsal border to the frontal is bow-shaped.

The dermopterotic is nearly rectangular; it is slightly deeper posteriorly than anteriorly. Near the ventral border of the dermopterotic, the main sensory canal is visible, which extends from the dermosphenotic to the extrascapular.

A small portion of the parasphenoid is visible along the lower border of the orbit. On the holotype, small teeth are visible along the parasphenoid. Since the suborbitals are missing in MB.f.3849 due to preservation, a large part of the hyomandibular is visible. The visible part anterior to the operculum looks like an hourglass.

Circumorbital series and suborbitals: At least four or five supraorbitals are visible in NHMUK PV OR 37931, but due to the poor preservation of the specimens, the exact number cannot be counted. At the anterior end of the eye, however, there appears to be one larger supraorbital.

An antorbital is not fully observable in any of the specimens; only in MB.f.3849 does it almost reach the orbit. A small portion of the parasphenoid is visible along the lower border of the orbit. Parts of the sclerotic ring are visible at the dorsal border of MB.f.3849 and NHMUK PV OR 37931.

The infaorbitals are not well preserved in any of the specimens and can best be seen in MB.f.3849. There appear to be four infraorbitals in total. As is usual in Caturidae, the lacrimal (first infraorbital) is somewhat smaller than the eye; it is slightly wider anteriorly and tappers posteriorly. The subinfraorbital (second infraorbital) is a thin, elongated bone at the ventral border of the orbit. The third infraorbital is about half the size of the eye with a rounded, convex posterior border not reaching to the preoperculum. Only a faint impression of the fourth and final infraorbital can be seen.

The suborbital bones are not clearly visible in any of the specimens. There is probably one large ventralmost suborbital that covers most of the quadrate.

Opercular series, branchiostegals, and gular: No tubercles were observed on the opercular bones, which are absent in other Caturidae of comparable size as well. None of the opercular bones have serrated borders.

The shape of the preoperculum is not visible in any of the specimens.

The operculum is large, about double the size of the suboperculum. Its antero-posterior width reaches nearly its dorsal-ventral extension. The ventral border of the operculum is nearly straight, except on its anterior part, where it bends dorsally, corresponding to the shape of the dorsal border of the suboperculum. The anterior border of the operculum is straight. The posterior and dorsal borders of the operculum are convexly curved.

The suboperculum has a long anterodorsal process that inserts between the operculum and preoperculum. The suboperculum has a convexly curved posterior border, a straight anterior-ventral border that abuts the interoperculum, a posterodorsally directed anterodorsal border terminating in the anterodorsal process, and a dorsal margin bordering the operculum.

The interoperculum is triangular and relatively small.

There are 23–25 branchiostegals in the observed specimens. The gular plate is very well visible in SNSB-BSPG 1986 XV 136 and NHMUK PV OR 37931, where it is slightly disarticulated.

The gular plate is nearly twice as long as it is broad, with its anterior part smaller than the posterior part. Its antero-posterior length is as long as the orbital length and a little less than half the length of the lower jaw. The growth rings of the gular can be clearly seen in SNSB-BSPG 1986 XV 136.

Jaws: The upper jaw is not well preserved in any of the specimens; only in NHMUK PV OR 37931 (Figure 7A) it can be seen from a small part of the upper jaw that it was thin and rod-shaped, as is common in Caturidae. In this fragment, it can also be seen that the posterior end of the maxilla turns ventrally. The ventral border of the maxilla bears large, pointed teeth. The exact number of teeth on the maxilla is not countable in any of the specimens. In NHMUK PV OR 37931, only three maxillary teeth are preserved.

Shoulder girdle and axial skeleton: The supracleithrum is an elongated element at the posterior border of the operculum. The lateral line canal, which comes from the extrascapular and the posttemporal, extends through the dorsal half of the supracleithrum and continues then dorsally in the squamation. The posterodorsal border of the supracleithrum is not serrated.

There are three smooth and unserrated postcleithra visible in MB.f.3849 and NHMUK PV OR 37931, with the dorsalmost much larger than the two ventral to it. The cleithrum is overlapped dorsally by the operculum, in its median part by the suboperculum, and anteroventrally by the branchiostegal rays.

The axial skeleton is covered by amioid scales, but these scales are so thin and transparent that the axial skeleton is clearly visible through the scales, or even better, in most specimens, the scales are visible from the interior side and the axial skeleton is uncovered and clearly visible. Dorsal to the notochord there are 50–52 neural spines between the cranium and the caudal fin. No hints of vertebrae centra are visible. There are 26 paired, long pleural ribs in the stomach area anterior to the anal fin, 23 haemal spines posterior to the anal fin, and at least seven hypurals (more are covered by caudal fin rays). There are a total of 25–26 elongated supraneurals. They have approximately double the length of the neural spines. Apart from the anteriormost, the ventralmost parts of the supraneurals insert between the dorsalmost parts of the neural spines. The posteriormost five supraneurals insert dorsally between the dorsal pterygiophores.

Paired fins: The pectoral fin is short (best visible in NMS 1905.65.5, NMS 1891.42.1, and SNSB-BSPG 1986 XV 136, Figure 5D). In NMS 1905.65.5 there are 20 rays, with the fifth ray being the longest. One basal fulcrum preceding the first ray. The rays are segmented and rarely branched; they only branch once near the proximal tips of the rays (best visible in SNSB-BSPG 1986 XV 136). Fringing fulcra on the pectoral fin are not observable at any of the specimens.

The pelvic fin originates behind the 37th to 40th vertical scale row, slightly posterior to the position of the origin of the dorsal fin. In the specimens where this fin is preserved, eight to ten segmented rays are visible, with the third ray being the longest. In the holotype, seven small basal fulcra precede the first segmented ray. The rays only branch once near the proximal tips of the rays (best visible in SNSB-BSPG 1986 XV 136). Fringing fulcra on the pectoral fin are not observable at any of the specimens.

Median fins: The dorsal fin (Figures 5 and 8) is located behind the 49th to 51th vertical scale row. The origin of the dorsal fin is located slightly anterior to the height of the pelvic fin origin. There are 20–21 dorsal pterygiophores and 19–20 corresponding segmented dorsal fin rays. The dorsal fin is as high as it is long, forming a triangle. The anterior edge is stiffened by six to eight basal fulcra, preceded by around three small oval scales (best visible in the holotype), which are thicker and smaller than the normal body scales. Fringing fulcra are absent. The fifth segmented and branched ray is the longest; from the eighth ray onward, the rays shorten quickly. The unsegmented basal part of the fin rays is long and takes up about the lower half of the fin. The rays only branch once near the proximal tips (best visible in SNSB-BSPG 1986 XV 136, Figure 5D).

The anal fin is in shape and dimension very similar to the pelvic fin. There are 11–12 anal pterygiophores and 11–12 corresponding segmented rays (best visible in SNSB-BSPG 1986 XV 136, Figure 5D). Anterior to these branched rays, there are two to four unsegmented basal fulcra. Fringing fulcra are upsent. Here too, the unsegmented basal parts of the lepidotrichia are long, and the rays only branch once near the proximal tips.

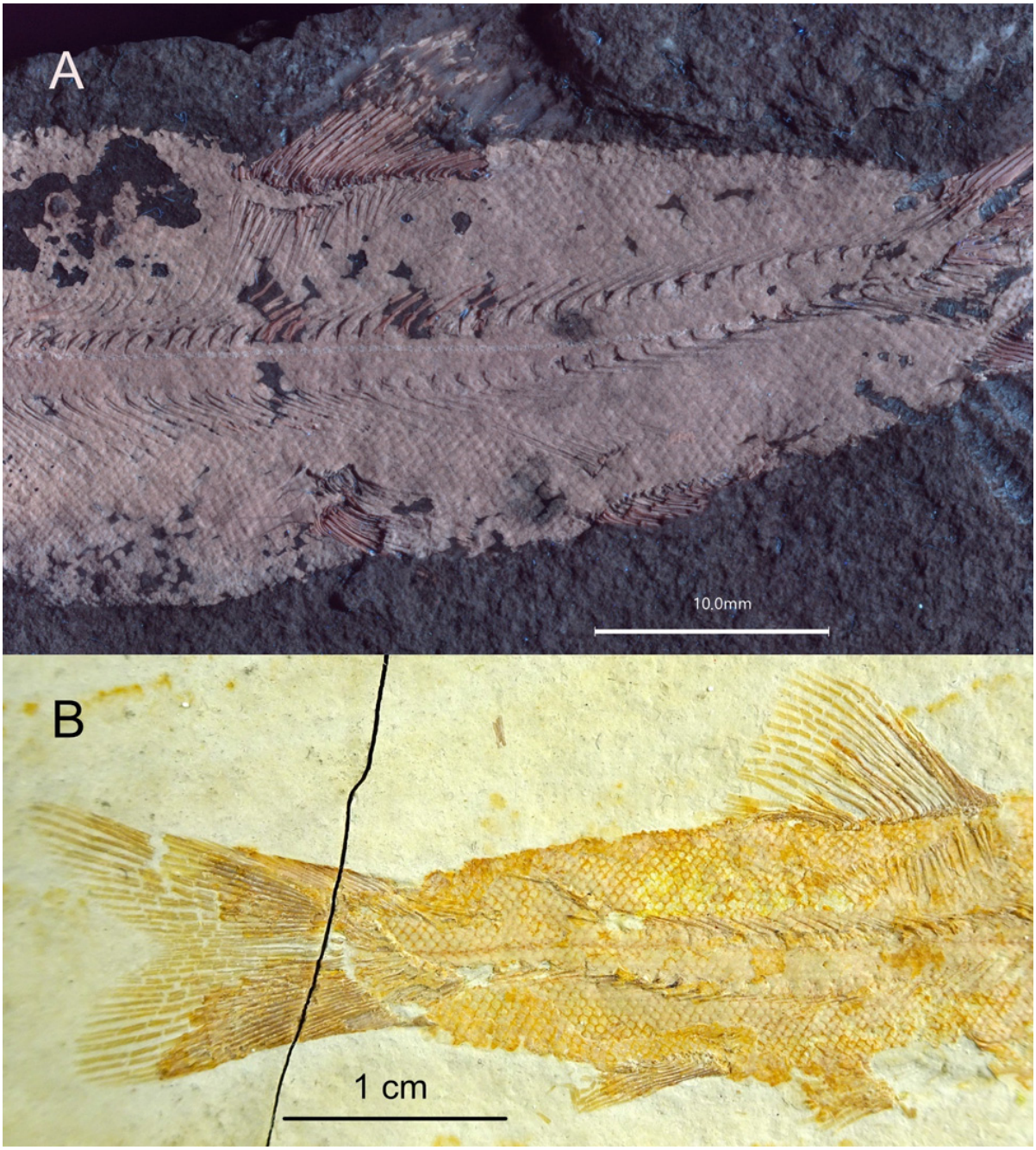

Figure 8. *Caturus brevicostatus* [10] posterior body region. (**A**) posterior body region with dorsal-, pelvic-, and anal fin of the holotype (MB.f.3849) from Kelheim, Bavaria, Germany; (**B**) posterior body region with dorsal-, pelvic-, anal-, and caudal fin of NHMUK PV OR 37931 from Solnhofen, Bavaria, Germany. (Photos: M. Ebert).

The caudal fin is only slightly forked (best visible in BSPG 1986 XV 136 (Figure 9B), NMS 1905.65.5, and JME-SOS4787). On the caudal fin there are 22–24 principal rays. The dorsalmost ray, which is the first principal ray, is dorsally flanked by eleven basal fulcra. Ventral of the ventralmost principal ray, there are about six segmented but unbranched rays, which are called procurrent rays. The segments of the rays are elongate (more than three times longer than deep), and the rays only branch once near the proximal tips. Three fringing fulcra are visible on the dorsal lobe of the holotype; fringing fulcra on the ventral lobe are absent. At least five urodermals are visible on the holotype (Figure 9A).

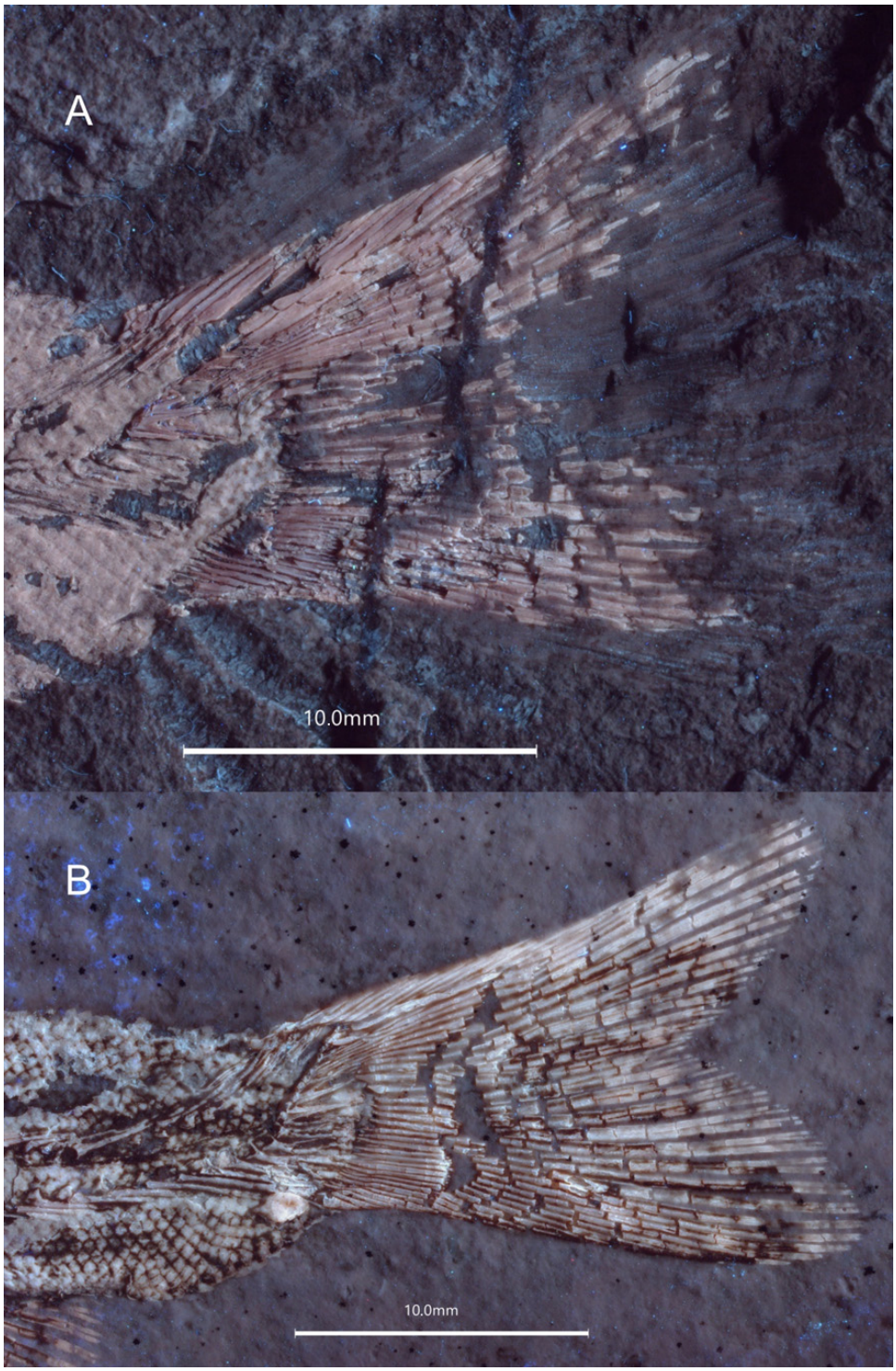

Figure 9. UV photos of the caudal fin of *Caturus brevicostatus* [10]. (**A**) holotype (MB.f.3849) from Kelheim, Bavaria, Germany; (**B**) SNSB-BSPG 1986 XV 136 from Eichstätt, Bavaria, Germany with long median fin rays. (Photos: M. Ebert).

Squamation: There are 49–51 transverse scale rows between postcleithra and dorsal fin origin, and 95–97 vertical rows of scales between the shoulder girdle and the caudal fin origin (best countable on MB.f.3849 (holotype, Figure 5B); JME-SOS4308; NMS 1891.42.1; NHMUK PV OR 37931; NHMUK PV P.912 and SNSB-BSPG 1986 XV 136; for a comparison with other Caturidae see Figure 20). Anterior to the dorsal fin, one single vertical scale row dorsal of the lateral line has a maximum of approximately 21 scales per row. The scales of

the body are of amioid type (Figures 3C and 10). On the holotype, the scales are visible from the interior side, and the lateral line is clearly observable from the posttemporal, nearly to the caudal area (Figure 5B).

Figure 10. Scales of *Caturus brevicostatus* [10] holotype (MB.f.3849) from Kelheim, Bavaria, Germany, visible from the interior side of the body (cranium to the right, UV Photo M. Ebert).

Family indet.

Genus *Nasrinsotoudehichthys*, gen. nov.

Zoobank registration of genus: urn:lsid:zoobank.org:act:0B744A60-413C-4B19-8E1C-26FF564B74B6

Etymology: To honor the Iranian lawyer, 2012 winner of the Sakharov Prize for Freedom of Thought and 2020 winner of the Right Livelihood Award Nasrin Sotoudeh (cf. https://en.wikipedia.org/wiki/Nasrin_Sotoudeh accessed on 1 May 2024.).

Diagnosis: As for type and only species.

4.2. Nasrinsotoudehichthys sprattiformis [2] (Figures 11–19)

1863 *Liodesmus sprattiformis* [2]: 713; pl. 5, fig. 1 (specimen missing).

v. 1992 *Liodesmus* [2]; [56]: figs. 29a (JME-SOS3453).

v. 1992 *Liodesmus sprattiformis* [2]; [56]: figs. 29b, 37 (SNSB-BSPG 1986 XV 113).

vp. 1999 *Liodesmus sprattiformis* [2]; [8]: fig. 5 (SNSB-BSPG 1986 XV 113).

Neotype: SNSB-BSPG 1986 XV 113 (Figures 11A,B, 15A,B and 18C), from Zandt, Bavaria, Germany (labeled *Liodesmus sprattiformis*). Specimen in lateral view, with 6.2 cm standard length (SL).

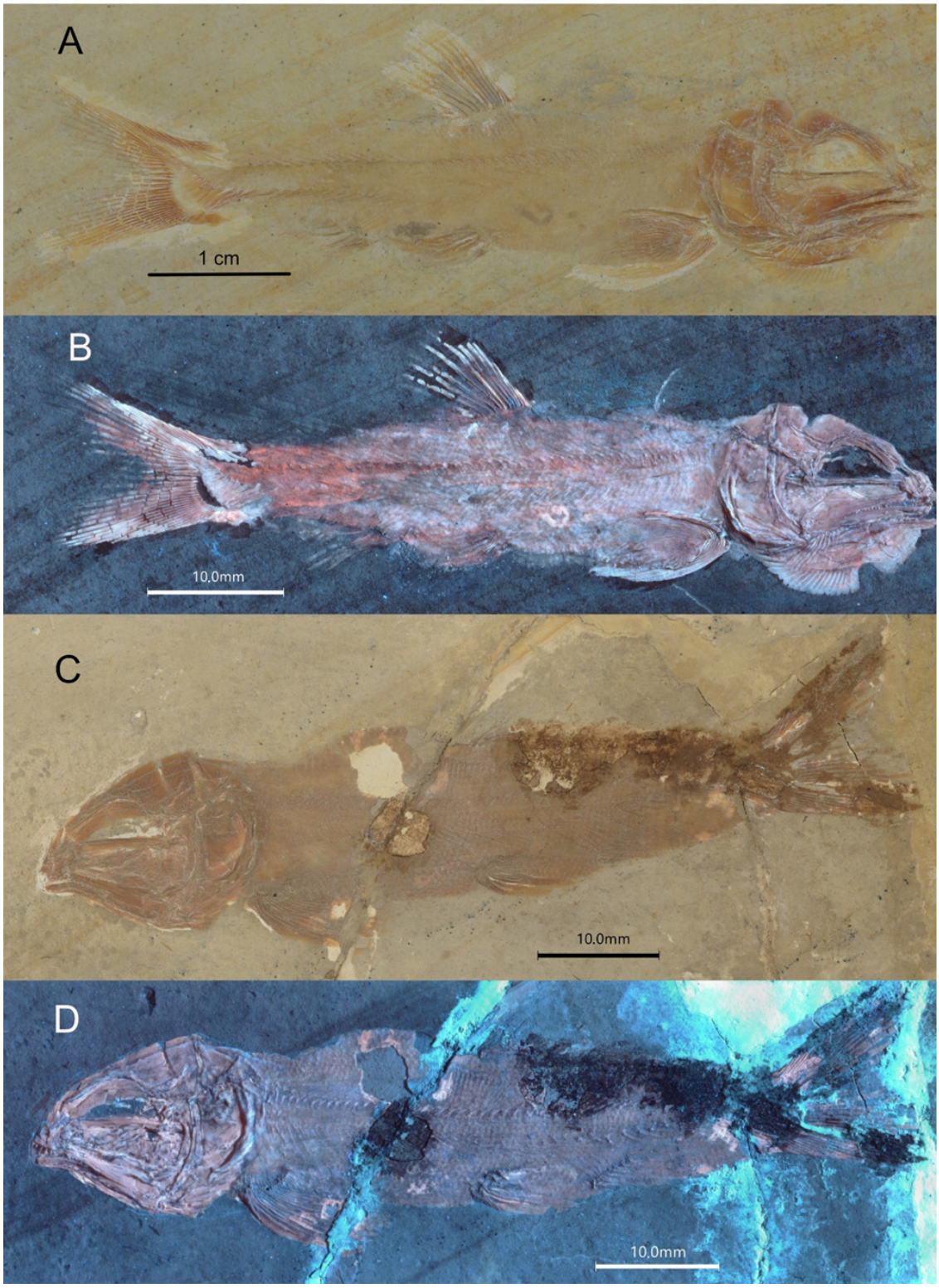

Figure 11. *Nasrinsotoudehichthys sprattiformis* [2] new gen. from the lower Tithonian of Zandt, Bavaria, Germany. (**A**) holotype (SNSB-BSPG 1986 XV 113) original photograph; (**B**) holotype (SNSB-BSPG 1986 XV 113) UV photograph; (**C**) JME-SOS3453 original photograph; (**D**) JME-SOS3453 UV photograph. (Photos M. Ebert).

Additional material: JME-SOS3453 from Zandt (Figure 11C,D; labeled *Liodesmus gracilis*); JME-SOS2602 (Figures 14A–C, 17 and 19) (from Breitenhill, Zandt Basin); LF 6037

(Figures 13A,B, 16C,D and 18B); LF 6068 (Figures 13C,D, 16A,B and 18A) (both from Zandt); SNSB-BSPG 1967 I 280 (from Zandt); and probably the two casts in NHMUK PV OR 37367, 37998 (Wagner [2] mentioned the locality of the original specimen as "Solnhofen", but this could be elsewhere in the Solnhofen Archipelago, for example, from Zandt, and the indicated stripes on the cast (NHMUK PV OR 37998) indicate the Liesegang rings typical for the material from Zandt).

Type locality: Zandt (Zandt basin), Solnhofen Archipelago, Bavaria, Germany. It is interesting that so far, all specimens of this taxon come from the Zandt Basin.

Type horizon: From the *eigeltingense* α horizon of the lower Tithonian.

Remarks: The original type specimens of "*Liodesmus sprattiformis*" [2] (pl. 5, fig. 1; Figure 12A) are missing; only casts in London are still available (NHMUK PV OR 37367 (Figure 12B); NHMUK PV OR 37998 (Figure 12C), therefore, we propose a neotype.

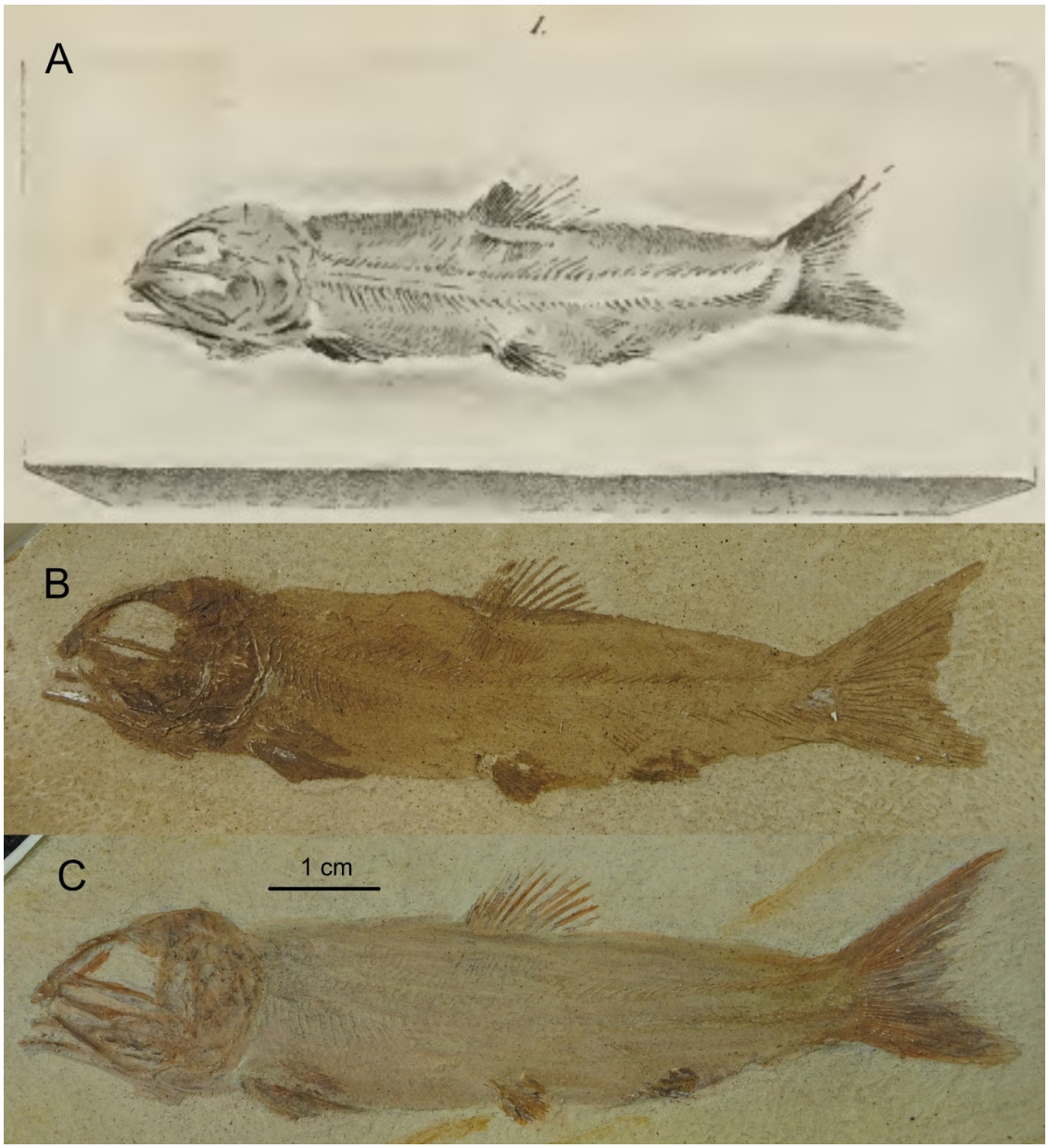

Figure 12. Missing holotype of *Liodesmus sprattiformis* [2] from the Solnhofen Archipelago, Bavaria, Germany. (**A**) drawing in [2] (pl. 5, fig. 1); (**B**) cast NHMUK PV OR 37367; (**C**) cast NHMUK PV 37998. (Photos: M. Ebert; to be able to compare it better with the drawing, the photos of the casts are mirrored).

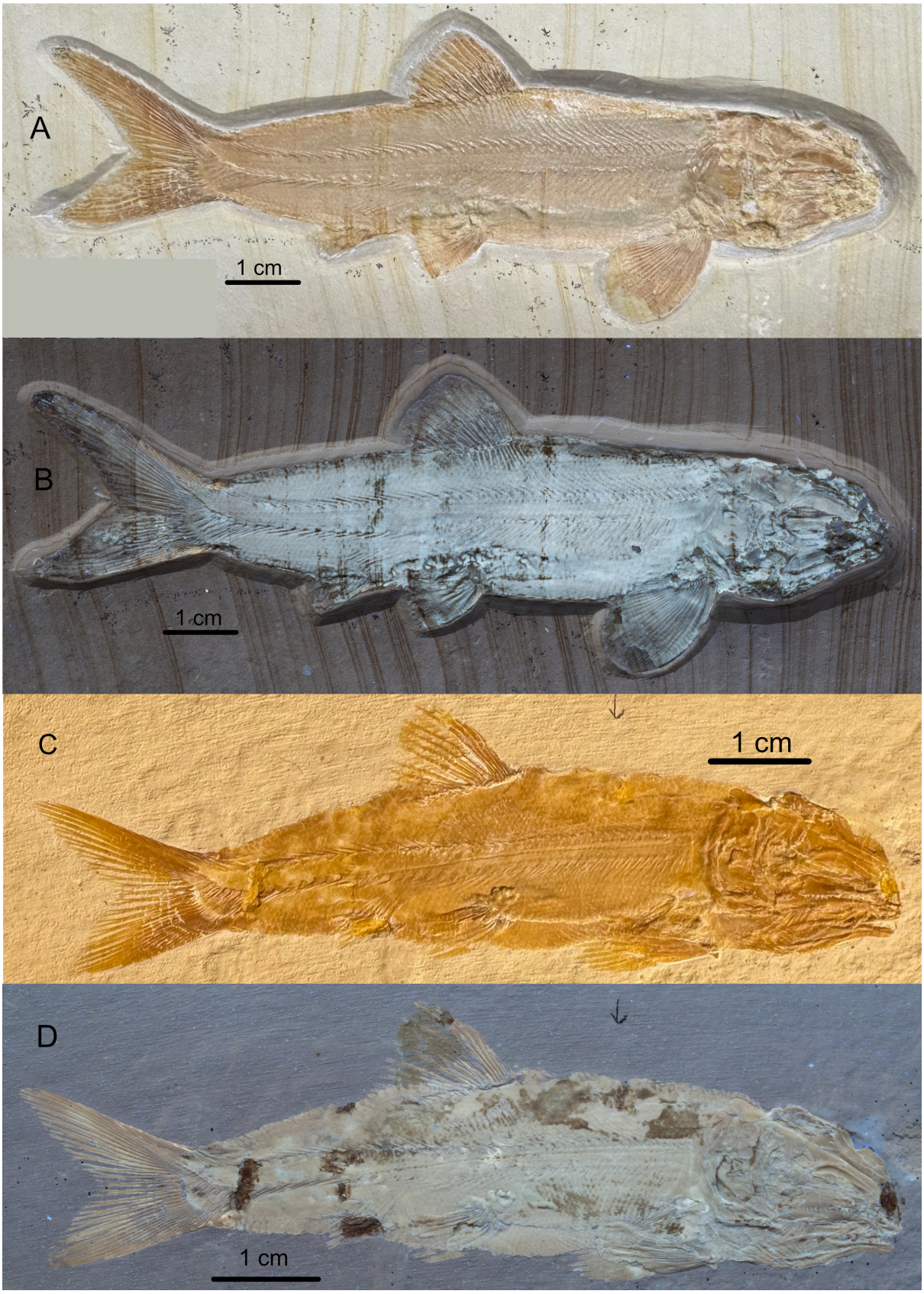

Figure 13. *Nasrinsotoudehichthys sprattiformis* [2] new gen. from the lower Tithonian of Zandt, Bavaria, Germany. (**A**) LF 6037 original photograph; (**B**) LF 6037 UV photograph; (**C**) LF 6068 original photograph; (**D**) LF 6068 UV photograph. (Photos: R. Lauer).

Species diagnosis: Small Caturoidea with the following unique combination of characters; possible apomorphies are identified with an asterisk *: maximum body depth in proportion to SL is 19–32%; four infraorbitals; posteriordorsalmost infraorbital directed posterodorsally; two suborbitals; one posteriorly unserrated extrascapular; three or four supraorbitals, of which the anteriormost is large, reaching nearly half the length of the eye; sclerotic ring absent; anterior part of the lower jaw slightly curved ventrally; teeth on maxilla and dentary small, maxilla gradually increasing in width posteriorly, with small postmaxillary notch, and maxillary canal; postmaxillary process without teeth; 40–41 vertical scale rows between the cranium and the insertion of the dorsal fin and approximately 80 scale rows from the cranium to the caudal fin; fringing fulcra on all fins present but only on large specimens; short dorsal fin (approximately 20% of SL), with 16–17 dorsal pterygiophores; *6–7 anal pterygiophores; caudal fin forked, with approximately 28–30 segmented caudal fin rays; amioid type of scales; ~16 branchiostegals.

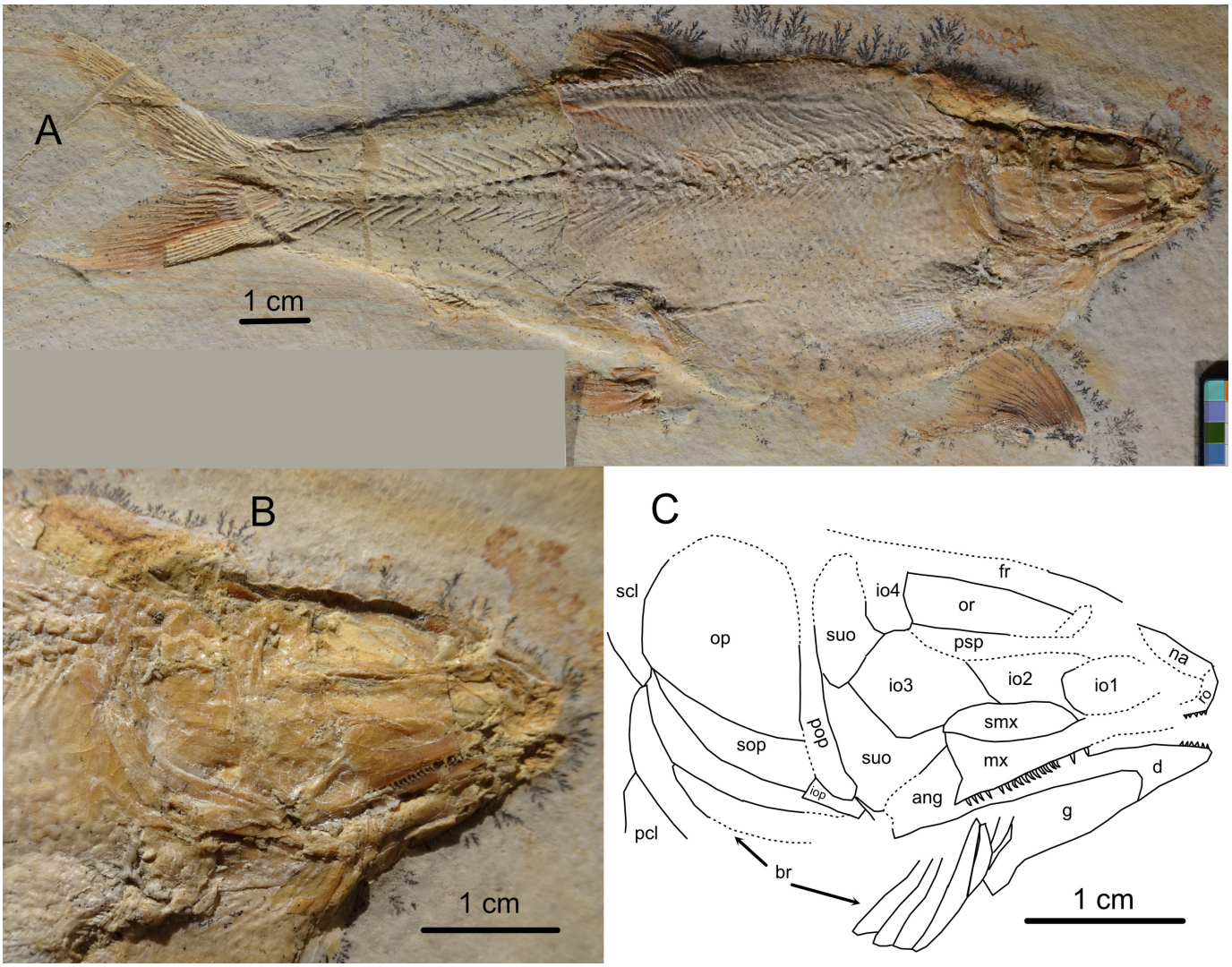

Figure 14. *Nasrinsotoudehichthys sprattiformis* [2] new gen. (JME-SOS2602) from the lower Tithonian of Breitenhill, Zandt Basin, Bavaria, Germany. (**A**) original photograph of complete specimen; (**B**) cranium; (**C**) drawing of cranium. (Photos: M. Ebert).

Morphological Description (If Not Otherwise Mentioned, the Description Is from the Holotype)

General features: *Nasrinsotoudehichthys sprattiformis* is a small Halecomorphi with 17.4 cm total length (standard length SL = 14.7 cm) in the largest specimens (JME-SOS2620). The maximum body depth is 19–32% SL. The fins are relatively short. The deepest part of the body is slightly anterior to the dorsal fin. The head, including the opercular series, measures approximately 26% of SL (for measurements of different species see Table 1).

Skull roof: The skull roof is well preserved in SNSB-BSPG 1986 XV 113 (holotype), where the right side of the skull roof is visible (Figure 15A,B) and in JME-SOS3453, where the left side of the skull roof is visible (Figure 15C,D). The skull roof bones and the operculum are smooth, without ridges or tubercles. The nasal is very well visible as small, triangular bone dorsally to the antorbital. The antorbital is a small, elongated, rectangular bone between the praemaxilla and the orbit. In the center of the antorbital and the nasal a sensory canal is visible, running from anteroventral to posterodistal.

The elongated frontals are the largest bones of the skull roof, as usual in Halecomorphi. The supraorbital sensory canal is visible on the posterior-ventral part of the frontal, passing above the dorsal border of the eye and then curving ventrally through the dermosphenotic into the dermopterotic. Another branch of the supraorbital sensory canal runs directly into the parietal.

The parietal is nearly quadrangular and has straight borders to the frontal, dermopterotic, and extrascapular.

There is a single extrascapular on each side, which reaches the dorsal midline of the skull. The anteroventral part of the extrascapular is overlapped by the dermopterotic. The extrascapulae completely enclose the occipital sensory canal (=supratemporal commissural canal), which is visible as a groove along the midline of the bone. The supratemporal sensory canal is only weakly visible along the ventral border of the extrascapular.

The posttemporal has about the same size as the extrascapular. Posttemporal and extrascapular are not serrated posteriorly. The anterior border of the posttemporal is overlapped by the extrascapular.

The dermopterotic is nearly triangular; it is deeper posteriorly than anteriorly. On the ventral half of the dermopterotic, the main sensory canal, which extends from the dermosphenotic is visible.

The dermosphenotic is fully incorporated into the skull roof. The visible part is ventrally smaller than dorsally. Posteroventral, the dermosphenotic contacts the dorsalmost infraorbital at the anterior-dorsal border. In SNSB-BSPG 1986 XV 113 and LF 6068, the uppermost part of the hyomandibular is visible.

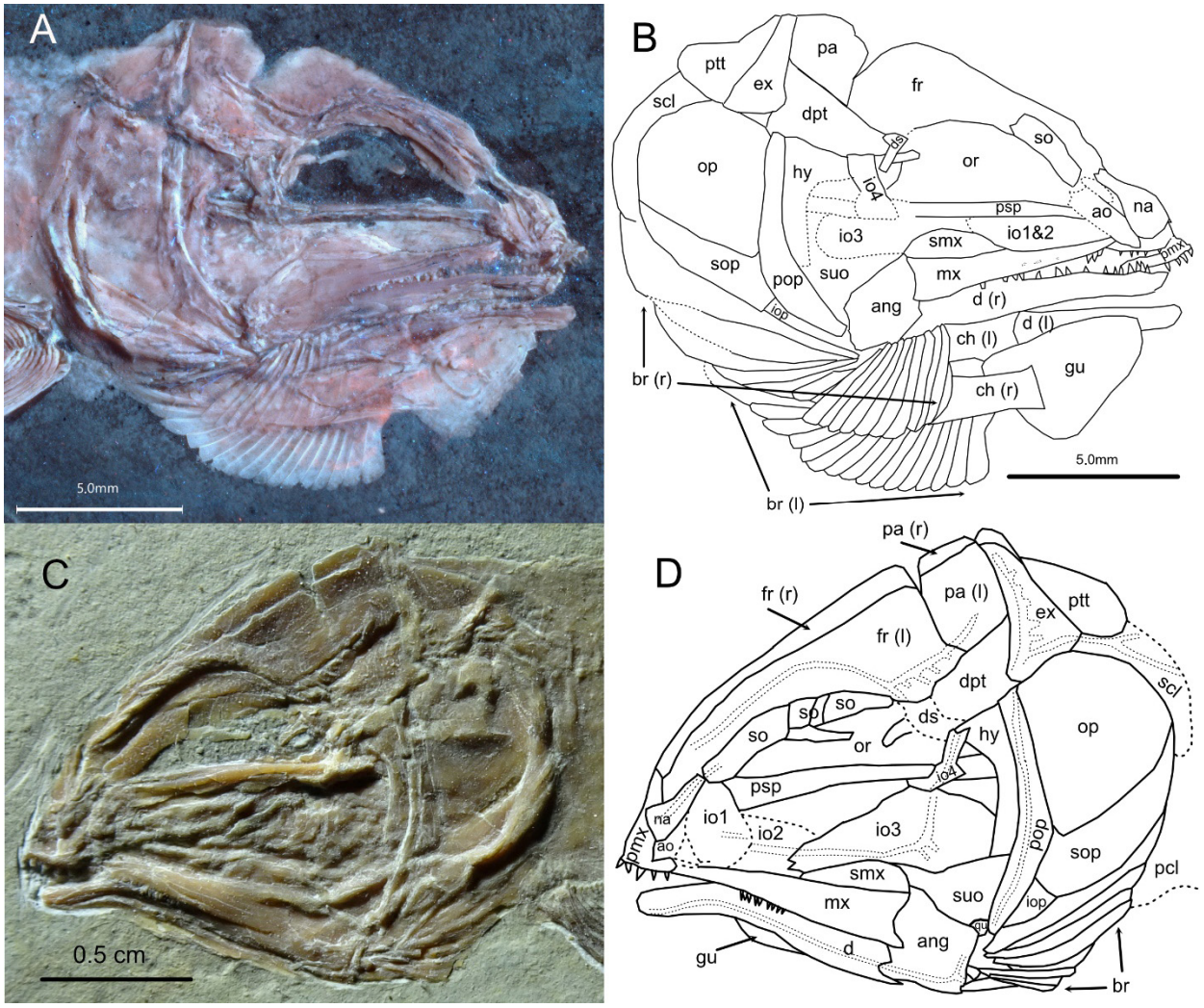

Figure 15. Cranium of *Nasrinsotoudehichthys sprattiformis* [2] new gen. from the lower Tithonian of Zandt, Bavaria, Germany. (**A**) holotype (SNSB-BSPG 1986 XV 113) UV photograph; (**B**) holotype (SNSB-BSPG 1986 XV 113) drawing; (**C**) JME-SOS3453 photograph; (**D**) JME-SOS3453 drawing. (Photos: M. Ebert).

Circumorbital series and suborbitals: There are four supraorbitals visible in JME-SOS3453 (Figure 15C,D and [56] fig. 29a). The anteriormost supraorbital is very large, with nearly half the length of the eye. The median two supraorbitals are much smaller, reaching not ¼ of the size of the anteriormost one. The posterior supraorbital nearly reaches half the length of the anteriormost. In LF 6037 and LF 6068 there are three large supraorbitals, with the anteriormost being twice as large as the following (Figure 16A–D).

The antorbital and the rostral bones are not clearly observable in any of the specimens.

A small portion of the parasphenoid is visible along the lower border of the orbit.

There are a total of four infraorbitals. The preservation of the anterior-most or first infraorbital (=lacrimal) and the second infraorbital (subinfraorbital) in none of the specimens is good enough to give a precise description of their dimensions. The third infraorbital is large with a rounded, convex posterior border. It is elongated posteriorly, reaching almost the preoperculum. The fourth and last infraorbital is a narrow, nearly rectangular bone, much deeper (dorso-ventrally) than it is wide (antero-posteriorly). Its upper part is directed posterodorsally, as in Ophiopsidae; see [9,57–59]. This bone forms the posterior border of the orbit and contacts the dermosphenotic dorsally and the third infraorbital ventrally. The infraorbital sensory canal passes in the ventral 1/3 of the first two infraorbitals, then curves dorsally on the third infraorbital, where it splits to a posteriorly directed branch and the

main branch of the sensory canal that passes dorsally onto the anteroventral part of the fourth infraorbital before continuing onto the dermosphenotic.

There are two large suborbitals best to be seen on the largest specimen, JME-SOS2602. One suborbital is posterioventrally to the third infraorbital, bordered by the angular posterodorsaly and the preopercle posteriorly. There is a second large suborbital posterodorsaly to the region to the third infraorbital. In the small specimens, this suborbital is hardly visible, and a large part of the hyomandubular is to be seen.

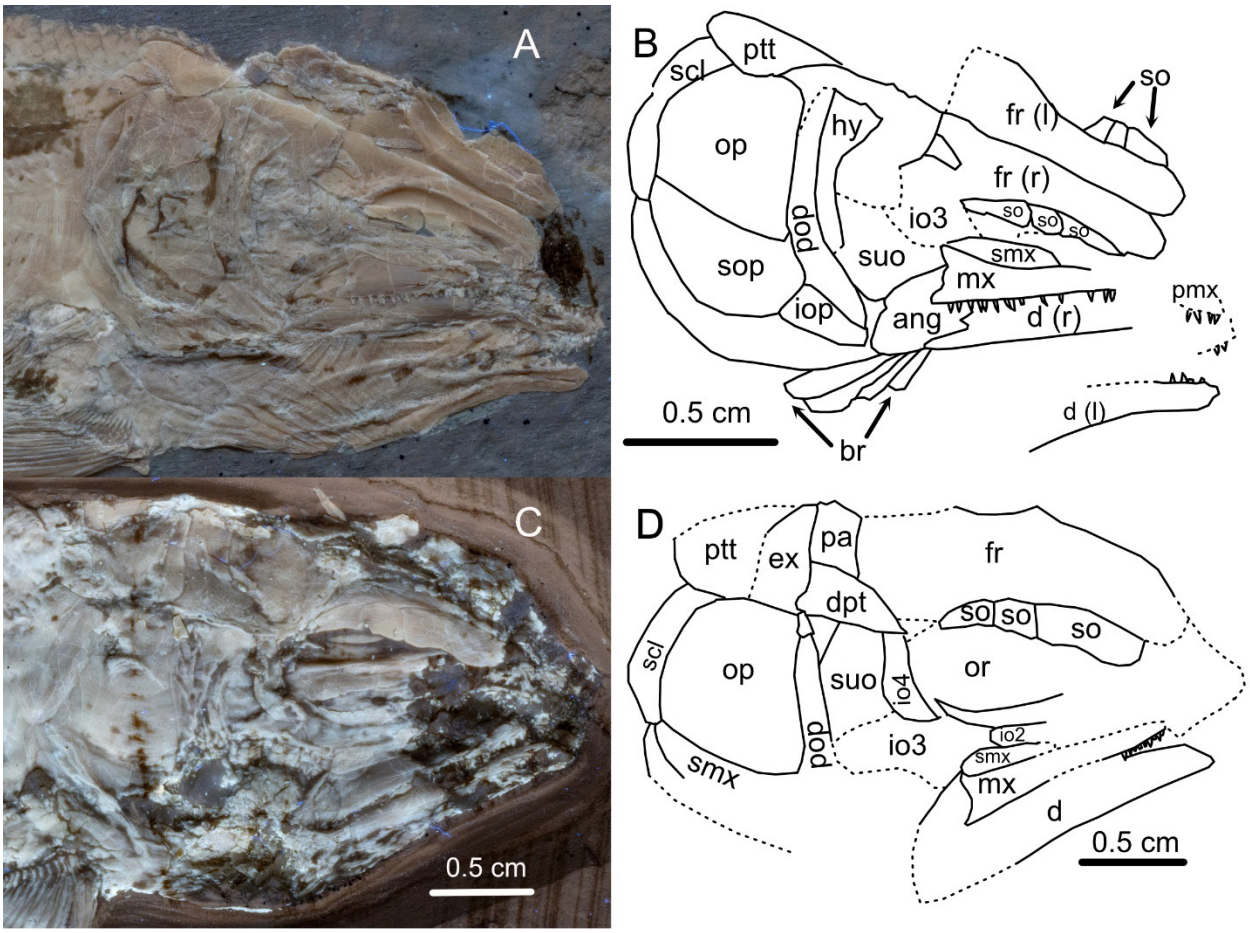

Figure 16. Cranium of *Nasrinsotoudehichthys sprattiformis* [2] new gen. from the lower Tithonian of Zandt, Bavaria, Germany. (**A**) LF 6068, UV photograph; (**B**) LF 6068, drawing; (**C**) LF 6039, UV photograph; (**D**) LF 6039, drawing. (Photos: R. Lauer).

Opercular series branchiostegals and gular: No tubercles were observed on the opercular bones. None of the opercular bones have serrated borders.

The preoperculum is a narrow, elongate, curved bone, reaching the dermopterotic dorsally. Its antero-posterior width is approximately the same at the anterior and posterior 1/3 of the bone. In the middle, at the height of the suboperculum, the antero-posterior width of the preoperculum doubles. The preopercular canal is to be seen at the entire length of the preoperculum.

The operculum is large, about double the size of the suboperculum. Its antero-posterior width reaches nearly its dorsal-ventral extension. The ventral border of the operculum is nearly straight, except on its anterior part, where it bends dorsally, corresponding to the shape of the dorsal border of the suboperculum. The anterior border of the operculum is straight. The posterior and dorsal borders of the operculum are convexly curved.

The suboperculum has a long anterodorsal process that inserts between the operculum and preoperculum. The suboperculum has a convexly curved posterior border, a

straight anterior-ventral border that abuts the interoperculum, a posterodorsally directed anterodorsal border terminating in the anterodorsal process, and a dorsal margin bordering the operculum.

The interoperculum is triangular and relatively small. Ventrally, the interoperculum overlaps the dorsalmost branchiostegal.

There are 15 branchiostegal rays from the right side countable on SNSB-BSPG 1986 XV 113. The length of the branchiostegals increases from the first to the posteriormost, which is 2.5 times as long and about three times as broad as the first branchiostegal. Between the branchiostegals of the left and right side, two broad ceratohyals are visible in SNSB-BSPG 1986 XV 113.

The gular plate is very well visible in SNSB-BSPG 1986 XV 113, where it is slightly disarticulated. The gular plate is nearly twice as long as it is broad, with its anterior part smaller than the posterior part. Its antero-posterior length is as long as the orbital length and a little less than half the length of the lower jaw. The growth rings of the gular can be clearly seen in SNSB-BSPG 1986 XV 113.

Jaws: The maxilla is clearly shorter than the mandible, reaching nearly the posterior border of the orbit. The maxilla is narrow anteriorly but rapidly widens posteriorly (different to Caturidae). The ventral border of the maxilla is nearly straight and bears at least 16 small, robust, pointed teeth in the largest specimen (Figure 14C), but some more are missing. The exact number of teeth on the maxilla is not countable in any of the specimens. The characteristic feature of advanced halecomorphs of having a concave curve posteriorly (postmaxillary notch) is present in this species as well. *Nasrinsotoudehichthys sprattiformis* has a short postmaxillary process beneath this postmaxillary notch, which is characteristic for halecomorphs as well. This process has no teeth. The maxilla is tapered anteriorly, but the anteroventral tip is covered by the antorbital. The dorsal border of the maxilla is straight as well, and a supramaxillary process is absent. A maxillary canal is best observable on SNSB-BSPG 1986 XV 113 (Figure 15A).

There is a single supramaxilla, which borders a little less than half of the posterodorsal part of the maxilla. The supramaxilla is broad, with the broadest part at the posterior two-thirds, and its entire dorsal border is convexly curved. The ventral border of the supramaxilla is relatively straight.

The premaxilla with four to five teeth is very well visible in SNSB-BSPG 1986 XV 113 and JME-SOS3453. The teeth on the premaxilla are medium in size and are not remarkably larger than the maxilla or dentary teeth.

The dentary is relatively long, and except for the anteriormost ¼, which curves slightly downwards, its ventral surface is straight. As in other halecomorphs [9], the quadrate articulation is located behind the posterior border of the orbit. The mandibular sensory canal is visibly along the whole length of the dentary (best visible in JME-SOS3453); it extends to the middle of the bone, between the dorsal and ventral borders of the dentary. There are at least 13 teeth on the dentary visible in SNSB-BSPG 1986 XV 113, and a few more may have been present in the middle and anterior parts. The teeth on the dentary are slightly larger than those on the maxilla.

The quadrate is nearly covered by a suborbital; only the ventralmost part of the quadrate is exposed in some of the specimens.

Shoulder girdle and axial skeleton:

The supracleithrum is an elongated element at the posterior border of the operculum. The lateral line canal, which comes from the extrascapular and the posttemporal, extends through the dorsal half of the supracleithrum and continues then dorsally in the squamation. The posterodorsal border of the supracleithrum is not serrated.

There are some postcleithra ventral to the supracleithrum, but the exact number is not countable due to the preservation of the specimens.

The cleithrum is overlapped dorsally by the operculum, in its median part by the subopercular, and anteroventrally by the branchiostegal rays.

The axial skeleton is covered by amioid scales, but these scales are thin and transparent, and most of the axial skeleton is visible through the scales. No hints of vertebrae centra are visible in the small specimens; only in the anterior halve of the body of the largest specimen (JME-SOS2602) halve ring centra are developed.

There are 47–48 neural spines countable in LF 6037, LF 6068, SNSB-BSPG 1986 XV 113, and the cast in London (NHMUK PV OR 37367).

There are approximately 20 elongated supraneurals, visible through the slightly transparent scales in LF 6037. They have two to three times the length of the neural spines. Apart from the anteriormost, the ventralmost parts of the supraneurals insert between the dorsalmost parts of the neural spines. The posteriormost three supraneurals insert dorsally between the dorsal pterygiophores.

There are 14 unpaired haemal spines without contact to the caudal fin. The median haemal spines are near the caudal peduncle region, strongly inclined to a nearly horizontal orientation as in Caturidea.

Paird fins: The pectoral fin is slightly larger than the pelvic or anal fins (good visible in JME-SOS2602 (Figure 17C), JME-SOS3453, LF 6037 (Figure 17A), and SNSB-BSPG 1986 XV 113). In JME-SOS2602 and LF 6037, there are approximately 22 pectoral rays and two basal fulcra. The first ray is very wide, with segments at least three times longer than broad, but the rays in the anterior halve of the fin are unbranched. Branching of fin rays on the pectoral fins is only present in large specimens and there only in the posterior half of the fin.

In the largest specimen, JME-SOS2602, the most posterior basal fulcrum is partially split, forming two fulcra-like ends, followed by two separate fringing fulcra.

In SNSB-BSPG 1986 XV 113, there are approximately 26 rays.

The pelvic fins are, together with the anal fin, the smallest fins (Figure 17B–D). The pelvic fins originate slightly posterior to the position of the origin of the dorsal fin. The posteriormost fin tips reach almost the anal fin origin. The pelvic fin has seven or eight segmented fin rays, followed by approximately seven basal fulcra. Here too, as in the pectoral fin, the first segmented fin ray is broad but unbranched, followed by up to eight fringing fulcra in the larger specimens.

Median fins: The dorsal fin is as high as it is long, forming a triangle (Figure 17E,F). In the largest specimen (JME-SOS2602), the anterior edge is stiffened by six basal fulcra and 12 fringing fulcra. There is one fringing fulcra between the posteriormost basal fulcra and the anteriormost segmented ray, three fringing fulcra between the first and second rays, and eight fringing fulcra between the second and third rays. In the smaller specimens, fringing fulcra are absent. The first three segmented rays are unbranched and short. The fourth segmented ray is the longest; subsequent rays slightly shorten. There are 16 to 18 dorsal pterygiophores and approximately 13 or 14 corresponding segmented dorsal fin rays.

The anal fin is not well preserved in larger specimens. On the anal fin, there are seven or eight segmented rays. Anterior to these segmented rays, there are at last four short basal fulcra. Dorsal to the anal fin there are six or seven anal pterygiophores.

The caudal fin in *Nasrinsotoudehichthys* is clearly forked, but the central rays are long. On the caudal fin there are 29 (LF 6068, Figure 18A) or 30 (SNSB-BSPG 1986 XV 113, Figure 18C) segmented rays. The dorsalmost ray is the axial caudal fin ray. The segments of the axial ray appear as a continuation of the urodermals at the tip of the axial lobe, and this axial ray has been identified as the 'scale-like ray' [60,61]. The 12th ray is the median ray; the ventral lobe consists of 17 or 18 segmented rays. The dorsal margin of the caudal fin is dorsally flanked by one median dorsal scute, eight basal fulcra, and at least seven fringing fulcra (LF 6037, Figure 18B). Ventral of the segmented rays there are one or two unsegmented basal fulcra and one or two basal scutes (Figure 18A). The segments of the rays of the dorsal and ventral lobe are at least five times longer than deep. Segments of the median rays are as long as deep (in the largest specimen, JME-SOS2602) or two times longer than deep in the smaller specimens. As in other Caturoidea, the segments of the ventralmost rays, the fulcra, and the scutes are covered with a thin ganoin coating, best visible by the read to yellow color in the UV photo of LF 6037 (Figure 18B).

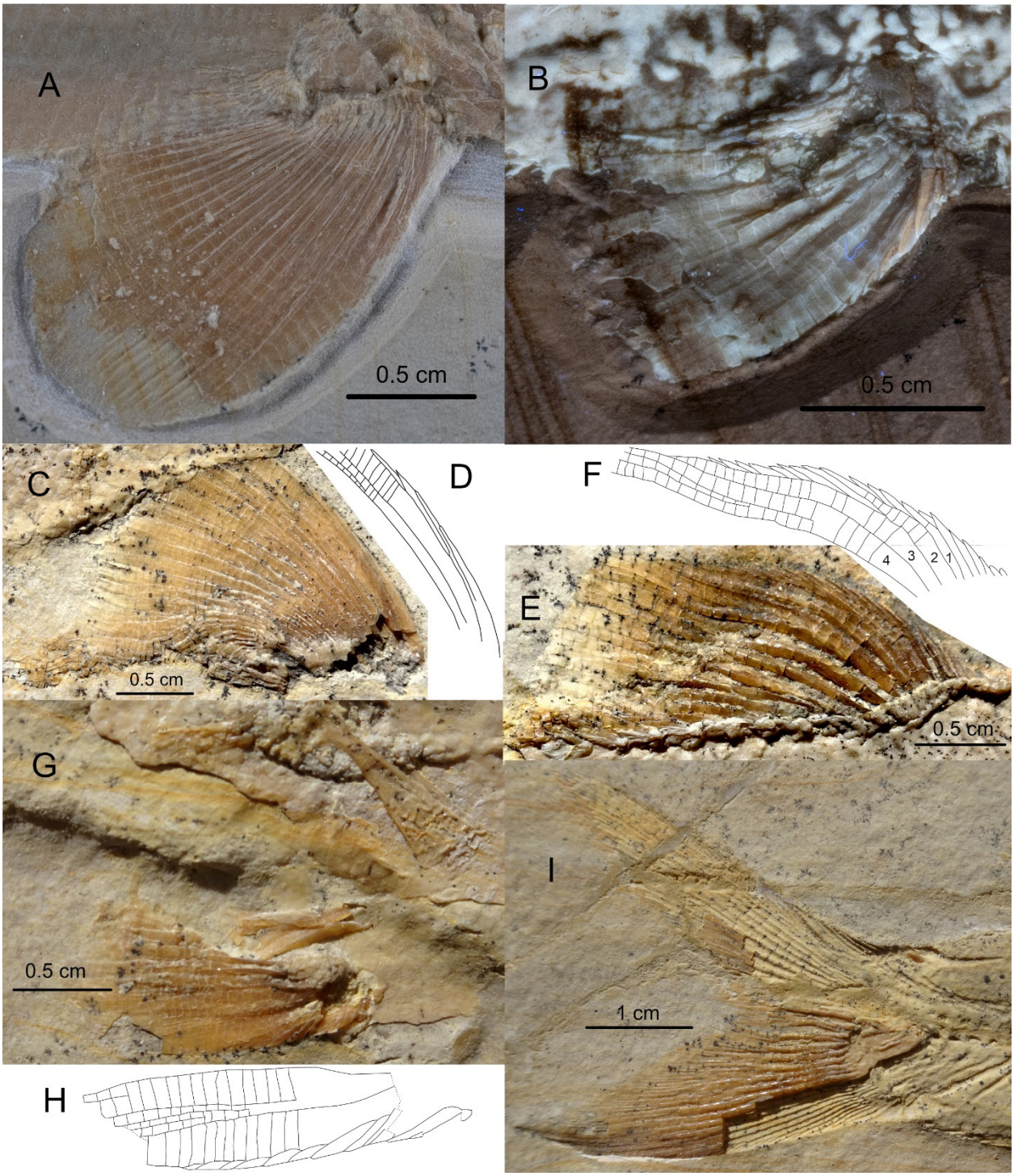

Figure 17. Fins of *Nasrinsotoudehichthys sprattiformis* [2] new gen. from the lower Tithonian of the Zandt Basin, Solnhofen Archipelago, Bavaria, Germany. (**A**) pectoral fin of LF 6037; (**B**) pelvic fin of LF 6037; (**C**) pectoral fin of JME-SOS2602; (**D**) drawing of the anteriormost rays and fulcra on the pectoral fin of JME-SOS2602; (**E**) dorsal fin of JME-SOS2602; (**F**) drawing of anteriormost rays and fulcra on the dorsal fin of JME-SOS2602; (**G**) pelvic fin of JME-SOS2602; (**H**) drawing of anteriormost rays and fulcra on the pelvic fin of JME-SOS2602; (**I**) caudal fin of JME-SOS2602. (Photos: (**A**,**B**) R. Lauer; (**C**–**I**) M. Ebert).

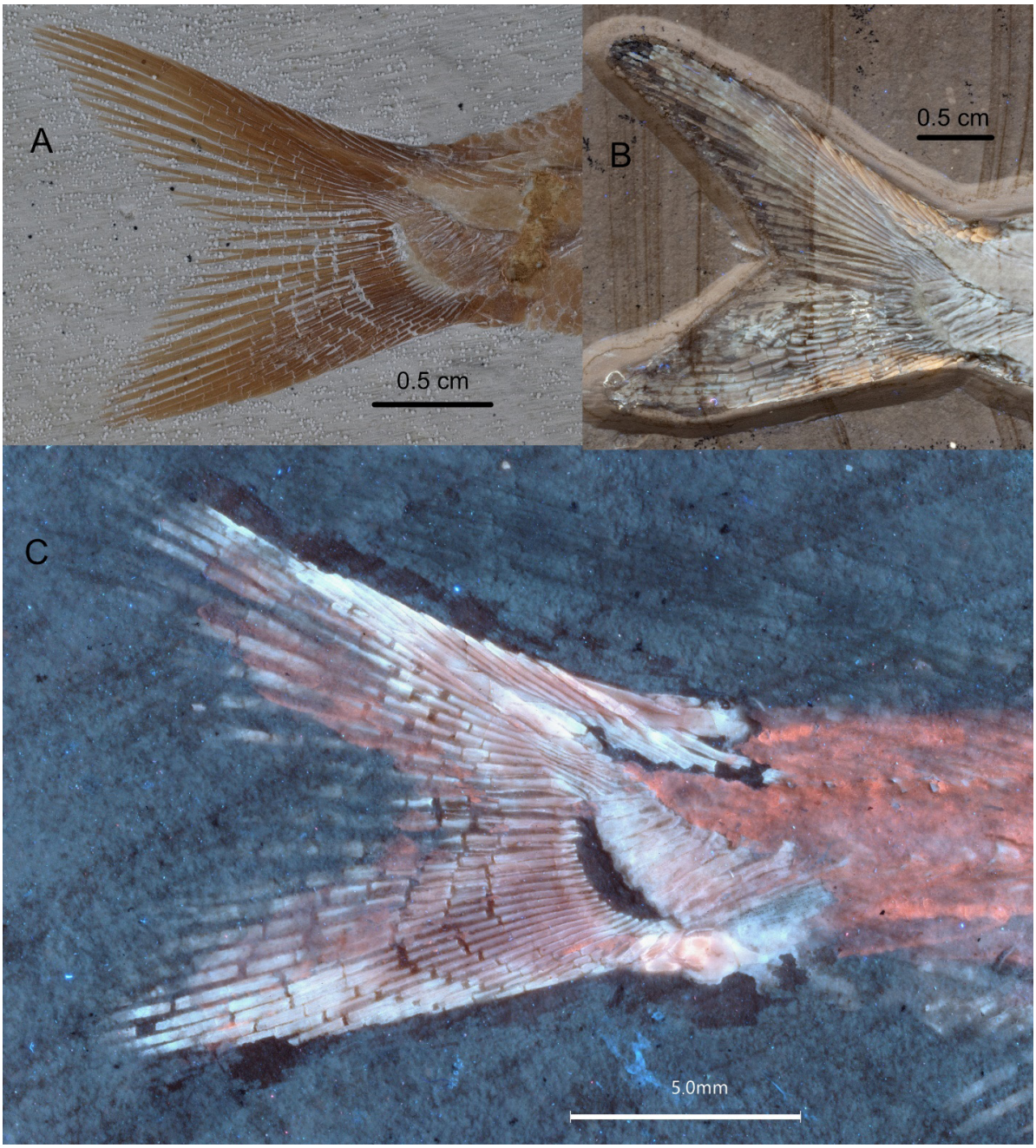

Figure 18. Caudal fin of *Nasrinsotoudehichthys sprattiformis* [2] new gen. from Zandt, Bavaria, Germany. (**A**) LF 6068; (**B**) LF 6037 (UV photo); (**C**) SNSB-BSPG 1986 XV 113 (UV photo). (Photos: (**A**,**B**) R. Lauer; (**C**) M. Ebert).

The caudal skeleton is best visible in Figure 18, where at least 18 haemal bones with contact to caudal fin rays are visible (see [56] fig. 37 as well). The dorsalmost are nearly completely covered by fin rays; therefore, an exact count of the hypurals is not possible.

Squamation: The scales of the body are of amioid type (Figure 19). On the surface of most scales of the body of the largest specimen (JME-SOS2602), there are ridges that end in spines at the posterior end of the scales (Figure 19A,B). Only in the anterior ventral most body part, near the pectoral fin, there are normal rounded thin amioid-like scales without ridges or spines (Figure 19C). There are approximately 40 ± 1 transverse scale rows between the cranium and the dorsal fin origin, best countable in LF 6037 (Figure 13A,B), LF 6068 (Figure 13C,D), and JME-SOS2602 (Figure 14A), and approximately 80 scale rows

between the cranium and the caudal fin origin (best countable in LF 6037). The lateral line is clearly visible along its entire length (best visible in LF 6068; Figure 13C,D). In most specimens, the lateral line is visible through the transparent scales as a lighter line. The lateral line, as is normal, extends parallel to the body axis in one of the median scale rows, nearly to the beginning of the caudal fin. The posteriormost end of the notochord, which goes into the upper lobe of the caudal fin, is covered by two rows of large, diamond-shaped scales (urodermals) (Figure 18A,B; [56] fig. 37). Both rows, which run from anteroventrally to postreodorsally, contain three or four scales, the most posterior being the largest, which are very elongated anteriorly posteriorly. Additionally, there is a row of thick, rounded scales with ganoin coating running from the dorsal scute to the posteriormost urodermals (Figure 18B).

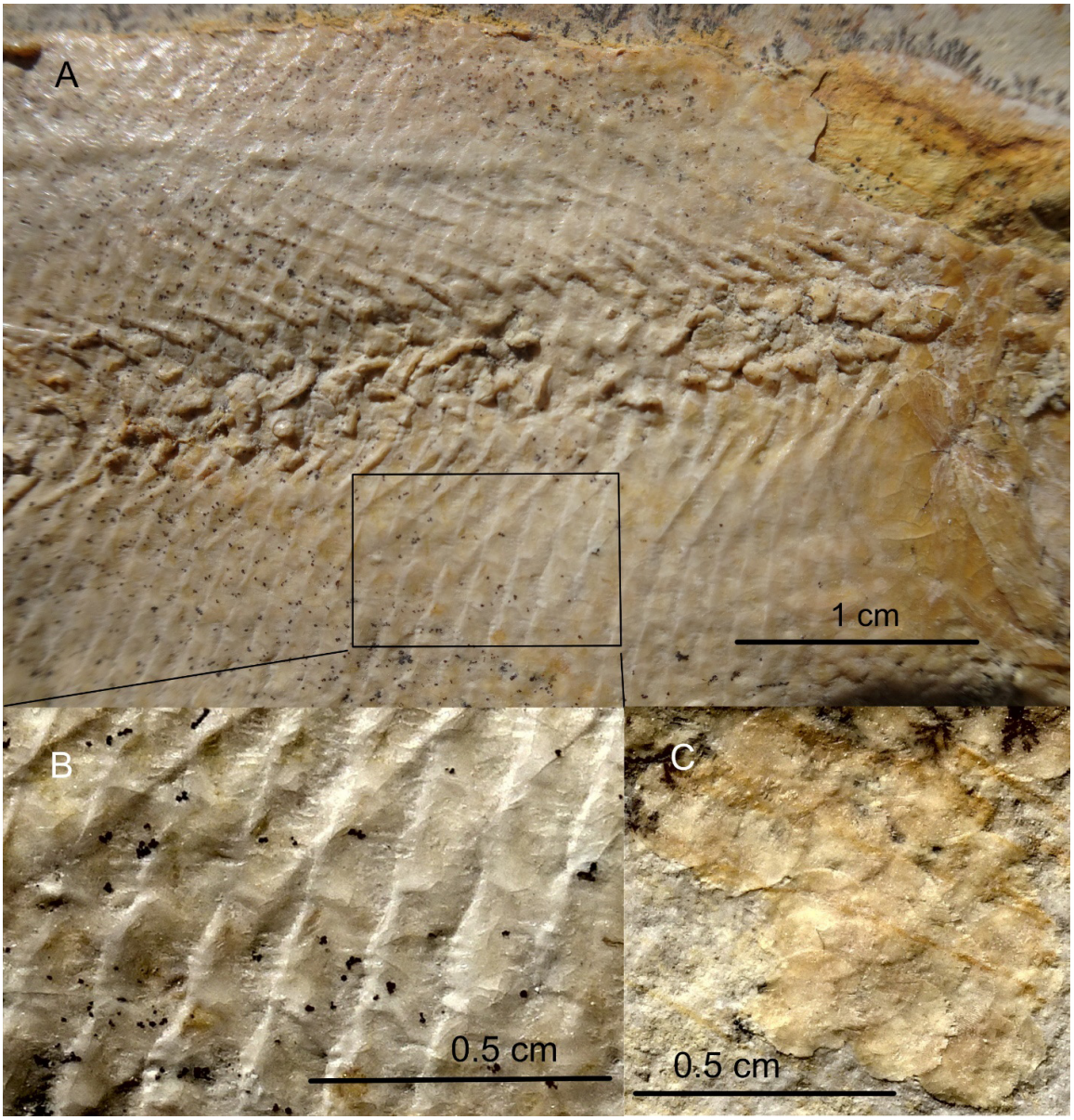

Figure 19. Scales of *Nasrinsotoudehichthys sprattiformis* [2] new gen. (JME-SOS2602) from Zandt, Bavaria, Germany. (**A**) squamation and underneath the translucent interior skeleton of the anterior part of the body (the rectangle shows the section of Figure 18B; (**B**) scales in the anterovenral body part with spines at the posterior border; (**C**) typical rounded amioid scales in the anterovenral body part near the pectoral fin. (Photos: M. Ebert).

5. Discussion

5.1. Historical Overview of the Taxonomic Position of Liodesmus [2]

Originally Wagner [2] (p. 697) placed his new genus *Liodesmus* in the family "Caturini Salmschupper", which he characterized as "Gestalt oval, Zähne spitz und in einfacher Reihe auf den Kiefern; die nackte Rückensaite mit getrennten Halbwirbeln oder ringförmigen Hohlwirbeln. Hieher gehören die 3 Gattungen *Caturus*, *Eurycormus* und *Liadesmus* [*Liodesmus*]; mit letzterer dürfte wahrscheinlich *Coccolepis* zu verbinden sein".

Woodward [4] placed *Liodesmus* in the Amiidae, particularly because there are no fulcra on the fins. However, fulcra are absent in nearly all Halecomorphi of this size.

Jordan [48] distinguished the Liodesmidae from the Amiidae, his argument being "the notochord is persistent, its sheath without ossification" [48] (p. 34). However, this applies to all other Amiidae or Caturidae of this body size and very probably to all juvenile Halecomorphi.

Lambers [56] (p. 332) was the first who returned *Liodesmus* to the original classification of Wagner (1863), stating *Liodesmus* "is related to the caturids, rather than the amiiforms".

Grande and Bemis [9] were the first who placed Caturidae and Liodesmidae under Caturoidae.

Lambers [8] thought that *Liodesmus* is closely related to the Caturidae.

We have shown here that all specimens described so far under *Liodesmus* either belong to other, previously described genera, belong to new genera clearly outside the description of the genus *Liodesmus*, or are nomina dubia (including the type species *Pholidophorus gracilis*). Consequently, we now think that the genus *Liodesmus* and the Liodesmidae are nomina dubia as well.

5.2. Anatomical Comparisons (An Overview of the Most Important Features, Gives Table 1)

5.2.1. Comparison of *Pholidophorus gracilis* [3] and *Liodesmus gracilis* [2]

Recently one of the authors (ME) discovered the specimen MB.f.15598 (Figure 2A) in the collection of the Museum für Naturkunde in Berlin and recognized this specimen to be the type specimen for *Pholidophorus gracilis* [3] (described in [7] and figured in [3] Atlas Tome II, pl. 42, fig. 2; see Figure 2B). According to Wagner [2], *Pholidophorus gracilis* [3] is a species of his new genus *Liodesmus* [2], which he called *Liodesmus gracilis* [3]. Moreover, Woodward [4] determined *Liodesmus gracilis* as the type species of the genus *Liodesmus*. However, Wagner [2], Woodward [4], and all subsequent authors who worked on the genus *Liodesmus* (see list of synonyms of *Caturus brevicostatus* (*Liodesmus gracilis*) above) incorrectly described the specimen SNSB-BSPG AS VII 1122 (Figure 2C) from the Munich collection as a holotype of *Pholidophorus gracilis* [3]. SNSB-BSPG AS VII 1122 is figured as a holotype of *Liodesmus gracilis* for the first time in [9] fig. 406a.

Moreover, the holotype of *Pholidophorus gracilis* [3] (MB.f.15598) has diamond-shaped ganoid scales (Figure 3A,B), as Agassiz [7] already described and figured ([3] Atlas Tome II, pl. 42, fig. 2), and SNSB-BSPG AS VII 1122 has amioid scales (Figure 3C). Agassiz [7] p. 285) reported about the holotype of *Pholidophorus gracilis.* "M. le comte de Münster désigne sous ce nom un petit poisson du calcaire de Kelheim, qui fait partie de sa collection. Ce savant, qui a bien voulu m'en communiquer de dessin. observe positivement que les écailles, qui sont petites et minces, ne montrent aucune trace de dentelure. L'original est couché sur le dos, de manière qu'on reconnaît, près de la tête, les deux pectorales. Le tronc est d'égale largeur, et la colonne vertébrale est grêle et composée d'un grand nombre de vertèbres. La tète a dû être assez large. Les Figure a et b représentent des écailles grossies d'après le dessin que m'en a communiqué M. le comte de Münster. Il est probable que la Figure b indique la face externe, la Figure a, la face interne. La forme pentagonale de ces écailles est encore un problème pour moi."

The shape of the scales leads us now to the conclusion that the holotype of *Pholidophorus gracilis* does not belong to the Caturoidea at all. In our opinion, the holotype of *Pholidophorus gracilis* (MB.f.15598) belongs to the Ophipsiformes [33], and SNSB-BSPG AS VII 1122 with

amioid scales belongs to the Amiiformes and is most probably a junior synonym of *Caturus brevicostatus* [10].

Therefore, *Pholidophorus gracilis* [3] cannot be the type of *Liodesmus* [2] (as wrongly declared by Woodward [4]). The type species of *Liodesmus* is *Liodesmus gracilis* [2].

So, *Pholidophorus gracilis* [3] and *Liodesmus gracilis* [2] are completely different taxa. Both specimens, the Munich specimen of *Liodesmus gracilis* [2] (SNSB-BSPG AS VII 1122; Figure 2C) and the type specimen of *Pholidophorus gracilis* [3] (MB.f.15598; Figures 2A and 3A), lie on his back, and only the ventral side is visible. Therefore, apart from the scales, these specimens do hardly show any features important for a diagnosis and are therefore nomina dubia.

Furthermore, it is not entirely clear which specimen Woodward [4] (pp. 361–362) meant when he established the holotype of *Liodesmus gracilis*. On the one hand, he wrote of the specimen in the "Palaeontological Museum, Munich", referring to the description by Wagner [2], which corresponds to SNSB-BSPG AS VII 1122; on the other hand, he first listed "1838-44. *Pholidophorus gracilis*, L. Agassiz (ex Münster, MS.), Poiss. Foss. vol. ii. pt. i. p. 285, pl. xlii. fig. 2" in his synonym list, which, however, corresponds to MB.f.15598. Woodward [4] incorrectly assumed that many of the specimens that Wagner described from the Münster collection were now in the collection in Munich. However, some of them, which were missed in Munich (suspected losses in WWII), are now found in the collection of the Museum für Naturkunde in Berlin.

5.2.2. Comparison of *Caturus brevicostatus* with the Other Caturidae of the Upper Jurassic of the Solnhofen Archipelago (For the Taxonomic Status of the Caturid Genera See [44]; for the Most Distinguishing Features See Table 1)

Amblysemius granulatus [10] differs from *Caturus brevicostatus* and the other species of *Caturus* in the following features: 26–27 supraneurals; the teeth are larger and broader than in other Caturoidea; the dorsal fin origin is posterior to pelvic fin origin; the anterior edge of the dorsal fin is slightly curved posteriorly; the dorsal lobe of the caudal fin is slightly longer than the ventral lobe; and the scales are smaller and more numerous, with 57–61 transverse scale rows between postcleithra and dorsal fin origin and 94–101 transverse scale rows from postcleithra to caudal fin origin.

Both *Caturus* and *Amblysemius* have a long, slender, rod-like maxilla with more than 20 teeth; a high number (>20) of branchiostegals; extrascapular bones with smooth posterior borders (present in many actinopterygian groups); 18–23 dorsal pterygiophores (present in many fish groups); and amioid type of scales.

The species of Caturidae are best distinguished by the number of transverse scale rows. The number of scale rows is best countable from the postcleithra to the dorsal fin origin (Figure 20); only in some specimens was it possible to count the scale rows from the postcleithra to the caudal fin origin (=to the first procurrent ray or basal fulcra of the ventral lobe of the caudal fin). Here is the information for the Caturidae of the Upper Jurassic Solnhofen Archipelago (a publication to the as yet undescribed Caturidae is in preparation by the authors):

***Caturus latus* [21]**: 24–29 scale rows between the cranium and the insertion of the dorsal fin, 50–57 between the cranium and the insertion of the ventral lobe of the caudal fin, and a maximum of 11–13 scales per scale row dorsal to the lateral line.

***Caturus furcatus* [19]**: 35–40 scale rows between cranium and dorsal fin, 64–72 between cranium and caudal fin, and a maximum of 17–19 scales per scale row dorsal to the lateral line.

***Caturus* n. sp. 1**: 36–42 scale rows between cranium and dorsal fin; 66–74 between cranium and caudal fin; and a maximum of 17–19 scales per scale row dorsal to the lateral line.

***Caturus brevicostatus* [10]**: 49–51 scale rows between cranium and dorsal fin. 96–97 between cranium and caudal fin and a maximum of approximately 21 scales per scale row dorsal to the lateral line.

***Caturus* n. sp. 2**: 51–57 scale rows between cranium and dorsal fin, 91–99 between cranium and caudal fin; and a maximum of 26–29 scales per scale row dorsal to the lateral line.

***Amblysemius granulatus* [10]**: 57–61 scale rows between cranium and the dorsal fin, 94–101 between cranium and caudal fin, and a maximum of 18–20 scales per scale row dorsal to the lateral line.

Caturoidae gen. et sp. nov.: 68–77 scale rows between cranium and dorsal fin, >130 between cranium and caudal fin, and a maximum of ~30 scales per scale row dorsal to the lateral line.

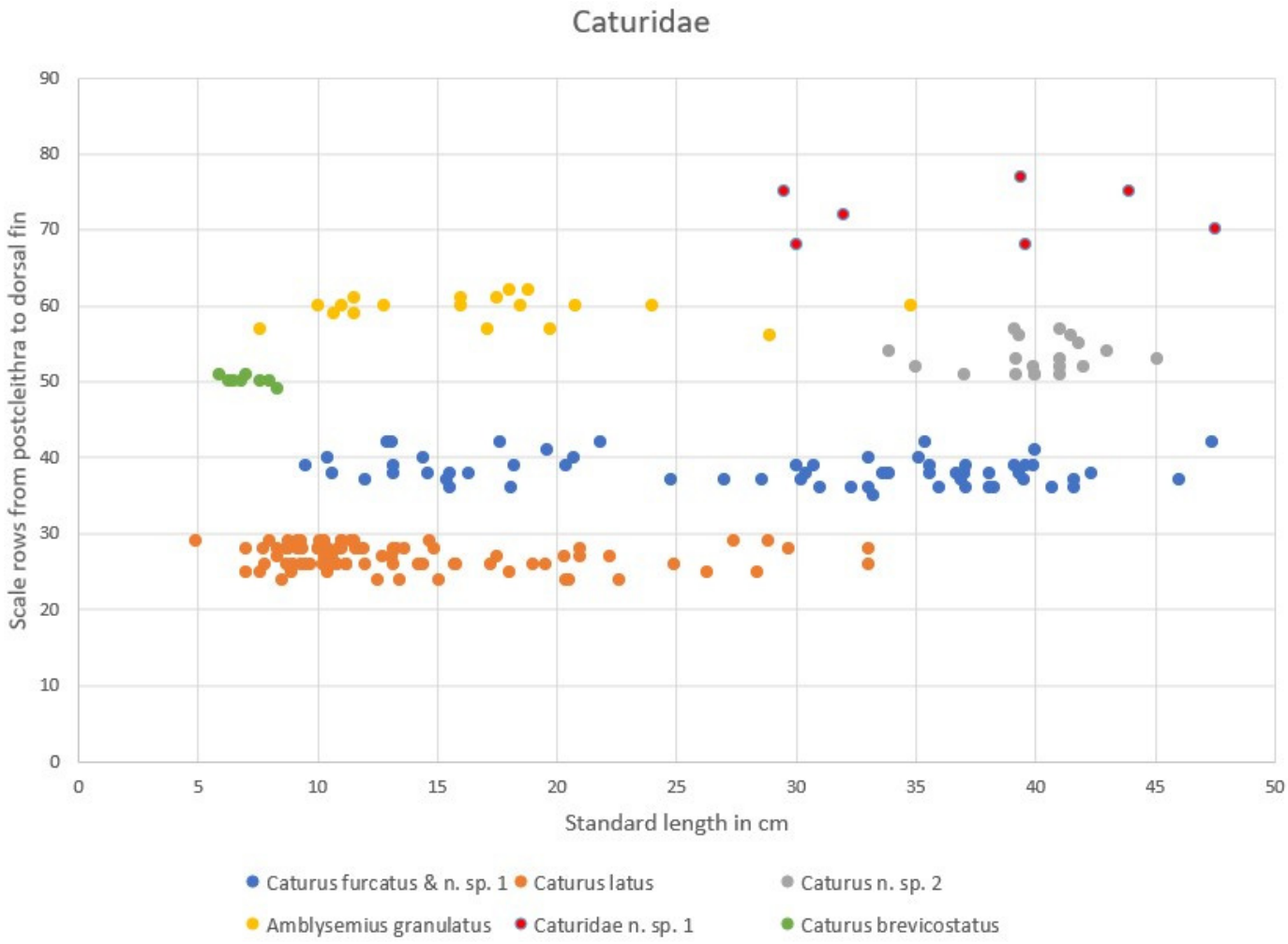

Figure 20. Species of Caturidae distinguished by the number of transverse scale rows from postcleithra to dorsal fin (# 209 specimens).

5.2.3. Comparison of *Nasrinsotoudehichthys sprattiformis* New Gen. with the Other Caturoidea

Specimens of *Nasrinsotoudehichthys sprattiformis* [2] were described and figured by [2] (pl. 5, fig. 1, specimen missing) and [8] (fig. 5 specimen SNSB-BSPG 1986 XV 113) under the taxon name *Liodesmus sprattiformis* [2]. In this article, we decided to describe this taxon as a new genus, which is excluded from the Caturidae but included in the Caturoidea [43]. *Nasrinsotoudehichthys* new gen. is separated from the Caturidae due to the following combination of features (for comparison of the most important features, see Table 1): posteriordorsalmost infraorbital directed posterodorsally; only three or four supraorbitals, of which the anteriormost is large, reaching nearly half the length of the eye; sclerotic ring absent; anterior part of the lower jaw slightly curved ventrally; teeth on maxilla and

dentary small; maxilla gradually increasing in width posteriorly; 6–7 anal pterygiophores*; ~16 branchiostegals.

Nasrinsotoudehichthys within Caturoidae requires some changes in the diagnoses of Caturoidea and Caturidae (see in Systematic Palaeontology above). The characters extremely slender rod-like maxilla, relatively high number of branchiostegal rays (22 or more on each side), and shape of haemal spines broadly spatulate in the transverse plane now apply only to Caturidae and no longer to Caturidea.

Nasrinsotoudehichthys is a Caturoidea sensu [9] within the Amiiformes because the superfamily Caturoidea is apomorphy-based, defined by the following features: Amiiformes without solid perichordally ossified centra; higher number of supraneurals (19–27); pre-ural haemal and neural spines near the caudal peduncle region strongly inclined to a nearly horizontal orientation; presence of sharply carinate acrodin tooth caps on the larger jaw teeth.

Grande and Bemis [9] give only (20–22) supraneurals for Caturidea, but in *Caturus latus* there are specimens with 19 and some specimens of *Amblysemius* have up to 27 supraneurals.

Sharply carinate acrodin tooth caps are not visible in *Nasrinsotoudehichthys* new gen., but in all other species of Caturidea this feature is likewise hardly visible in specimens of similar size.

Nasrinsotoudehichthys thus far is limited to the Zandt Basin and the *Lithacoceras eigeltingense* α Horizon of the *L. riedense* Subzone (Altmühltal Formation, *Hybonoticeras hybonotum Zone*; [62]).

5.3. More Taxa Mentioned under the Genus Liodesmus and Liodesmidae

Wagner [2] incorrectly believed that *Coccolepis bucklandi* [7] might also belong to the new genus *Liodesmus*. However, the genus *Coccolepis* is a chondrostean and has recently been described and figured by [11].

Woodward [4] (p. 362) thought that *Lophiurus minutus* [63] "seems to be referable to the genus *Liodesmus*". However, this taxon does not belong to the Caturidae. We consider it possible that the holotype from Vetter [63] is a juvenile specimen of *Callopterus* [64].

Nybelin [65] (figs. 18, 22a) figured SNSB-BSPG 1953 I 126, another specimen from Zandt, described its caudal fin, and named it *Liodesmus* sp. It is very similar to *Nasrinsotoudehichthys sprattiformis*. However, it differs from this taxon in having a higher number of anal fin rays supported by 13 pterygiophores. In the number of anal pterygiophores it resembles the other Caturidae (see Table 1); in *Nasrinsotoudehichthys sprattiformis* we only have six or seven anal pterygiophores. The description of this specimen (SNSB-BSPG 1953 I 126) in [65] is also mentioned in [8,9,66].

6. Conclusions

The rediscovery of the holotype of *Pholidophorus gracilis* [3] in the collection of the Museum für Naturkunde in Berlin (MB.f.15598) and the confusion with *Liodesmus gracilis* [2] by Wagner and all subsequent authors who worked on the genus *Liodesmus* (for example [4,8,9]) led us to re-examine the genus *Liodesmus* [2] and all specimens that had previously been included in this genus.

The holotype of *Pholidophorus gracilis* [3] (MB.f.15598) belongs to the Ophipsiformes [33]. Agassiz [7] already describes the diamond scales of this specimen and depicts them [3] (pl. 42, figs. 2a,b). Wagner [2] was surprised by this, claiming that the specimen, he thought to be the holotype, had no scales at all. Clearly a mix-up by Wagner [2]—unnoticed for almost 200 years—due to the fact that both specimens from Münster are labeled *Pholidophorus gracilis*.

The specimen in the Munich collection (SNSB-BSPG AS VII 1122), which has been described since Wagner [2] and Woodward [4] as the holotype of *Liodesmus gracilis* [2], has amioid scales (Figure 3C) and is most probably a specimen of *Caturus brevicostatus* [10]. *Caturus brevicostatus* is described in detail here for the first time.

The holotype of *Pholidophorus gracilis* Agassiz, 1838 (MB.f.15598) and the Munich specimen of *Liodesmus gracilis* cannot be clearly identified on genus or species level due to their preservation and are considered nomina dubia.

Consequently, the genus *Liodesmus* [2] and the Liodesmidae [48] are now considered to be nomina dubia as well.

Megalurus intermedius Münster in [6] taken by Wagner [2] as one of the specimens of *Liodesmus gracilis* [2] is considered *Nomen dubium* as well and probably a juvenile of *Caturus latus*. All other taxa assigned by Wagner [2] to the genus *Liodesmus* belong to different genera outside Caturidae.

Nasrinsotoudehichthys sprattiformis [2], a taxon previously described under *Liodesmus* as well, is described here as a new genus, which is excluded from the Caturidae but included in the Caturoidea [43]. This new taxon, so far, is limited to the Zandt Basin of the Solnhofen Archipelago, Bavaria, Germany. *Nasrinsotoudehichthys* new gen. is separated from the Caturidae because of the following combination of features: posteriordorsalmost infraorbital directed posterodorsally; only three or four supraorbitals, of which the anteriormost is large, reaching nearly half the length of the eye; sclerotic ring absent; anterior part of the lower jaw slightly curved ventrally; teeth on maxilla and dentary small; maxilla gradually increasing in width posteriorly; 6–7 anal pterygiophores*; ~16 branchiostegals.

An overview of the different Jurassic Caturidae is provided in Table 1.

Table 1. Features to distinguish the different genera (*Amblysemius*, *Caturus*, *Strobilodus*, and *Nasrinsotoudehichthys*) and species of Upper Jurassic Caturoidea (taxa sorted by the number of scale rows).

Species Name	Max. TL	Max. SL	SO	SR-D	SR-C	D to P	SU	SCL	AP	MS
C. latus	37	33	many	24–29	50–57 (59 *)	anterior	19–21	yes	12–15	slender
C. furcatus Ei/So	53	44	many	36–40	64–72	anterior	22–23	yes	9–11	slender
C. furcatus Kelheim	40	33	many	~35	~66	anterior	?	yes	13	slender
C. furcatus Cerin	62	48	many	39–42	71–74	anterior	~22	yes	10	slender
N. sprattiformis	17	15	3–4	40–41	~80	anterior	~20	no	6–7	broad
S. giganteus	124	104	~5	?	?	anterior	?	yes	?	broad
C. brevicostatus	10	8	?	49–51	95–97	anterior	25–26	yes	11–12	slender
A. granulatus	56	48	?	57–61	94–101	posterior	26–27	yes	12–14 (10 *)	slender

Abbreviation: AP: number of anal pterygiophores; D to P, position of dorsal fin in relationship to pelvic fin; max. TL, maximal total length (cm); max. SL, maximal standard length (cm); MS, maxilla shape; SCL, sclerotic ring; SO, number of supraorbitals; SR-C, number of scale rows from postcleithra to the insertion of the ventral lobe of the caudal fin; SR-D, number of scale rows from postcleithra to the insertion of the dorsal fin; SU, number of supraneurals. Remarks *: 10 * anal pterygiophores in *A. granulatus* are only present in a single specimen (JME-ETT3369), which is the only specimen from the locality Ettling. A count of 59 * scale rows in *C. latus* is only present in the locality of Cerin (France).

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