# The genus Belonostomus AGASSIZ, 1834 (Neopterygii, Aspidorhynchiformes) in the late Jurassic of the Solnhofen Archipelago, with a focus on Belonostomus kochii MÜNSTER, 1836 from Ettling (Germany)

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#### Abstract

The aim of this work is to give a comparison of the different species of the genus *Belonostomus* in the late Jurassic and discuss the stratigraphic range and distribution of these species in the Plattenkalk basins of Southern Germany. These species remain poorly known, because L. AGASSIZ never fixed a type specimen for the first described species *B. tenuirostris* and the types of the other *Belonostomus* species are badly preserved.

Belonostomus kochii is here described in detail for the first time, based on new and excellently preserved material from the late Jurassic of Ettling (Solnhofen Archipelago) and compared to other late Jurassic *Belonostomus* species from the various Plattenkalk basins of Southern Germany.

A type specimen of *Belonostomus tenuirostris* is also designated and a description of *B. tenuirostris* is provided based on newly prepared material. The characteristic features of *B. muensteri* are clarified and current understanding of *B. sphyraenoides* and *B. speciosus* is discussed.

Based on the combination of features, there appear to have been two species groups of *Belonostomus* in the late Jurassic. One species group with a length difference of 0–20% between the upper and lower jaw (measured from the anterior rim of the orbit to the jaw tips) and two rows of teeth in the premaxilla, (representing *B. kochii, B. sphyraenoides* and *B. muensteri*). The second species group is represented by *B. tenuirostris* with length difference of 28-44% between the upper and lower jaw and only one row of teeth in the premaxilla.

#### Zusammenfassung

Das Ziel dieser Arbeit ist es, die unterschiedlichen Arten der Gattung *Belonostomus* im oberen Jura zu vergleichen und die stratigraphische Reichweite und die Verteilung dieser Arten in den Plattenkalkwannen Süddeutschlands zu diskutieren. Über diese Arten ist bisher nur wenig bekannt, da L. AGASSIZ für die zuerst beschriebene Art *B. tenuirostris* kein Typusexemplar bestimmt hat und das Typenmaterial der anderen *Belonostomus*-Arten schlecht erhalten ist. Belonostomus kochii wird hier zum ersten Mal ausführlich beschrieben, basierend auf neuem und hervorragend erhaltenem Material aus dem oberen Jura von Ettling (Solnhofen-Archipel), und wird mit den anderen oberjurassischen Belonostomus-Arten der verschiedenen Plattenkalkwannen Süddeutschlands verglichen.

Ein Typusexemplar für *Belonostomus tenuirostris* wird ebenfalls benannt und eine Beschreibung von *B. tenuirostris* basierend auf neu präpariertem Material beigefügt. Die charakteristischen Merkmale von *B. muensteri* werden erläutert und das gegenwärtige Verständnis von *B. sphyraenoides* und *B. speciosus* wird diskutiert. Nach Sichtung der zur Verfügung stehenden Exemplare, sieht der Autor *Belonostomus kochii* MÜNSTER, 1836, *Belonostomus tenuirostris* (AGAS-SIZ, 1833) und *Belonostomus muensteri* AGASSIZ, 1844 als begründete Arten an. *Belonostomus sphyraenoides* AGASSIZ, 1844 und *Belonostomus speciosus* WAGNER, 1863 werden als *nomina dubia* beschrieben.

Belonostomus kochii ist im Solnhofen-Archipel nur aus den älteren Plattenkalken der Kelheimer Wanne wie Kelheim-Kapfelberg (Typlokalität) und aus dem Steinbruch von Ettling (Hartheimer Wanne) bekannt. Das Alter von Kelheim-Kapfelberg ist spätes Kimmeridgium bis zum eigeltingense Horizont, der untersten Zone des Tithoniums. Diese Art ist damit bisher die stratigraphisch älteste Belonostomus-Art in den bayerischen Plattenkalken. Belonostomus kochii ist ein schlanker Belonostomus mit einer Längendifferenz zwischen Ober- und Unterkiefer von weniger als 20% (Abb. 7-12). Die Prämaxilla hat zwei Reihen Zähne, eine Reihe von großen Zähnen an der inneren Seite und eine zusätzlichen Reihe von sehr kleinen Zähnen an der äußeren Seite (Abb. 7c und 11). Belonostomus kochii hat 68-71 Wirbel und 71-73 Seitenlinienschuppen. Die Pterygial-Formel von Belonostomus kochii ist:

$$\frac{D51-54}{P30-31\,A45-48\,C64-68} T71-73$$

*Belonostomus sphyraenoides* AGASSIZ, 1844 ist nur aus der Plattenkalkwanne von Eichstätt bekannt. *Belonostomus*-Exemplare sind in der Plattenkalkwanne von Eichstätt sehr selten und gehören nach Ansicht des Autors alle zu *B. sphyraenoides.* Die Plattenkalke von Eichstätt werden in den Horizont *eigeltingense*  $\beta$  des Tithoniums datiert (SCHWEIGERT et al. 2013). *Belonostomus sphyraenoides* hat ungefähr 71 Wirbel und 71 Seitenlinienschuppen.

**Belonostomus tenuirostris** (AGASSIZ, 1833) ist nur aus den eigentlichen Solnhofener Plattenkalken sensu stricto von Solnhofen/Langenaltheim sowie aus dem Plattenkalkwannen von Schamhaupten/Öchselberg/Zandt und Painten bekannt. Das Alter dieser Plattenkalke ist spätes Kimmeridgium bis zum *eigeltingense*-Horizont, der untersten Zone des Tithoniums. *Belonostomus tenuirostris* ist ein schlanker *Belonostomus* mit einer Längendifferenz zwischen Ober- und Unterkiefer von 28-44% (Fig. 2 und 3). Die Prämaxilla trägt nur eine Reihe von größeren Zähnen (Fig. 3b). *Belonostomus tenuirostris* hat 77-78 Wirbel und 77-78 Seitenlinienschuppen. Die Pterygial-Formel von *B. tenuirostris* ist:

Von **Belonostomus speciosus** WAGNER, 1863 ist bisher nur ein einziges Exemplar aus den Solnhofener Plattenkalken *sensu stricto* (*rueppellianus*-Horizont des Tithoniums) bekannt. Verglichen mit den anderen Arten hat *Belonostomus speciosus* (Fig. 14) kurze Ober- und Unterkiefer, die fast gleichlang sind. *B. speciosus* besitzt zwei Reihen von Prämaxillarzähnen. Die Zähne der Reihe mit größeren Zähnen sind vergleichsweise größer (besonders auf der Prämaxilla) und ihre Anzahl ist geringer als in den anderen Arten von *Belonostomus*.

**Belonostomus muensteri** AGASSIZ, 1844 ist die stratigraphisch jüngste Art der Gattung *Belonostomus* im Solnhofen-Archipel. Der Holotyp stammt aus den Mörnsheimer Schichten der Solnhofener Gegend. Die Mörnsheimer Schichten sind die Typus-Schichten des *moernsheimensis*-Horizonts des Tithoniums. Die Fossilien der Mörnsheimer Schichten kommen von Daiting, Mörnsheim, Mülheim und aus der Gegend von Solnhofen/Langenaltheim und in all diesen Lokalitäten ist *Belonostomus muensteri* recht häufig.

Belonostomus muensteri hat eine Längendifferenz zwischen Ober- und Unterkiefer von weniger als 20% (Fig. 5a). Die Prämaxilla hat zwei Reihen Zähne (Fig. 5b), wie bei Belonostomus kochii. Im Gegensatz zu B. kochii, haben die Schuppen von B. muensteri jedoch kleine Tuberkel auf ihrer Oberfläche.

Basierend auf der Kombination der Merkmale lässt sich feststellen, dass im oberen Jura zwei Gruppen von *Belonostomus* existierten. Eine Arten-Gruppe, charakterisiert durch eine Längendifferenz zwischen dem Ober- und Unterkiefer von 0-20% (gemessen vom Augenvorderrand bis zu den Kieferspitzen) und zwei Reihen von Zähnen an der Prämaxilla (repräsentiert durch *B. kochii, B. sphyraenoides* und *B. muensteri*) und eine zweite Arten-Gruppe, repräsentiert durch *B. tenuirostris,* mit einer Längendifferenz zwischen dem Ober- und Unterkiefer von 28-44% (Abb. 16 und Tab. 4) und nur einer Reihe von Zähnen an der Prämaxilla.

### Introduction

Fossils from the Late Jurassic Plattenkalk of Bavaria have been known since the mid-18th century. Many authors who worked on the taxonomy of fishes from this area attributed them to the locality of "Solnhofen" without providing further information about which of the various Plattenkalk basins the fishes specifically came from. In recent years and prompted by excavations in new Plattenkalk quarries, some authors (ARRATIA 1997, 2000, Ebert 2012, Ebert & Kölbl-Ebert 2012, LANE & EBERT 2012, LANE & EBERT 2014, LÓPEZ-AR-BARELLO & SCHRÖDER 2014) began to point out the exact distribution of fish species in the various Plattenkalk basins of different ages within the Solnhofen Archipelago (a term coined by M. RÖPER). For current knowledge about the ages of the various Plattenkalk basins see Schweigert (2007) and Schweigert et al. (2013).

Among the first to publish on fishes from the Solnhofen Archipelago was KNORR (1755). KNORR (1755) was also the first author to figure a specimen of the family Aspidorhynchidae. Based upon this figured specimen, BLAINVILLE (1818) described Esox acutirostris (later Aspidorhynchus acutirostris). This, as well as all other type specimens from KNORR (1755), is lost and a neotype of Aspidorhynchus acutirostris was assigned recently by López-Arbarello & Schröder (2014). AGASSIZ (1834b) separated "Aspidorhynchus" tenuirostris and some new species from the genus Aspidorhynchus AGASSIZ, 1833 and referred these species to his new genus Belonostomus. The characters of this new genus given in AGASSIZ (1834b) in comparison to the genus Aspidorhynchus are "sehr lang gezogene Kiefer zu haben, die beinahe gleich lang sind, und von welcher der Oberkiefer keine Kerbe hat zur Aufnahme der Unterkiefers. Auch ist bei diesen Arten die Afterflosse schmäler als bei Aspidorhynchus, und der Leib allgemein gestreckter." This translates: "... they have very elongated jaws, which are nearly of the same length and the upper jaw does not have a notch for the lower jaw. Also in these species, the anal fin is narrower than in Aspidorhynchus and the body is generally more elongated."

The genus *Belonostomus* AGASSIZ, 1834b is one of four genera of the extinct family Aspidorhynchidae NI-CHOLSON & LYDEKKER 1889. The other three are the type genus *Aspidorhynchus* AGASSIZ, 1833 from mid to late Jurassic marine deposits of the Tethys (Cuba, France, Germany, Great Britain), *Vinctifer* JORDAN, 1919 from Cretaceous marine deposits of the Gondwana coasts (Antarctica, Argentina, Australia, Brazil, Columbia, Equatorial Guinea, Mexico and Venezuela) and *Rich-mondichthys* BARTHOLOMAI, 2004 from marine deposits of the Cretaceous (Albian) of Queensland (Australia).

The genus *Belonostomus* is widespread, ranging from the late Jurassic (Kimmeridgian to Tithonian of England, France and Germany) to the Cretaceous (England, Germany, Italy, Lebanon, North and South America) and maybe even up to the Paleocene (BRY-ANT 1987; however *cf.* BOGAN et al. 2011).

The first to figure a specimen of *Belonostomus* was BAIER (1757: 10, pl. VI, fig. 4), who called his figured specimen Serpens marinus. MÜNSTER (1842: 45) mentioned twelve species of Belonostomus from his collection, most of them without description. AGASsız (1833-1844) described six species from the Plattenkalk of Southern Germany, whereas WAGNER (1863) regarded only four to be well founded. However, WAGNER (1863: 688) also acknowledged: "Eine grosse Schwierigkeit ist die Bestimmung der Arten, indem die Exemplare gewöhnlich sehr beschädigt sind, zumal an ihren Kieferteilen, wo dann eine sichere Deutung unsicher oder selbst unmöglich gemacht wird." This translates: "A great difficulty is the determination of the species, because the specimens are normally badly damaged, especially in the jaws, which then makes the interpretation uncertain or even impossible."

Further details of the late Jurassic genus Belonostomus were reported by VETTER (1881), REIS (1887), WOODWARD (1895), SAINT-SEINE (1949), SCHULTZE & Stöhr (1996), Brito (1997, 1999), Arratia (1999, 2008), BRITO & MEUNIER (2000) and EBERT & KÖL-BL-EBERT (2010a). BRITO (1997) in his Révision des Aspidorhynchidae described only two species of Belonostomus in the late Jurassic Plattenkalk of southern Germany, B. tenuirostris and B. muensteri Agassiz, 1844, noting that he was not sure whether B. kochii and B. sphyraenoides Agassiz, 1844 are synonyms of B. muensteri or not. Up to the present, there is no satisfying description of the various species of Belonostomus, which made it also impossible to determine which species are native to which of the Plattenkalk basins of the Solnhofen Archipelago (Fig. 1), which cover an age range of 17 ammonite horizons (see Schweigert 2007). In the late Jurassic French locality of Cerin, matters were no better. THIOL-LIÈRE (1848, 1850, 1873) mentioned from Cerin B. tenuirostris, B. muensteri and B. sphyraenoides (?). WAGNER (1860: 403) regarded his specimens from Cerin as identical to B. kochii. EASTMAN (1914a) considered most of the specimens from Cerin in the Carnegie museum as belonging to B. muensteri and one specimen possibly to B. tenuirostris. SAINT-SEINE (1949) and BRITO (1997) assigned all specimens from Cerin to *B. tenuirostris*.

Therefore, a clear definition of these species was necessary.

Fig. 1: Map of the upper Jurassic Plattenkalk region of Bavaria, Southern Germany, showing the localities yielding *Belonostomus* material (redrawn after Röper et al. 2000). Abb. 1: Karte der Plattenkalk-Regionen Bayerns: Aufgeführt sind alle Lokalitäten in denen *Belonostomus* gefunden wurde (umgezeichnet nach Röper et al. 2000).



(From the Kimmeridgian of Dorset (England), the genus *Belonostomus* is only present with isolated cranial bones. This species, *Belonostomus dorsetensis* WOODWARD, 1895 and the Cretaceous species (see BRITO 1997) are excluded from this study.)

### Material and methods

The historical specimens were often prepared rather coarsely or simply split in half. Some Belonostomus specimens from NHMUK like P.3802 and P.7661 were acid prepared, after the method of TOOMBS & RIXON (1959). The fossil fishes from Ettling come from the excavation site of the Jura-Museum Eichstätt (EBERT & KÖL-BL-Ebert 2008b, 2009, 2010b, 2011, 2012, 2013, Ebert et al. 2014). The fishes from Ettling are preserved in fine-laminated Plattenkalk and the quality after mechanical preparation is sometimes better than acid prepared specimens. This, of course, is aided by the exceptional preservation of the Ettling material (TISCHLINGER 1998, EBERT et al. 2014). All examined Belonostomus specimens from Ettling in the Jura-Museum Eichstätt were mechanically prepared under the microscope with the aid of air-pressure vibration tools, scalpels and tiny, soft paintbrushes by the author. Specimens were examined using a Leica M80 microscope, a Leica Wild M3Z microscope and a PZO 20138 microscope. The drawings were made with a camera lucida attached to the Leica M80 microscope. Photographs were made using a Canon EOS 450D digital camera. A Kappa Zelos microscope camera with Leica 10447367 camera attachment was used for photographing small-scale anatomical details.

Skull bones are named according to López-AR-BARELLO & SCHRÖDER (2014). Fulcra and fin rays are named according to Arratia (2008).

*Anatomical Abbreviations*—ang, angular; br, branchiostegal ray; cl, cleithrum; d, dentary; dpt, dermopterotic; dsp, dermosphenotic; fr, frontal; io, infraorbitals; iop, interoperculum; ll, lateral line; mx, maxilla; n, nasal; op, operculum; pa, parietal; par, parasphenoid; pcl, postcleithrum; pd, predentary; pmx, premaxilla; pop, preoperculum; ptt, posttemporal; q, quadrate; ro, rostral; r, fin ray; s, scale; scl, supracleithrum; so, supraorbital; sop, suboperculum; suo, suborbital.

# *The studied material belongs to the following institutions*

BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

CAM SM: The Sedgwick Museum of Earth Sciences, University of Cambridge, UK

CMNH: Carnegie Museum of Natural History, Pittsburgh, USA

FSL: Collections de Géologie, Université Claude Bernard – Lyon1, France GPIT: Geologisch-Paläontologisches Institut Tübingen, Germany

JME: Jura-Museum Eichstätt, Germany

MB: Museum für Naturkunde der Humboldt Universität, Berlin, Germany

MHNL: Museum d'Histoire naturelle de Lyon, France MMG-SNSD: Museum für Mineralogie und Geologie – Senckenberg Naturhistorische Sammlungen Dres-

den, Germany MNHN: Muséum d'Histoire Naturelle Paris, France NMP: National Museum of Prague, Department of

Palaeontology, Czech Republic NKMB: Naturkunde-Museum Bamberg, Germany NHMUK: Natural History Museum, London, UK

NHMW: Naturhistorisches Museum Wien, Austria SMF: Senckenberg Forschungsinstitut und Naturmuseum Frankfurt a. M., Germany

SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany

SNSB: Staatliche Naturwissenschaftliche Sammlungen Bayerns, Germany

TM: Teylers Museum, Haarlem, Netherlands

*Fossil material examined* (the best preserved specimens of *Belonostomus* with their main characters are listed in Tab. 1)

*Aspidorhynchus acutirostris* (BLAINVILLE, 1818): BSPG 2012 I 1 (neotype); JME-SOS2827; JME-SOS2856; JME-SOS3180.

*Aspidorhynchus ornatissimus* AGASSIZ, 1834: BSPG AS VII 1106; BSPG AS VII 1109 (holotype); GPIT-OS-782.

Aspidorhynchus sanzenbacheri BRITO & EBERT, 2009: JME-ETT1 (holotype); JME-ETT2; JME-ETT18; JME-ETT84; JME-ETT85; JME-ETT88; JME-ETT102; JME-ETT140; JME-ETT221; JME-ETT565; JME-ETT851; JME-ETT1586; JME-ETT1599; JME-ETT1797; JME-ETT1897; JME-ETT2744; JME-ETT2936; JME-ETT3483; JME-ETT3485; JME-ETT3911.

Belonostomus kochii Münster, 1836: BSPG AS VII 1068 (neotype); BSPG AS VII 1070; CAM SM F11124; CAM SM F11126; JME-ETT16; JME-ETT17; JME-ETT49; JME-ETT50; JME-ETT117; JME-ETT123; JME-ETT128; JME-ETT137; JME-ETT271; JME-ETT882; JME-ETT893; JME-ETT981; JME-ETT1355; JME-ETT1581; JME-ETT1582; JME-ETT1798; JME-ETT1900; JME-ETT1941; JME-ETT2170; JME-ETT2544; JME-ETT2638; JME-ETT2870; JME-ETT2938; JME-ETT2939; JME-ETT2965; IME-ETT3342; JME-ETT3372; JME-ETT3378; IME-ETT3463; JME-ETT3673; JME-ETT3912; MB. f. 1378; MB. f. 3508; MB. f. 3543; MB. f. 3544; MMG-SNSD Ba J 1761; NHMW 8625.

*Belonostomus muensteri* AGASSIZ, 1844: BSPG 1964 XXIII 519 and counterpart BSPG 1964 XXIII 520;

name & number	locality	total length / cm	standard length / cm	PM: ante- rior rim of the eye to premaxilla tip / cm	PD: ante- rior rim of the eye to predentary tip / cm	PM/PD	rows of teeth on premaxilla	
B. kochii	B. kochii							
BSPG AS VII 1068 holotype	Kelheim	~29	~26.5					
JME-ETT16	Ettling	32	30	6.3	5.1	1.24 =81%	2	
JME-ETT17a	Ettling	34	32.5	5.9	5	1.18 =85%	2	
JME-ETT49a	Ettling	23.5	22	3.8	3.7	1.03 =97%	2?	
JME-ETT117	Ettling	29	27.5	5.3	5	1.06 =94%	2	
JME-ETT123a	Ettling	13.5	12.5		2.5			
JME-ETT128	Ettling	26	24.5	3.8	3.3	1.15 =87%	2	
JME-ETT882	Ettling	13	12	3.1	2.5	1.24 =81%	1 juvenile	
JME-ETT981	Ettling			3.3 bro- ken?	3.2	1.03 =97%	2?	
JME-ETT1900	Ettling	25.5	23.5	4.5	4	1.13 =89%		
JME-ETT2170a,b	Ettling	20	19	4.2	3.5	1.2 =83%		
JME-ETT2544	Ettling			3.5	3.5	1 =100%	2	
JME-ETT3463	Ettling	20.5	19	4.9	4			
JME-ETT3673	Ettling		~18	4.6	3.5			
MB. F. 3508	Kelheim		~25	5.2	4.9		2	
NHMW 8625	Kelheim?	21	19	4.6	3.9	1.18 =85%		
B. muensteri								
MB. f 4994	Mörn- sheim Lay- ers	~45	~40				2	
BSPG 1964 XXIII 520a,b	Daiting			7.5	6.7	1.12 =89%	2	
BSPG 1964 XXIII 527a,b	Daiting						2	
JME-Moe114	Mülheim			5.1	5	1.02 =98%	2	
JME-Moe145	Daiting?			5.5	4.7	1.17 =85%		
JME-SOS2849	Eichstätt? Moe			6.7	5.4	1.24 =81%	2	
NHMUK 505 counterpart of holotype	Solnhofen						2	
NHMUK 3801 holotype	Solnhofen						2	
NHMUK 3802	Solnhofen						2	
NHMUK 37796 & 37798	Solnhofen	~38	~35	5.8	5.2	1.12 =89%		
B. tenuirostris								
BSPG AS I 1207	Solnhofen	~34.5		6.4	4.6	1.39 =72%	1	
BSPG 1957 I 339a,b	Zandt	37.5	34.5	6.3	4.5	1.4 =71%	1	

JME-SOS2735	Langenal- theim	36.5	34.5	7.8	5	1.56 =64%	
JME-SOS2841	Langenal- theim	~37	~34.5				
JME-SOS2844	Solnhofen	~35	~33	8.2	5.6	1.46 =68%	1?
JME-SOS2845	Öchselberg	~27	~25				
JME-SOS2850	Zandt	~15	~13.5				1
JME-SOS2851a,b	Zandt						1
JME-SOS3258	Zandt	~18	~16.5				
JME-SOS4074a,b	Hummel- berg			7.5	5	1.5 =67%	
JME-SOS8088				7.1	5		1
MB. F. 3578	Solnhofen			5.4	3.2		1
NHMUK P962	Solnhofen			5.8	3.5	1.66 =60%	
NHMUK P962a	Solnhofen			7.3	4.1	1.78 =56%	
NHMUK P7661	Solnhofen	~30	~28	6.8	4.6	1.48 =68%	1
NHMUK P12762	Zandt						1
NHMUK 35014	Solnhofen			~5.3	~4.0		
NHMUK 36029	Solnhofen			6.1	3.6	1.69 =59%	
JME-Scha45a,b	Scham- haupten	12	11	2.4	1.7	1.41 =71%	1?
JME-Scha1466a,b	Scham- haupten						1
JME-Scha1467	Scham- haupten	15.5	14	3.6	2.1	1.71 =58%	1
SMF- P.9633	Scham- haupten	32	30.3	5.9	4.4		
TM 6847	Solnhofen			5.6	4	1.4 =71%	
SMNS55675	Solnhofen			8	5.2		1?
SMNS55676	Solnhofen			9.5	6.4		1
SMNS86367	Zandt						1
Belonostomus aus	Cerin						
MHNL20015041	Cerin			4.5	3.8	1.18 =85%	
MHNL20015043	Cerin			7			
MHNL20015045	Cerin			6.2	4.8	1.29 =77%	
MHNL20015049	Cerin			6.3	4.1	1.54 =65%	
MHNL20015054	Cerin	33	31	6.6	4.5	1.47 =68%	
MHNL20015055	Cerin			5.4	4.6	1.17 =85%	
MHN- L20015315A,B	Cerin	33.5	32	7.4	5.3	1.4 =71%	
MHNL20015520	Cerin			6.3	4.9	1.29 =77%	
MHNL20015588	Cerin		30	5.7	4.9	1.16 =86%	
MHNL20150356	Cerin			6.5	4.4	1.48 =68%	
MHNL20150467	Cerin		28	5.9	4.8	1.23 =81%	
NHMUK P2001	Cerin			6.8	4.2	1.62 =62%	

B. speciosus								
BSPG AS VII	Solnhofen		~33	6.2	5.7		2	
1069 holotype								
B. spyraenoides	B. spyraenoides							
BSPG AS VII	Eichstätt	~21	~18.5	3.6	3.6			
1066 holotype								
CAM SM F11098								
counterpart of								
holotype								
JME-SOS3044a,b	Schernfeld	~33	31	?5.3	5	?1.06	2	
						=94%		
SMNS86704	Wintershof						2	
B. sp.								
JME-SOS2842a,b	Breitenhill			5.8	5.4	1.07 =93%	1	

Tab. 1: Skeletal measurements of available Belonostomus specimens from the following collections: BSPG, CAM SM, JME, MB, MHNL, NHMUK, NHMW, SMF, SMNS, TM.

Tab. 1: Messungen aller verfügbaren Belonostomus-Exemplare aus folgenden Sammlungen: BSPG, CAM SM, JME, MB, MHNL, NHMUK, NHMW, SMF, SMNS, TM.

Tab. 2: Comparison of aspidorhynchid genera (modified after BARTHOLOMAI 2004). Information on *Vinctifer* and *Richmondich-thys* is based on diagnoses and descriptions in BARTHOLOMAI (2004) and BRITO (1997).

Tab. 2: Vergleich der Gattungen der Aspidorhynchidae (modifiziert nach BARTHOLOMAI 2004). Die Informationen über *Vinctifer* und *Richmondichthys* basieren auf Angaben und Beschreibungen von BARTHOLOMAI (2004) und BRITO (1997).

Charac- ters	Rich- mondich- thys	Vinctifer	Belono- stomus species group A	Belono- stomus species group B	Aspidorhyn- chus
Premax- illary teeth	absent	absent	two rows	one row	one row
Max- illary teeth	absent	present	present	present	present
Supra- maxilla	absent	absent	absent	absent	present
Maxilla	very ex- tended	large	slender	slender	slender
Premax- illa	short	elongat- ed	very elongat- ed	very elongat- ed	elongated
Paras- phenoid	edentulate	edentu- late	toothed	toothed	toothed
Anterior infraor- bitals	much ex- panded	small	small	small	small
Preden- tary	minute	small	very elongat- ed	very elongat- ed	small
Scale ganoin	very orna- mented	not or- nament- ed	slightly orna- mented	not orna- mented	absent

BSPG 1964 XXIII 527; CAM SM F11127; GPIT 8105a,b; JME-Moe114; JME-Moe145; JME-Moe148; JME-SOS2849; MB. f. 3540; MB. f. 4994; MB. f. 5086; MNHN SLN 174; NHMUK PV P.505 and counterpart NHMUK PV P.3801 (holotype); NHMUK PV P.3802; NHMUK PV 37796 and counterpart 37798; NHMUK PV 37799; NHMUK PV 37801; NHMW 7985; NHMW 7986; SMNS 89169.

Belonostomus speciosus WAGNER, 1863: BSPG AS VII 1069 (holo-type).

*Belonostomus* sphyraenoides AGASSIZ, 1844: BSPG AS VII 1066 (holotype) and counterpart CAM SM F11098; JME-SOS3044a,b; SMNS 86704.

*Belonostomus tenuirostris* (AGAS-SIZ, 1833): BSPG AS I 1207; BSPG 1956 I 422; BSPG 1957 I 339a and counterpart 1960 XVIII 60; CAM SM F11475; GPIT 7167; GPIT 8103; JME-Scha45a,b; JME-Scha1466; JME-Scha1467; JME-SOS2735; JME-SOS2841; JME-SOS2844; JME-SOS2845; JME-SOS2850; JME-SOS2851a,b; JME-SOS3258; JME-







Fig. 2: Designated neotype of *Belonostomus tenuirostris* (BSPG AS I 1207) from Solnhofen: a) Complete specimen. b) Cranium. c) Detail of the cranium with the dentition of the premaxilla and the predentary.

Abb. 2: Neuernannter Neotypus von *Belonostomus tenuirostris* (BSPG AS I 1207) von Solnhofen: a) Gesamtübersicht des Exemplars. b) Schädel. c) Detail des Schädels mit der Bezahnung der Prämaxilla und des Prädentale. SOS4074a,b; JME-SOS8088; MB. f. 3535; MB. f. 3569; MB. f. 3570; MB. f. 3578; MNHN SLN 7a,b; MNHN SLN 162; MNHN SLN 164; NHMUK PV P.962a; NHMUK PV P.962; NHMUK PV P.2001; NHMUK PV P.7661; NHMUK PV P.12762; NHMUK PV 35014; NHMUK PV 36029; NHMW 7918; NMP UC 89; SMF-P.9633; SMNS 18889; SMNS 55675; SMNS 55676; SMNS 86367; TM6847; TM13253.

Belonostomus sp. (from Cerin): FSL 1066; FSL 93082; FSL 93408; FSL 93409; FSL 503602; FSL 503634; FSL 503816; FSL 504133; FSL CRN 400054; MHNL20015041; MHNL20015042 and counterpart MHNL20015043; MHNL20015045; MHNL20015046; MHNL20015047; MHNL20015049; MHNL20015054; MHNL20015055; MHNL20015056 and coun-MHNL20015059; MHNL20015315A,B; terpart MHNL20015520; MHNL20015588; MHNL20150356; MHNL20150467; MHNL20150967; MNHN CRN 7; MNHN CRN 8; MNHN CRN 81. Belonostomus sp. (from Breitenhill): JME-SOS2842 a,b.

### Systematic Palaeontology

Neopterygii REGAN, 1923 (sensu PATTERSON 1973) Aspidorhynchiformes Bleeker, 1859 Aspidorhynchidae NICHOLSON & LYDEKKER, 1889 Genus *Belonostomus* AGASSIZ, 1834b Name: similar to the recent fish genus *Belone* 

*Diagnosis of the genus* (amended from BRITO 1997): A very slender and elongated Aspidorhynchidae, with a maximum depth (MD) of about 6-9% of standard length (SL). The cranium is also slender and elongate with both jaws of great length. The main characteristic feature is an elongated predentary, which is nearly as long as the dentary. A supramaxilla does not exist.

The maxilla is pointed at the ends with a laterally expanded lamella at the dorsal border. Ganoin on the scales is present. There are three dorsoventrally elongated flank scales in the middle of the body, of which the median one is the lateral line scale, which is two to three times higher than long. All fins are reduced in size and have fewer rays than in other members of Aspidorhynchidae. (A comparison of the aspidorhynchid genera is provided in Tab. 2, modified from BART-HOLOMAI 2004).

Type species: *Belonostomus tenuirostris* (AGAS-SIZ, 1833)

*Belonostomus tenuirostris* (AGASSIZ, 1833) (Fig. 2, 3) 1833 *Aspidorhynchus tenuirostris* AGASSIZ p. 478 1833-44 *Aspidorhynchus tenuirostris* AGASSIZ vol. 2, pt. 1, p. 14

1834a Aspidorhynchus tenuirostris AGASSIZ p. 70 1834b Belonostomus tenuirostris AGASSIZ p. 388 1837 Belonostomus tenuirostris AGASSIZ p. 127



Fig. 3: *Belonostomus tenuirostris*, NHMUK PV P.7661 (acid prepared specimen) from Solnhofen: a) Complete specimen.
b) Cranium with one row of teeth in the premaxilla.
Abb. 3: *Belonostomus tenuirostris*, NHMUK PV P.7661 (säure-präpariert) von Solnhofen: a) Gesamtübersicht des Exemplars.
b) Schädel mit einer Reihe von Zähnen auf der Prämaxilla.

1837 Belonostomus tabulatus AGASSIZ p. 127

*Belonostomus tenuirostris* AGASSIZ vol. 2, pt. 2, p. 143, 165, 297

*Belonostomus tenuirostris* Agassiz; Thiollière p. 111

*Belonostomus tenuirostris* Agassiz; Wagner p. 691

*Belonostomus tenuirostris* Agassiz; Thiollière p. 24

*Belonostomus tenuirostris* Agassiz; Vetter p. 85 (part)

*Belonostomus tenuirostris* Agassiz; Woodward p. 431, pl. 17 fig. 12

*Belonostomus tenuirostris* Agassiz; Saint-Seine p. 257, fig. 114

*Belonostomus muensteri* AGASSIZ; BARTHEL pl. 18, fig. 1

1985 Aspidorhynchus sp. Müller fig. 322





Fig. 4: Holotype of *Belonostomus muensteri* from Solnhofen: a) NHMUK PV P.505 holotype. b) NHMUK PV P.380 (Counterpart of the holotype).

Abb. 4: Holotypus von *Belonostomus muensteri* von Solnhofen: a) NHMUK PV P.505 Holotypus. b) NHMUK PV P.380 (Gegenplatte des Holotypus).

*Belonostomus muensteri* Agassiz; Frickhinger fig. on p. 447

*Belonostomus muensteri* AGASSIZ; LAMBERS p. 301 (only pl. 6a)

*Belonostomus tenuirostris* Agassiz; Brito p. 729, fig. 42-45

*Belonostomus muensteri* Agassiz; Frickhinger fig. 426

1999 Belonostomus tenuirostris Agassiz; Frick-Hinger fig. 183

*Belonostomus tenuirostris* Agassiz; Brito p. 253 fig. 4A,B

*Belonostomus tenuirostris* Agassiz; Arratia p. 305, fig. 16A

*Belonostomus tenuirostris* AGASSIZ; PHILIPPE et al. fig. on p. 74-75

*Belonostomus muensteri* Agassiz; Arratia p. 79, fig. 21





Fig. 5: Cranium of *Belonostomus muensteri*: a) BSPG XXIII 527a, from Daiting. b) NHMUK PV P.3802, from Solnhofen, with two rows of teeth in the premaxilla. Abb. 5: Schädel von *Belonostomus muensteri*: a) BSPG XXIII

527a von Daiting. b) NHMUK PV P.3802 von Solnhofen mit zwei Reihen von Zähnen auf der Prämaxilla.

2010 *Belonostomus muensteri* AGASSIZ; RESCH & RÜCKERT p. 9

*Neotype:* AGASSIZ or later authors never decided on a type specimen. Therefore, according to Article 75 of the International Code of Zoological Nomenclature, BSPG AS I 1207 is here designated as the neotype (Fig. 2).

This specimen is chosen as the neotype because: a) It is the best preserved *B. tenuirostris* specimen known to the author from the type locality of Solnhofen. After a new preparation of the dentition by the author, this main distinctive feature is now very well visible.

b) This specimen belongs to the old collection of the BSPG and is probably one of the specimens studied by Agassiz. The label of this specimen and the catalogue of this collection, however, were destroyed in World War II.

*Type horizon and locality:* The newly designated neotype is from Solnhofen (*rueppelianus* horizon), the original type locality of AGASSIZ.

*Distribution:* From the southern German Plattenkalk basins of Solnhofen/Langenaltheim (Tithonian, *rueppelianus* horizon), Zandt (Kimmeridgian, *eigeltingense* horizon), Schamhaupten and Painten (both Kimmeridgian, *rebouletianum* horizon; for the localities see Fig. 1).

**Emended Diagnosis** – as in BRITO (1997), but with the following emendations:

- Up to 35 cm standard length (SL).
- 77-78 vertebrae (Fig. 3a).

• About 77-78 lateral line scales (this number is identical to the number of transverse scale rows).

• The upper jaw (premaxilla) is 28-44% longer than the lower jaw (predentary), (measured from the front of the orbit to the front tips of the jaws) (Fig. 2b, 3b).

• The predentary is shorter in *B. tenuirostris* compared to the same cranial length in *B. kochii*.

• The premaxilla of each side bears only one row of larger teeth (Fig. 2c, 3b). The tiny teeth, present external to the larger teeth in the other species of this genus, are completely missing.

• Scales and cranial bones are without tubercles.

• The pterygial formula in *B. tenuirostris* is:

*Belonostomus muensteri* AGASSIZ, 1844 (Fig. 4, 5) 1834a *Aspidorhynchus Münsteri* AGASSIZ p. 70 (name only)

1837 Belonostomus Münsteri AGASSIZ p. 127 (name only)

1844 *Belonostomus Münsteri* AGASSIZ p. 141, pl. 47a fig. 2

1863 *Belonostomus Münsteri* Agassız; Wagner p. 689

1895 *Belonostomus muensteri* Agassiz; Woodward p. 429

1997 Belonostomus münsteri Agassız; Brito p. 736 (part)

1999 *Belonostomus tenuirostris* Agassiz; Frick-Hinger fig. 180, 181

2010 Belonostomus sp. Resch & Rückert p. 9, fig. 6-7

*Holotype*: NHMUK PV P.3801 = Fig. 4a, (counterpart NHMUK PV P. 505 = Fig. 4b)

*Type horizon and locality*: From the Mörnsheim Layers (Tithonian, *moernsheimensis* horizon) of Solnhofen. *Distribution*: From the Mörnsheim Layers (*moernsheimensis* horizon) of Daiting, Mülheim and the Solnhofen area. There is much confusion about this species in more recent literature. BARTHEL (1978) and FRIC-KHINGER (1991, 1994) figured BSPG 1957 I 339 from



Fig. 6: Holotype of *Belonostomus kochii*, BSPG AS VII 1068, from Kelheim. Abb. 6: Holotypus von *Belonostomus kochii*, BSPG AS VII 1068, von Kelheim.

Zandt and named this specimen *B. muensteri*. The same diagnosis of this specimen was given by BRITO (1997). However, according to the descriptions of AGASSIZ (1833-44), this specimen belongs to *B. ten-uirostris*. Already AGASSIZ (1833-44: 297) and WAG-NER (1863: 689) mentioned that *B. muensteri* comes especially from Daiting, the active quarry in the Mörnsheim Layers at that time.

**Emended Diagnosis** – as in BRITO (1997), but with the following emendations:

• Up to 40 cm standard length.

• The upper jaw is 0–20% longer than the lower jaw, measured from the front of the orbit to the front tips of the jaws (Fig. 5a).

• The premaxilla on each side bears two rows of teeth, one row of larger teeth on the interior side and an additional row of tiny teeth on the exterior side (Fig. 5b).

• All scales and posterior dermal bones of the skull (e.g., operculum, preoperculum) have tiny tubercles on the surface.

# Belonostomus kochii Münster, 1836 (Fig. 6-12)

1836 Belonostomus Kochii Münster p. 581

1844 *Belonostomus Kochii* Münster, Agassiz p. 143, 165, 297

1863 *Belonostomus Kochii* Münster; Wagner p. 689 1895 *Belonostomus kochi* Münster; Woodward p. 431

1996 *Belonostomus münsteri* Agassız; Schultze & Stöhr fig. 6b

1997 Belonostomus kochii Münster; Brito p. 736

2008a *Belonostomus tenuirostris* Agassiz; Ebert & Kölbl-Ebert fig. 8

2008b *Belonostomus* cf. *tenuirostris* Agassiz; Ebert & Kölbl-Ebert fig. 13

2010b *Belonostomus* cf. *tenuirostris* Agassiz; Ebert & Kölbl-Ebert fig. 7, tab. 1

2010a *Belonostomus* cf. *tenuirostris* Agassiz; Ebert & Kölbl-Ebert fig. 14-16

2011 *Belonostomus kochi* Münster; Ebert & Kölbl-Ebert tab. 2

2013 *Belonostomus tenuirostris* Agassiz; Kogan & Licht fig. 1

2015 Belonostomus kochi Münster; Ebert et al., fig. 11

*Holotype*: BSPG AS VII 1068, from Kelheim (Fig. 6) *Type horizon and locality*: The label of the type specimen is simply marked "Kelheim." The lithology makes it most likely that this specimen came from the Kapfelberg layers, which are Upper Kimmeridgian up to the *eigeltingense* horizon (lowermost horizon of the Tithonian).

**Distribution:** Known only from the older strata of the Kelheim basin, such as Kelheim-Kapfelberg and from the quarry of Ettling.

- Diagnosis
- Up to 33 cm standard length
- 68-71 vertebrae
- Approximately 71-73 lateral line scales (this number is identical to the number of transverse scale rows)





- Length difference of 0-20% between upper and lower jaw (Fig. 7–12).
- The premaxilla on each side bears two rows of teeth, one row of larger teeth on the inner side and an additional row of tiny teeth on the outer side (Fig. 7c, 11b) like in *Belonostomus muensteri*.

• The predentary in *B. kochii* is longer, comparably than in *B. tenuirostris*.

- Scales and cranial bones without tubercles (Fig. 10a).
- The pterygial formula in *Belonostomus kochii* is:

# Anatomical description and comparison of the genus *Belonostomus*

The description is mainly based on *B. kochii* due to the much better preservation of the specimens from Ettling. The other species of *Belonostomus* are mentioned where differences from *B. kochii* are present.

# Cranium

The cranium of *B. kochii* is very well preserved in specimens JME-ETT16 (Fig. 7), JME-ETT17, JME-ETT49, JME-ETT117, JME-ETT123 (Fig. 9), JME-ETT128 (Fig. 8), JME-ETT882 (Fig. 12), JME-ETT981 (Fig. 10), JME-ETT1900, JME-ETT2170, JME-ETT2544 (Fig. 11), JME-ETT2638, JME-ETT3463. The following descriptions and figures based on the best-preserved specimens (i.e., JME-ETT16 (Fig. 7), JME-ETT981 (Fig. 10), JME-ETT2544 (Fig. 11) and JME-ETT3463), in which nearly all bones of the cranium are clearly visible for the first time.

# Skull roof

The rostral bone is unpaired and elongated like the premaxilla. The rostral covers the dorsal border of

Fig. 7: *Belonostomus kochii*, JME-ETT16, from Ettling:
a) Complete specimen. b) Cranium.
c) Camera lucida drawing of the cranium.
Abb. 7: *Belonostomus kochii*, JME-ETT16, von Ettling:
a) Gesamtübersicht des Exemplars. b) Schädel.
c) Camera lucida-Zeichnung des Schädels.



the premaxilla with the exception of the anteriormost part. It sutures with the frontal posteriorly. In the rostral the ethmoidal commissure is visible running from the left side of the cranium to the right, perpendicular to the body axis in the position of the posterior end of the predentary. At the ventral border of the rostral the ethmoidal commissure ends in a pore. In some specimens, however, at the position of this ethmoidal commissure, the rostral has an indentation (JME-ETT16 (Fig. 7), JME-ETT981 (Fig. 10)). The frontals cover the dorsal part of the cranium above the orbit. Anteriorly there is a zigzag-shaped suture with the rostral and posteriorly with the dermopterotic. In the frontal, dorsal to the dermosphenotic, the connection of the supraorbital canal, the temporal canal and the infraorbital canal is clearly visible (best observed in JME-ETT16 (Fig. 7), JME-ETT 882 and JME-ETT2544 (Fig. 11)). In many specimens the dorsalmost suborbital covers a part of the frontal dorsoventrally. The dermosphenotic lies at the posterodorsal end of the orbit and has a canal inside, running from the infraorbitals to the frontal. The dermopterotic and the parietal are fused into a single bone, which lies posterior to the frontal. The dermopterotic has a lateral expansion alongside the ventral border and is best recognizable by the junction of the temporal canal and the supraoccipital canal. The temporal canal runs close to the ventral margin of the dermopterotic. The junction between the temporal and supraoccipital canal and the lateral line occurs approximately at the centre of the ventral border of the dermopterotic at a position dorsal to the dorsalmost tip of the preoperculum. The extrascapulars are not clearly visible in any of the specimens. The posttemporals are orientated and ornamented like larger dorsal body scales. At their ven-



Fig. 8: *Belonostomus kochii*, JME-ETT128, from Ettling. Abb. 8: *Belonostomus kochii*, JME-ETT128, von Ettling.

tral borders the lateral line canal is clearly visible. Posterior to the posttemporals the first scales of the body appear. Along the complete skull roof, from the anterior tip of the premaxilla to the posttemporals, all bones are ornamented with longitudinal ridges, which are strongest in adult specimens.

#### Circumorbital bones

There are four to six infraorbitals visible in known specimens of *B. kochii* (four in JME-ETT2544 (Fig. 11); five in JME-ETT16 (Fig. 7), JME-ETT128 and JME-ETT3673; six in JME-ETT117 and JME-ETT981 (Fig. 10)). The first infraorbital is a rectangular to ovoid bone, which lies at the anterior part of the orbit. A Y-shaped antorbital with a similarly Y-shaped sensory canal connecting to the infraorbital and supraorbital sensory canals and the ethmoidal commissure, which was described in *Aspidorhynchus* (LÓPEZ-AR-BARELLO & SCHRÖDER 2014), is not present in *Belonostomus*. The second infraorbital is a triangular bone,

Fig. 9: *Belonostomus kochii*, JME-ETT123a, from Ettling, with *Orthogonikleithrus hoelli* ARRATIA, 1997 as prey in the mouth: a) Complete specimen. b) Cranium of this juvenile specimen, with only one row of teeth in the premaxilla. Abb. 9: *Belonostomus kochii*, JME-ETT123a, von Ettling, mit *Orthogonikleithrus hoelli* ARRATIA, 1997 als Beutefisch im Maul: a) Gesamtübersicht des Exemplars b) Schädel dieses juvenilen Exemplars mit nur einer Reihe von Zähnen auf der Prämaxilla.





slightly more than twice as long as the first infraorbital. It begins on the anterior margin of the orbit and curves down nearly to the ventralmost point of the orbit, where it ends in an elongated tip. In JME-ETT981 (Fig. 10b), a third elongated infraorbital follows on the ventral rim of the orbit. One to three more rectangular infraorbitals follow on the posterior part of the orbit. In JME-ETT2544, with only one infraorbital behind the posterior border of the orbit, a fusion of infraorbitals may have occurred. The ventralmost of these three infraorbitals is not elongated caudally, unlike Aspidorhynchus. Only in JME-ETT2544 (Fig. 11), where a fusion of infraorbitals may be present, a caudal expansion is faintly discernible. But there is still a suborbital between the infraorbital and the preoperculum and there is no connection between this infraorbital and the preoperculum as in Aspidorhynchus.

There are two supraorbitals on the dorsal border of the orbit. One large, triangular supraorbital begins at the anterior dorsal margin of the orbit and extends over more than two-thirds of the dorsal rim of the orbit. It ends posteriorly in a sharp pit. A second smaller, more ovoid supraorbital lies posterior to this



large supraorbital. In the ventral part of the orbit two sclerotic plates are visible in well preserved specimens (e.g., JME-ETT981, Fig. 10; JME-ETT2544, Fig. 11). Between the rostral and the first supraorbital and dorsal to the first infraorbital there is a small bone that is probably the nasal. A large part of this bone is covered by the supraorbital.

#### **Cheek bones**

There are three to four large suborbitals (three in JME-ETT117, JME-ETT128, JME-ETT1900 and JME-ETT3673; four in JME-ETT16), which in larger specimens are slightly ornamented with wavy ridges. The preopercular presents two well-defined parts: a vertical dorsal ramus and an expanded ventral part. In the well-preserved specimen of Belonostomus tenuirostris (BSPG 1957 I 339a) there are two tiny spines at the posteroventral edge of the preopercular. In JME-ETT981 there is a separate bone between the preopercular and the ventralmost suborbital (Fig. 10). This separate bone is part of the preopercular in all other specimens, which is clear because this bone bears parts of the preopercular canal. In the preopercular the main preopercular canal runs from the dorsal edge vertically downwards and then with a kink in the middle of the bone horizontally to the anteroventral edge. The preopercular canal (like all cranial sensory canals) is visible as an indentation in the bone and the colour of the bone above the canal is somewhat lighter. From the main preopercular canal there run some unbranched canalicules to the surface, which end in single pores. The vertical dorsal ramus of the preopercular has four to seven pores and the expanded ventral part has up to ten pores, depending on the ontogenetic stage of the speci-

Fig. 10: Cranium of *Belonostomus kochii*, JME-ETT981, from Ettling. a) Photo. b) Camera lucida drawing. Abb. 10: Schädel von *Belonostomus kochii*, JME-ETT981, von Ettling. a) Foto. b) Camera lucida-Zeichnung.



men. Anterodorsal to the point were the main preopercular canal bends in a sharp angle, there is a second canal. This second canal is smaller and bow-shaped, and curves in the opposite direction to the main preopercular canal (Fig. 7b, 11a). This second canal was present in all specimens of *Belonostomus* and *Aspidorhynchus* where the preservation is sufficient.

# **Opercular series**

The operculum is large and nearly ovoid. In most specimens (e.g., JME-ETT2544, Fig. 11) the posterior part of the operculum completely covers the cleithrum, except in JME-ETT981 in which the operculum ends anterior to the cleithrum (Fig. 10).

The suboperculum is reduced in size, with a maximum depth between 0.2 and 0.25 the depth of the operculum. The suboperculum is triangular, with a well-developed ascending process. The anteroventral edge of the suboperculum ends at the posteroventral edge of the preoperculum. An interoperculum as figured by GARDINER (1960, fig. 76) could not be observed with certainty. A thin elongated bone is visible on the ventral rim of the preoperculum in JME-ETT128 and JME-ETT2544 (Fig. 11), which could be an interoperculum. The preoperculum covers a large part of this bone. In a single specimen (JME-ETT981), the suboperculum does not reach the posteroventral edge of the preoperculum and a bone is visible more posteriorly in direct elongation of the suboperculum which could be an interoperculum or a further branchiostegal (Fig. 10). In JME-ETT3463, an interoperculum is clearly not developed.

Fig. 11: Cranium of *Belonostomus kochii*, JME-ETT2544, from Ettling. a) Photo. b) Camera lucida drawing. Abb. 11: Schädel von *Belonostomus kochii*, JME-ETT2544, von Ettling. a) Foto. b) Camera lucida-Zeichnung.

# Jaws

The upper jaw consists of the premaxilla and the maxilla. As in the Aspidorhynchid genus *Vinctifer* (BRITO 1997: 698) and *Richmondichthys* (BARTHOLOMAI 2004: 531), there is no supramaxilla in any specimen of *Belonostomus*. This readily distinguishes the genus *Aspidorhynchus* from *Belonostomus*, because in *Aspidorhynchus* a supramaxilla is present (see, e.g., *Aspidorhynchus sanzenbacheri* BRITO & EBERT 2009, figs. 4, 5).

The premaxilla in *Belonostomus* is an elongated, narrow bone, which is half of the length of the skull or even slightly more. The premaxilla in *B. tenuirostris* is 28–44% longer than the lower jaw (predentary), measured from the anterior rim of the orbit to the tips of the jaws (Fig. 2b, 3). In *B. kochii* and *B. muensteri* the premaxilla is in most cases somewhat longer than the predentary (up to 20% longer). In some cases the jaws are of nearly the same length, but in these cases tip of the premaxilla looks somewhat worn – as in JME-ETT49, JME-ETT981 (Fig. 10) and JME-ETT2544 (Fig. 11). In







Fig. 12: *Belonostomus kochii*, JME-ETT882, from Ettling. Juvenile specimen, with premaxillae not yet fused to form a single element.

Abb. 12: *Belonostomus kochii*, JME-ETT882, von Ettling. Juveniles Exemplar mit zwei getrennten Prämaxillas, die noch nicht zu einem Knochen verwachsen sind.

one specimen (JME-ETT3372) the premaxilla is broken off, probably during life, either by predation or fighting among rivals. The left and right premaxillae seem to be fused into a single element in adult specimens, forming a single "rostrum." In some juveniles in which the jaws are a bit squeezed, it becomes apparent that the jaws in juveniles are not yet fully fused (see JME-ETT882, Fig. 12). The posterior two-thirds of the premaxilla is covered dorsally by the rostrum. In B. *tenuirostris* the premaxilla of each side bears only one row of larger teeth (Fig. 3b); in adult specimens such as BSPG AS I 1207 there are about fifty teeth. The anterior tip of the premaxilla in B. tenuirostris, which protrudes over the predentary, is either completely toothless (as in NHMUK P7661) or the teeth are noticeably smaller and only the anterior three quarters of the space are without teeth (as in BSPG 1957 I 339 and BSPG AS I 1207).

In adult specimens of *Belonostomus kochii* (Fig. 7c, 11b), as well as *B. muensteri* (Fig. 5b), the premaxilla bears two rows of teeth: One row of larger teeth that slightly increases in size caudally (about 30 teeth in JME-ETT2544) and external to the larger teeth another row of numerous tiny teeth, one-fourth to onefifth the size of the large teeth. However, in juveniles of *B. kochii* such as JME-ETT123 (Fig. 9) and JME-ETT882, the second row of tiny teeth is missing. In sub-adults such as JME-ETT2544 and JME-ETT3463 (about 20 cm in total length), these tiny teeth are only present in the posterior two-thirds of the premaxilla (Fig. 11). Many of the larger premaxillary teeth, especially the largest, are curved, with the tip pointing to the front. According to Vetter (1881, p. 83), the length of the premaxilla ("rostrum") decreases with ontogeny in *Aspidorhynchus*. However, according to our studies, this is not the case in *Belonostomus*.

The maxilla is an elongated thin bone with an expansion projecting from the dorsal border. It begins anteriorly as a very thin bone in the same position as the beginning of the dentary below. Shortly after the frontal tip, the height of the maxilla slowly increases to a point anterior to the anteriormost infraorbital and then the height of the maxilla declines immediately, down to the same height as at the anterior end. This expansion at the dorsal border of the maxilla forms a thin lamella, which is anteroposteriorly more extended than in the genus Aspidorhynchus. The posteriormost part of the maxilla curves slightly downward and overlaps the dentary. The maxilla ends at the position of the posterior two-thirds of the orbit. The oral border of the maxilla bears a row of tiny teeth, all of nearly similar size (about 120 teeth counted in JME-ETT2544). The maxillary teeth are less than half the size of the dentary teeth, which lie opposite to them.



Fig. 13: Tubercles on the scales of *Belonostomus sphyraenoides* (JME-SOS3044b) are clearly visible as imprints in the matrix. Abb. 13: Die Tuberkel auf den Schuppen von *Belonostomus sphyraenoides* (JME-SOS3044b) sind klar als Abdrücke in der Matrix erkennbar.

An unpaired predentary and paired dentaries, angulars and surangulars, have been identified in the lower jaw. The predentary is elongate (8-13 times as long as high) and toothed along its total length. It is linked to the rest of the mandible by a triangular suture and is the same length as the dentary or slightly more. In all species of *Belonostomus*, the oral border of the predentary bears a sparse row of median large teeth, which slightly increases in size posteriorly (approximately 25 teeth in *B. tenuirostris*: BSPG AS I 1207 or *B.* kochii: JME-ETT2544 and about ten teeth in B. speciosus: BSPG AS VII 1069). These larger teeth are flanked on each side by a row of numerous small lateral teeth (in BSPG AS I 1207, a second row of small teeth is visible in the posterior part of the predentary). All of these smaller teeth are of nearly the same size (approximately 170-180 teeth in BSPG AS I 1207). Two rows of teeth on the predentary, visible in lateral view, can be found in all specimens of Belonostomus and Aspidorhynchus if the preservation is adequate. The larger teeth, which lie in a second row behind the small teeth, are always about twice the size of the premaxillary teeth on the opposite side of the jaw. Most of these larger predentary teeth, especially the largest, are curved, with the tip pointing to the front.

The dentary constitutes most of the mandible; it is five to six times as long as it is broad and approx-

imately the same height from anterior to posterior. It is toothed along its entire length, with numerous medium sized teeth (at least 70 in JME-ETT981), of which the largest teeth are located in the middle of the bone. Near the anterior tip of the dentary is one large tooth, representing the largest tooth in the entire cranium. This large tooth is no paired element but only present in one of the dentary bones. This large tooth on one of the dentary bones is also present in Aspidorhynchus. The posterior part of the dentary curves slightly upwards and the last teeth are visible dorsal to the maxilla in some specimens (JME-ETT981, JME-ETT16, JME-ETT117), the posteriormost part of which overlaps the dentary. The posteriormost bone in the lower jaw is the angular, which is connected to the dentary by a zigzag-shaped suture. The surangular, at the dorsal border of the angular, is not clearly visible.

# *Ornamentation of the cranial bones* (only visible in adult specimens)

In *Belonostomus tenuirostris* and *B. kochii*, the anterior part of the premaxilla is covered with grooves parallel to the body axis which continue caudally in longitudinal striations. A pattern of wavy, wrinkled striations, mostly orientated parallel to the body axis, is visible along the entire surface of the skull roof bones, i.e. the rostral, frontal, parietal, dermopterotic, extrascap-

ula and posttemporal. This pattern of wrinkled lines continues on the dorsal body scales. The dorsal lamella of the maxilla, the suborbitals and the opercular bones are in juvenile specimens completely smooth, whereas in adult specimens they can have a pattern of sparse wavy lines, mostly perpendicular to the body axis.

In *Belonostomus muensteri*, *B. speciosus* and *B. sphyraenoides*, the patterns on the anterior part of the cranium are the same as in *B. tenuirostris* and *B. kochii*, but posterior to the orbit all dermal bones of the skull and scales are covered with tubercles (Fig. 13), which are lacking in *B. tenuirostris* and *B. kochii*.

In all species of *Belonostomus*, the predentary has tiny horizontal (i.e. anteroposterior) striations, whereas the dentary is completely smooth.

### Palatal bones, jaw articulation and hyoid arch

The ectopterygoid, endopterygoid and metapterygoid are mostly covered by other cranial bones. Only in specimens where these overlying bones are removed (for example, by splitting the rock, as in JME-SOS2842) or when the mouth is widely open (as in JME-Moe114), an internal surface of these bones, with tiny teeth, is visible.

The quadrate is a fan-shaped, crenulated bone, which lies between the angular and the preoperculum. Dorsally it is overlapped in some specimens by the lowermost suborbital (e.g., JME-ETT981) or by an infraorbital (as in JME-ETT2544). The quadrate has a well-developed jaw articulation with the angular (best visible in JME-ETT3463). The posterior part of the quadrate is covered by the preoperculum.

The lower part of the hyoid arch is visible in JME-ETT3463 and JME-ETT128. The anterior ceratohyal is a nearly rectangular bone, four to five times as long as high. The posterior ceratohyal is much smaller and has a triangular shape, a convex border with the anterior ceratohyal a small fenestra in the anterior part, probably for the passage of the hyoidean artery. A very small bone is visible anterior to the anterior ceratohyal, which could be the hypohyal. A connection with the branchiostegal rays visible in JME-ETT2544 (Fig. 11); there are probably more, but these tiny and thin bones are hardly visible.

### Pectoral fin and girdle

There are one or two larger scales behind the extrascapular bone, with the lateral line at the ventral border; these are probably the posttemporal(s). Apart from the lateral line, these scales are indistinguishable from the other dorsal scales of the body. Posterior to the posttemporal and dorsal to the cleithrum, the lateral line can be followed along the dorsal border of the supracleithrum into the second row of enlarged body scales. The operculum partly overlaps the supracleithrum, which is an elongated scale at the posterior dorsal border of the operculum.

The cleithrum is a well ossified, bow-shaped bone at the posterior and ventral rim of the operculum. In

Tab. 3: Characteristic features of the different species of *Belonostomus* in the Solnhofen Archipelago (the ratio of upper to lower jaw length is measured from anterior rim of orbit to anterior tip of jaw).

Tab. 3: Charakteristische Merkmale der unterschiedlichen *Belonostomus*-Arten im Solnhofener Archipel (das Verhältnis der Ober- zur Unterkieferlänge wird vom Augenvorderrand bis zur jeweiligen Kieferspitze gemessen).

Species of the genus <i>Belonos-</i> tomus	length difference between the upper and lower jaw	rows of teeth in the pre- maxilla	number of verte- brae	num- ber of lateral line scales	pterygial formula		tubercles on scales
B. kochii	0-20 %	2	68–71	71–73	D51-54	- <i>T</i> 71–73	no
	0.00.00				P30-31 A45-48 C04-08		
B. sphyraenoi- des	0-20 %	2	71	71			yes
B. tenuirostris	28-44 %	1	77–78	77-78	D55–58		no
					P31-33 A49-52 C74-75	- 1//-/8	
B. speciosus	~10 % (both jaws relatively short)	2	77				yes
B. muensteri	0-20 %	2					yes

most specimens its upper arm is nearly completely covered by the operculum and its lower arm is covered by the suboperculum. Only in JME-ETT981 is the operculum a bit shorter, not covering the cleithrum posteriorly (Fig. 10). There are no prominent postcleithral scales in any observed specimen of *Belonostomus*.

The pectoral fins are small but longer than the pelvic, anal and dorsal fins and comprise as many as seven to eight rays (best visible in JME-ETT3463, in which the left and the right pectoral fins are separated). The second to sixth rays are broad and overlap each other in the anterior half. This and the fact that nearly the total length of these rays is unsegmented, help to stiffen these fins. Only the posterior-most parts of these rays are segmented and branched. The slender first ray is nearly as long as the second ray, slightly bowed and unsegmented. The base of this first ray is as broad as the second ray up to the first one-third of the ray, after which the first ray becomes narrower and tapers posteriorly. The second ray is the longest ray and branches two to three times in adult specimens, making it broader towards the posterior end. The shape and number of subsequent rays are difficult to study, because they are mostly covered by the aforementioned rays, but they are all segmented and branched posteriorly and rapidly decreasing in size. In Belonostomus kochii from Ettling, the leading edges of all fins have a rim of ganoin. Fine wavy "ridges" of ganoin have been described by Arratia (2008: 81) for the caudal fin of Belonostomus, but in the extraordinary preservation at Ettling a rim of ganoin is preserved along the leading edges of all fins. This rim of ganoin can easily be recognized by a locally confined swelling and darker colour on these rays (EBERT & KÖLBL-EBERT 2010a, figs. 14, 16). I am unable to observe a difference in the shape of the pectoral fin between the various species of Belonostomus reported by BRITO (1997: 736).

### Pelvic fins

The pelvic fin is similar to the pectoral fin but smaller. In *Belonostomus kochii* the pelvic fin originates after the 30–31<sup>th</sup> scale row and in *B. tenuirostris* it originates after the 31–33<sup>th</sup> scale row. Seven rays are visible in JME-ETT128.

### Dorsal and anal fins

Both the dorsal and the anal fins are triangular and located posteriorly on the body. In *Belonostomus kochii* the dorsal fin begins at the level of the 51<sup>st</sup>-54<sup>th</sup> transverse scale row and the anal fin at the 45-48<sup>th</sup> transverse scale row. In *B. tenuirostris*, the dorsal fin begins at the level of the 55-58<sup>th</sup> and the anal fin at the 49-52<sup>th</sup> transverse row of scales. The anal fin is somewhat longer and broader than the dorsal fin. The pterigophores are normally covered by scales, but in JME-ETT3463 thirteen anal pterigophores are clearly visible underneath the scales, whereas in JME-ETT128 the scales are removed at this position and thirteen anal pterigophores are visible. The anal fin comprises one to two basal fulcra, one or two segmented but unbranched rays and up to 14 branched fin rays (JME-ETT17). The third anal fin ray is the longest ray (best visible in JME-ETT17), after which the rays gradually decrease in length caudally. In adult specimens there are one to two elongate fringing fulcra anterior of each unbranched ray and a small number of fringing fulcra between the unbranched ray and the first branched ray. All fulcra have a rim of ganoin.

In the dorsal fin there are 9-11 fin rays and 1-2 dorsal basal fulcra. In JME-ETT941a there are two very short basal fulcra, one segmented but unbranched short ray and eight segmented and branched rays. The second and third rays are the longest, after which the rays gradually decrease in size. In JME-ETT17 there are two very short basal fulcra, three segmented but unbranched rays (each twice the size of the preceding ray) and eight segmented and branched rays. The last unbranched and first branched rays are the longest. In JME-ETT3463 eight dorsal pterigophores are visible underneath the scales and in JME-ETT117 seven dorsal pterigophores are visible (the anteriormost pterygophore may be hidden under the scales). In JME-ETT117 and JME-ETT16, the scales ventral to the dorsal fin are reduced in size or completely missing, so that a small scale-free area appears, under which several pterygopores are visible. Such a scale-free area ventral to the dorsal fin is known in other actinopterygians (for example, Macrosemius), in which it has been interpreted as contributing to increased fin mobility (EBERT et al. 2013).

### Caudal fin

The small caudal fin is forked, with both lobes of nearly the same length. In some specimens (e.g., JME-ETT128: Fig. 8), the ventral lobe is slightly longer than the dorsal lobe, but not as much as in the genus Aspidorhynchus where the ventral lobe is always distinctly longer. Very long fringing fulcra are present at the leading edge of the caudal fin (EBERT & KÖLBL-EBERT 2010a, fig. 15), which because of their exceptional length were termed "modified fringing fulcra" by AR-RATIA (2008: 81). The dorsal lobe comprises four to six basal fulcra, one to two procurrent rays and seven to eight principal rays. The ventral lobe comprises one to two basal fulcra, four to five procurrent rays and eight to ten principal rays. The total number of principal rays is 15–17 (15 in JME-ETT16, JME-ETT117, JME-ETT882, JME-ETT1900, JME-ETT1941, JME-ETT2170, JME-ETT3463, JME-SOS2841, JME-SOS2844, JME-SOS2845, JME-SOS3258 and NHMW

8625; 16 in BSPG 1957 I 339; 17 in JME-ETT17 and JME-ETT128). *Belonostomus* lacks an urodermal, which is present in *Aspidorhynchus* (EBERT & KÖL-BL-EBERT 2010a, figs. 4, 5b, 6, 7, 11, 12).

# Vertebrae

The total number of vertebrae is difficult to count, because in well-preserved specimens the vertebrae are covered by scales and in juveniles not all vertebrae are ossified (especially in the caudal area). In nearly all specimens of *Belonostomus tenuirostris* or *B. muensteri*, parts of the vertebral column are missing.

The total number of vertebrae in *B. tenuirostris* is about 78 (BRITO, 1997). For the present paper, 78 vertebrae were counted in BSPG AS I 1207; about 77 in BSPG 1957 I 339; about 79 in JME- SOS4074 and about 78 in the juvenile specimen JME-SOS3258. In specimens of *B. kochii* from Ettling, only 68-71 vertebrae were counted (68 in JME-ETT1941, about 71 in JME-ETT2170 and about 68 in JME-ETT3463). In *B. sphyraenoides*, about 71 vertebrae could be counted in specimen JME-SOS3044. For *B. muensteri* no specimen is well enough preserved to count the number of vertebrae.

The vertebrae in adult specimens of Belonostomus tenuirostris and B. muensteri are completely ossified and similar in colour to the other bones and the surface of the cylindrical vertebral centra is completely smooth. In specimens of B. kochii, nearly all vertebrae are covered by scales, but vertebrae of B. kochii from Ettling are black in colour (completely different from the brown colour of the other bones and covering scales) and are therefore clearly visible through the scales. In broken specimens such as JME-ETT3378, it is clearly observable that the vertebrae in adult specimens of B. kochii are not completely ossified, unlike in B. tenuirostris and B. muensteri. Comparable partially ossified vertebrae can be observed in adult specimens of Aspidorhynchus as well. A gap between the vertebrae lacking calcification, as described by SAINT-SEINE (1949), was found only in juvenile specimens. For the vertebrae in the caudal area, see BRITO (1999) and ARratia (1999).

Earlier authors, such as AGASSIZ (1833-44), WAG-NER (1863), WOODWARD (1895), EASTMAN (1914a, b) and BRITO (1997), tried to compare the different *Belonostomus* species with regard to the shape of the vertebral centra; some of them with contradictory results. Whereas AGASSIZ (1844) and WAGNER (1863) report that the vertebrae are longer than deep in *B. tenuirostris*, WOODWARD (1895: 432) claims that they are "much deeper than broad." One of the problems is that in all juvenile *Belonostomus* specimens, as in other actinopterygian fishes (see for example KONWERT, 2011, TISCHLINGER & ARRATIA, 2013), the vertebral centra are not fully developed and are always deeper than long. Even in some sub-adults of about one-half to twothirds of the maximum species length, the vertebrae are not as long as in large, fully adult specimens. This was quite problematic in classifying the different species (see below: *B. sphyraenoides*). The best-preserved vertebrae can be observed in acid-prepared, slightly disarticulated specimens (Fig. 3a), in which the scales have been removed from the body. Disarticulation is common in specimens from the Solnhofen Plattenkalk sensu stricto (Fig. 3a, 14) or the Plattenkalk of the Mörnsheim Layers (Fig. 4). From Ettling and Kelheim, however, disarticulation is unknown and in all specimens the vertebral column is completely covered by scales. In younger specimens, however, the vertebral column can be seen through the transparent scales. In all adult specimens of B. muensteri, the vertebral centra are longer than deep. In some specimens of B. ten*uirostris*, the vertebral centra are also longer than deep (for example, JME-SOS4074 from Mörnsheim-Hummelberg, or BSPG AS I 1207 from Solnhofen). In other adult B. tenuirostris specimens, the vertebral centra are as long as they are deep (for example, NHMUK P.7661, BSPG 1957 I 339a and MB. f. 3569), with the exception of some vertebrae in the posterior part of the body, which are longer than deep.

### Squamation

The shape and arrangement of the scales is similar in all species of the genus *Belonostomus*. They only differ in the number and ornamentation of the scales, which are characteristic features distinguishing the different species. In *B. muensteri*, *B. sphyraenoides* and *B. speciosus*, all scales are covered with tubercles (Fig. 13), whereas in *B. tenuirostris* and *B. kochii*, the scales are smooth or ornamented with elongated ridges. A caudal inversion of scale rows is absent.

Belonostomus tenuirostris has 77-78 transverse scale rows from the cranium to the caudal fin. This number is identical in all species to the number of lateral line scales (about 77 in BSPG 1957 I 339, about 78 in JME-SOS3258 and about 78 in JME-SOS2845). Belonostomus sphyraenoides JME-SOS 3044 has 71 or 72 scale rows. The number of scale rows or the number of lateral line scales is not countable in B. muensteri or B. speciosus due to preservation. B. kochii has 71-73 transverse scale rows and lateral line scales. The number of scales in one transverse scale row decreases from the abdominal region (max. 15) to the caudal fin base, where only one or two scales are present in a single scale row. In contrast to the genus Aspidorhynchus, all species of the genus Belonostomus and Vinctifer have a ganoin coating on their scales (SCHULTZE 1966, 1996; Brito 1997 and Brito & Meunier 2000). There are three larger flank scales in each transverse scale row, with the exception of the anteriormost postcranial area and the caudal area. In the anterior half of the body, the ventralmost of these flank scales is the largest, about three times higher than long. The central flank scale, which is the lateral line scale, is the largest flank scale from approximately the middle of the body (2.5 times higher than long) to the rear. The dorsalmost flank scales are the smallest (two times higher than long) and only elongated in the posterior two thirds of the body. Nearly in the middle of this dorsalmost flank scale, there is a horizontal ridge, which ends in a prominent spine on its posterior end. The surface of this ridge is also covered with tiny spines, which are orientated posteriorly as well. In Aspidorhynchus there are two elongated flank scales ventral to the lateral line scale; the second scale ventral to the lateral line scale is never elongated in the genus Belonostomus. Most of these flank scales in B. kochii are completely smooth ventral to the lateral line, but in some specimens (e.g., JME-ETT16 and JME-ETT1941) there a few tiny vertical ridges. Dorsal to the lateral line, all scales are ornamented with wavy ridges that are orientated horizontally. The lateral line is visible as a horizontal line along the dorsal two thirds of the lateral line scale and ends in each scale with a small indentation. In the anterior part of the body nearly every second lateral line scale has a pore in the middle, probably for the "Grübchenorgan" (see SCHULTZE 1966). Posteriorly, the number of lateral line scales with pores decreases, so that in the posterior part of the body only every fourth or fifth lateral line scale has a pore. Nearly all lateral line scales have a small spine directly dorsal to this indentation. A small number of lateral line scales are spineless and in large specimens (e.g., JME-ETT17) some lateral line scales have a second small spine at the posteroventral end. Dorsal to the flank scales, there are three rows of smaller ornamented scales (best seen in JME-ETT1941). Nearly all of these scales end posteriorly in a spine, but most of the dorsalmost scales in each scale row are spineless (best seen in JME-ETT1941). Ventral to the flank scales, there are up to nine small, rectangular, smooth scales, all having a small spine on their posterior end. The dorsalmost of these small rectangular scales is the largest and its spine is swollen in larger specimens to a horizontal ridge, which extends over the entire scale. The high number per scale row (up to nine) of these small rectangular scales is only present in the stomach region. Caudally, they decrease gradually to one scale. Like the row of spines along the uppermost flank scale, this second row of spines can be followed as a line along the body of *Belonostomus* kochii. Near the base of the ventral lobe of the caudal fin, the lower row of spinous scales ends in a ridge of thickened scale spines (EBERT & KÖLBL-EBERT 2010a, fig. 16). At the base of the dorsal lobe of the caudal fin and ventral to the dorsal fin, some scales are reduced in

size. Dorsal to the anal fin in JME-ETT1941, two scale rows merge at the position of the lateral line scale and continue dorsally as a single scale row.

#### Prey

EASTMAN (1912) and SAINT-SEINE (1949) described a specimen of Belonostomus from Cerin, France, containing prey. The specimen from the Carnegie Museum (described by EASTMAN) has a Homoeosaurus as stomach contents and the other specimen in the collection in Lyon (NHML 20015056, with counterpart 20015059) has a *Notagogus* specimen as pharyngeal contents. EBERT & KÖLBL-EBERT (2008a) first described prey in a specimen of *Belonostomus* from southern Germany. This specimen (JME-ETT123) is a *B. kochii* with a specimen of Orthogonikleithrus hoelli ARRATIA, 1997 as pharyngeal contents (Fig. 9). KOGAN & LICHT (2013) described a *Belonostomus* specimen from Kelheim, probably a specimen of *B. kochii*, with three prey fish in the abdomen. Two of the prey fish were interpreted as *Leptolepides* sp. and the third as a juvenile *Caturus* sp. From the new excavation site in Ettling, five specimens of B. kochii containing O. hoelli as stomach contents have been collected (JME-ETT893, JME-ETT1900, JME-ETT3378, JME-ETT3673 and JME-ETT3912). There is a further B. kochii specimen in Berlin (MB. f. 3544) with a small teleost in the stomach region.

#### Discussion

#### a) Problematic species

There are specimens, which cannot clearly be assigned to a specific species (mostly due to bad preservation and rareness of specimens). Nevertheless these specimens are important, because some of them have been described historically as separate species, because some of them show a combination of features, which places them somewhere between the above described species. However, whether *Belonostomus speciosus* and *Belonostomus sphyraenoides* (see below) represent valid species can only be studied satisfactorily, when more and better preserved material will become available. At the moment these species must be treated as *nomina dubia*.

The same problem of bad preservation likewise affects the assignment and description of *Belonosto-mus*-specimens from the French locality Cerin (see below).

Belonostomus speciosus WAGNER, 1863 (Fig. 14)

1863 Belonostomus speciosus WAGNER p. 689

1887 Belonostomus speciosus WAGNER; REIS pl. 1, fig. 4 1997 Belonostomus muensteri AGASSIZ, BRITO p. 763 (partim)

Holotype: BSPG AS VII 1069

*Type horizon and locality*: From the Tithonian (*ruep-pellianus* horizon) of Solnhofen.



Fig. 14: *Belonostomus speciosus*, BSPG AS VII 1069, from Solnhofen. Abb. 14: *Belonostomus speciosus*, BSPG AS VII 1069, von Solnhofen.

#### Characteristic features of B. speciosus (Fig. 14):

• Predentary only slightly shorter than premaxilla.

• Predentary and premaxilla shorter and more massive than in the other species and bearing two rows of teeth.

• Smaller number of large teeth, especially in the premaxilla (approximately ten teeth), which is a consequence of the shorter jaws and these teeth are more massive than in the other species.

• All scales and posterior dermal bones of the skull (e.g., operculum), have tiny tubercles on the surface *Comment:* WAGNER (1863) described only one specimen of his new species *Belonostomus speciosus* (Fig. 14), but considered *B. speciosus* to be a synonym of *B. muensteri*; i.e. he believed that *B. speciosus* was only the largest and most massive form in which *B. muensteri* occurs. However, the proportions of the predentary and premaxilla, which are shorter and more massive than in the other species, makes me assume that it is indeed a separate species. REIS (1887), who figured this specimen, accepted the name *Belonostomus speciosus* too.

*Belonostomus sphyraenoides* AGASSIZ, 1844 (Fig. 15) 1837 *Belonostomus sphyraenoides* AGASSIZ p. 127 (name only)

1837 *Belonostomus brachysomus* AGASSIZ p. 127 (name only)

1844 *Belonostomus sphyraenoides* AGASSIZ p. 140, 165, 296, pl. 47a fig. 5

1844 Belonostomus brachysomus Agassiz p. 143, 297 1863 Belonostomus sphyraenoides Agassiz; Wagner p. 690

*Holotype*: BSPG AS VII 1066 and counterpart CAM SM F11098

*Type horizon and locality*: AGASSIZ (1844: 140, 165) noted the type specimen of *Belonostomus sphyraenoides* as being from Solnhofen. On a newer label of the type specimen in Munich, the word "Kelheim" is written (see Fig. 15); however, this provenance is unlikely based on the structure of the sediment. On the reverse of the type specimen is an old, faded label, written in MÜNSTER's handwriting, which reads "Eichstätt." The labels of the counterpart in Cambridge also list Eichstätt as the locality. The oldest label on this counterpart is written in MÜNSTER's handwriting.

**Distribution:** All specimens here attributed to *Belonos-tomus sphyraenoides* come from Eichstätt (Tithonian, *eigeltingense*  $\beta$  horizon). Specimens of *Belonostomus* are extremely rare in the Plattenkalk of the Eichstätt basin and all three known specimens belong to *B. sphyraenoides*.

**Comment:** AGASSIZ (1844: 140-141) described, as one of the main characteristic features for *Belonostomus sphyraenoides*, that their vertebrae are taller than long (The same description was given by WAGNER, 1863). Comparing BSPG AS VII 1066, of approximately 21 cm total length, with numerous sub-adult specimens of similar length, it seems likely that the type and only specimen of *B. sphyraenoides* available to AGASSIZ lacks fully developed vertebrae and is therefore a juvenile. Juvenile fishes normally have shorter vertebrae (see, for example, KONWERT, 2011, TISCHLINGER & ARRATIA, 2013). Therefore, this feature should not be regarded as diagnostic.

The other major characteristic features for *B. sphyraenoides*, according to AGASSIZ (1844: 140-141), are the apparently equal length of the jaws and the short length of the head. The actual length of the jaws is only visible in the counterpart of the holotype (CAM SM F11098) and in JME-SOS3044. The tubercles on the scales and the posterior dermal bones of the skull (see Fig. 13) are another important feature of this species. Tubercles are also present in *B. muensteri* and *B. speciosus* but absent in *B. tenuirostris* and *B. kochii*.

Belonostomus sphyraenoides seems to form a connecting link between the Kimmeridgian *B. kochii* and *B. muensteri* of the *moernsheimense* horizon of the Tithonian. It is currently not possible to assess whether *B. sphyraenoides* is synonymous with *B. muensteri*, until better-preserved material becomes available.

#### Belonostomus specimens from Cerin

In the late Jurassic French locality of Cerin (late Kimmeridgian up to the *eigeltingense* horizon of the Tithonian; see ENAY et al. 1994) *Belonostomus* is common too, but it is not clear if there are the same species as in southern Germany. THIOLLIÈRE (1848, 1850, 1873) mentioned *B. tenuirostris*, *B. muensteri* and *B. sphyraenoides*(?). WAGNER (1860: 403) regarded his specimens from Cerin as identical to *B. kochii*. EASTMAN (1914a) considered most of the specimens from Cerin in the Carnegie museum as belonging to *B. muensteri* and one specimen possibly to *B. tenuirostris*. SAINT-SEINE (1949) and BRITO (1997) assigned all specimens from Cerin to *B. tenuirostris*.

From my own preliminary studies it is clear that there are two species in Cerin. The first species is sim-

Fig. 15: Holotype of *Belonostomus sphyraenoides* AGASSIZ, 1844 (BSPG AS VII 1066), from Eichstätt. Abb. 15: Holotypus von *Belonostomus sphyraenoides* AGASSIZ, 1844 (BSPG AS VII 1066), von Eichstätt.



ilar to *B. tenuirostris*, with a difference in jaw length of more than 20% and only one row of teeth in the premaxilla. However, contrary to the Bavarian *B. tenuirostris*, the scales and the posterior dermal bones of the skull are granulated. The second Cerin species is more similar to *B. kochii*, with a jaw difference of 0–20% and two rows of teeth in the premaxilla. However, the preservation of most specimens from Cerin is not well enough to compare them with the known species from southern Germany in more detail.

#### b) Comments on dentition and some cranial bones

The dentition of *Belonostomus tenuirostris*: AGASSIZ (1844: 297) wrote about *B. tenuirostris*. "... les deux mâchoires très-minces, armées les deux de dents conique à-peu-près d'égale grandeur, entre lesquelles il y en a de très-fines." (Translated: "... the two jaws are very slender and both are armed with conical teeth of about similar size, between which it [the species] has very fine ones"). SAINT-SEINE (1949) followed this description, presenting a drawing of the cranium of *Belonostomus tenuirostris* with two rows of teeth in the premaxilla (SAINT-SEINE, 1949, fig. 114). Unfortunately, he did not record which specimen was illustrated.

Both AGASSIZ' description and SAINT-SEINE'S drawing are contradicted by figure 34B in BRITO (1997), as well as the description given in the present paper, because *B. tenuirostris* has only tiny teeth anterior of the larger ones in the predentary (as do all other species of *Belonostomus* and *Aspidorhynchus*), but not in the premaxilla (unlike the other species of the genus *Belonostomus*). Remarkably, because of the better preservation, both SAINT-SEINE (1949) and BRITO (1997) based their descriptions and drawings of the cranium of *B. tenuirostris* on material from Cerin (France) and not on material from the type locality of Solnhofen (Germany).

A supramaxilla is not present in *Belonostomus*. A supramaxilla is, however, present in *Aspidorhynchus* (BRITO & EBERT, 2009, figs. 4, 5). This is contrary to SAINT-SEINE (1949, fig. 114) and BRITO (1997, fig. 43), who claimed that a supramaxilla was present in both *Belonostomus* and *Aspidorhynchus*. The "supramaxilla" figured in BRITO (1997) and SAINT-SEINE (1949) for *Belonostomus* specimens from Cerin is probably a small infraorbital, which lies at the posteroventral border of the dentary (see this infraorbital in *B. kochii* Fig. 7c, 10b, 11b).

The presence of an interoperculum in *Belonostomus* as figured by GARDINER (1960, fig. 76) is still questionable. A thin, elongate bone at the ventral border of the preoperculum could be the interoperculum (JME-ETT128, JME-ETT2544 (Fig. 11)). The preoperculum covers a large part of this bone. In a single specimen, JME-ETT981, the suboperculum does not reach the posteroventral edge of the preoperculum and a bone is visible more posteriorly in direct elongation of the suboperculum which could be an interoperculum or a further branchiostegal (Fig. 10). In JME-ETT3463, in which the region between the suboperculum, the quadrate and the lower part of the hyoid arch is very well preserved, no interoperculum is present. BRITO (1997) discussed the possibility of secondary loss of the interoperculum in Aspidorhynchidae, whereas LÓPEZ-ARBARELLO & SCHRÖDER (2014) described an interoperculum as present in *Aspidorhynchus*.

#### c) Comments on problems of identification

Why is it so difficult to decide how many species the genus *Belonostomus* contains?

1. The first difficulty is the poor preservation of many specimens, especially the type specimens. The difference in jaw length is one of the most characteristic features. However, the jaw tips are not preserved in the holotypes of *B. muensteri*, *B. kochii* and *B. sphyrenoides* (only on the counterpart of the holotype of *B. sphyrenoides* CAM SM F.11098, do the imprints show the jaw length with certainty).

2. The second difficulty in correctly identifying the different species of *Belonostomus* lies in the fact that AGASSIZ never named or figured a type specimen for *B. tenuirostris*, which is the type species of the genus. However, AGASSIZ named as a main characteristic of *B. tenuirostris* the clearly different lengths of the jaws.

3. Sometimes it is difficult to decide which strata or which basin a specimen actually came from. Some specimens (even types) are simply labelled "Solnhofen," which could be anywhere within the diachronous Solnhofen Archipelago. It is clear that the holotype of B. muensteri comes from the Mörnsheim Layers, which are coarser-grained and more recent in age than the normal Plattenkalk of Eichstätt and Solnhofen. The label of the holotype simply reads "Solnhofen," which may be correct, but at Solnhofen there is the slightly older Solnhofen Plattenkalk sensu stricto as well as the younger Mörnsheim Layers above it. In the Mörnsheim Layers of Daiting, Mülheim and in the vicinity of Solnhofen, a Belonostomus species of up to 50 cm in length is very common. Comparing these Belonostomus specimens with the description of AGASsiz (1844), it is clear that these specimens belong to *B*. muensteri.

4. There are large discrepancies between the description of the type material and specimens in collections later attributed to these species. Some of these specimens unfortunately were published with these incorrect names. The greatest problem is BSPG 1957 I 339 (from Zandt), in which the upper and lower jaws are of decidedly different lengths. Whereas the initial descriptions by AGASSIZ (1844) and WAGNER (1863: 691) describe jaws of nearly similar length as characteristic for *B. muensteri* and jaws of very different lengths as characteristic for *B. tenuirostris*, this specimen was nevertheless identified as *Belonostomus muensteri* by BARTHEL (1978), FRICKHINGER (1991, 1994) and BRITO (1997).

### Conclusion

*Belonostomus* is known in all late Jurassic Plattenkalk basins of Southern Germany. In the oldest Plattenkalk basins of southern Germany such as Brunn (Kimmeridgian: *kiderleni* horizon) and Wattendorf (Kimmeridgian: *pseudomutabilis* subzone), *Belonostomus* is present; however, it is currently not possible to describe these specimens.

From the knowledge of the available specimens, the author considers *Belonostomus kochii* MÜNSTER, 1836, *Belonostomus tenuirostris* (AGASSIZ, 1833) and *Belonostomus muensteri* AGASSIZ, 1844 as valid species, whereas *Belonostomus sphyraenoides* AGASSIZ, 1844 and *Belonostomus speciosus* WAGNER, 1863 are considered to be *nomina dubia*.

**Belonostomus kochii** MÜNSTER, 1836 is thus far the oldest known species of *Belonostomus* in the Plattenkalk of the Solnhofen Archipelago. *Belonostomus kochii* is known only from the older strata of the Kelheim basin such as Kelheim-Kapfelberg (the type locality) and from the quarry of Ettling (Hartheim basin). The age of Kelheim-Kapfelberg is late Kimmeridgian up to the *eigeltingense* horizon, the lowermost zone of the Tithonian. *Belonostomus kochii* is a slender *Belonostomus* with a length difference between the upper and lower jaws of less than 20% (Fig. 7-12). One single premaxilla bears two rows of teeth, one row of larger teeth on the interior side and an additional row of tiny teeth on the exterior side (Fig. 7c & 11). *Belonostomus kochii* has 68-71 vertebrae and 71-73 lateral line scales. The pterygial formula for *Belonostomus kochii* is:

$$\frac{D51-54}{P30-31\,A45-48\,C64-68} T71-73$$

**Belonostomus sphyraenoides** AGASSIZ, 1844 is known only from the Eichstätt basin. *Belonostomus* is very rare in the Plattenkalk basin of Eichstätt and as far as I know, all specimens belong to *B. sphyraenoides*. The Plattenkalk of Eichstätt is dated as *eigeltingense*  $\beta$ horizon of the Tithonian (SCHWEIGERT et al. 2013). *Belonostomus sphyraenoides* has about 71 vertebrae and 71 lateral line scales.

**Belonostomus tenuirostris** (AGASSIZ, 1833) is known from the Solnhofen Plattenkalk *sensu stricto* of Solnhofen/Langenaltheim, as well as from the basins of Schamhaupten/Öchselberg/Zandt and Painten. The age of these Plattenkalk deposits is from the late Kimmeridgian up to the *ruppellianus* horizon of the Tithonian. *Belonostomus tenuirostris* is a slender *Belonos*-

Tab. 4: Stratigraphic distribution of the different species of *Belonostomus* in the Solnhofen Archipelago (ages from SCHWEIGERT 2007 and SCHWEIGERT et al. 2013).

Tab. 4: Stratigraphische V	erteilung der unterschiedlichen	Belonostomus-Arten im	Solnhofener Archipel (A	Alter nach Schweigert
2007 und Schweigert et	al. 2013).			

Stage	Subzone	Horizon	Localities	Species group A	Species group B
Tithonian	Moernshei- mensis	moernsheimen- sis	Daiting, Mül- heim, Soln- hofen	B. muensteri	
Tithonian	Rueppelianus	rueppelianus	Solnhofen, Lan- genaltheim	B. speciosus	B. tenuirostris
Tithonian	Riedense	eigeltingense $\beta$	Eichstätt	B. sphyraenoi- des	
Tithonian	Riedense	eigeltingense $\alpha$	Zandt		B. tenuirostris
Kimmeridgian	Ulmense	rebouletiatum	Öchselberg, Schamhaupten, Painten (lower part)		B. tenuirostris
Kimmeridgian	Ulmense		Kelheim, Et- tling	B. kochii	
Kimmeridgian	Subeumela	kiderleni	Brunn		?
Kimmeridgian	Pseudomuta- bilis		Wattendorf		?

*tomus* with a length difference between the upper and lower jaws of 28-44% (Fig. 2b & 3b). One single premaxilla bears only one row of larger teeth (Fig. 2c, 3b). *Belonostomus tenuirostris* has 77–78 vertebrae and about 77-78 lateral line scales. The pterygial formula in *B. tenuirostris* is:

The pterygial formula of the other species of *Belonostomus* is unknown, because of the bad preservation of the specimens.

**Belonostomus speciosus** WAGNER, 1863 is thus far known only from a single specimen, from the Solnhofen Plattenkalk *sensu stricto* (*rueppellianus* horizon of the Tithonian). Compared to the other species, *Belonostomus speciosus* (Fig. 14) has short upper and lower jaws, which are of nearly the same length. It also has two rows of premaxillary teeth, but the larger row of larger teeth is comparably larger (especially on the premaxilla) and their number is lower, than in other *Belonostomus* species.

Belonostomus muensteri AGASSIZ, 1844 is the stratigraphically youngest species of the genus Belonostomus in the Solnhofen archipelago. The holotype comes from the Mörnsheim Layers of the Solnhofen area. The Mörnsheim Layers are situated above the Solnhofen Plattenkalk sensu stricto and are clearly distinguishable under the microscope as a result of their coarser grain size. The Mörnsheim Layers are the type layers for the moernsheimensis horizon of the Tithonian. The fossils of the Mörnsheim Layers come from Daiting, Mörnsheim, Mülheim and the area of Solnhofen/Langenaltheim and in all these localities Belonostomus muensteri is very common. Belonostomus muensteri has a length difference between the upper and lower jaws of less than 20% (Fig. 5a). One single premaxilla bears two rows of teeth (Fig. 5b), as in Belonostomus kochii. In contrast, however, the surfaces of the scales of B. muensteri have tiny tubercles.

For a synoptic overview of the characteristic features of the different species of *Belonostomus* in the Solnhofen Archipelago Germany, see Tab. 3.

Based on this combination of features, there appear to have been two species groups of *Belonostomus* in the late Jurassic.

Species Group A appeared in the late Kimmeridgian, with *B. kochii* evolving via *B. sphyraenoides* to *B. muensteri* in the *moernsheimensis* horizon of the Tithonian. Species Group A is characterised by the following features: Upper jaw is 0-20% longer than the lower jaw (measured from the front of the orbit to the front tips of the jaws) and each premaxilla bears two rows of teeth; one row of larger teeth on the interior side and an additional row of tiny teeth on the exterior side. Species group B is represented by *B. tenuirostris*, which appeared in the late Kimmeridgian and continued to the *rueppelianus* horizon of the Tithonian. Species group B is characterised by the following features: Upper jaw is 28-44% longer than the lower jaw and each premaxilla bears only one row of teeth (see Fig. 16 & Tab. 4).

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Fig. 16: Variation of the two species groups of *Belonostomus* in the Solnhofen Archipelago with respect to their jaw lengths (cf. text): a) length of lower jaw versus length of upper jaw. b) ratio of jaw lengths versus skull length.

Abb. 16: Variation der beiden Arten-Gruppen von *Belonostomus* im Solnhofen-Archipel in Bezug auf ihre Kieferlängen (vgl. Text): a) Unterkieferlänge gegen Oberkieferlänge. b) Verhältnis von Ober- zu Unterkieferlänge gegen Schädellänge.

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