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***Trigonodon oweni* and *Asima jugleri* are different parts of the same species *Trigonodon jugleri*, a Chiseltooth Wrasse from the Lower and Middle Miocene in Central Europe (Osteichthyes, Labridae, Trigonodontinae)**

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(With 2 Plates)

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Abstract

The fossil oral jaw teeth traditionally known as *Trigonodon oweni* and the pharyngeal tooth plates known since SCHULTZ 1978 as *Asima jugleri*, but before described as *Radamas jugleri*, *Taurinichthys Sacheri* and *Stylodus Lebescontei*, are all parts of the same fossil fish, and bear a close similarity to the Recent Chisel-tooth Wrasse *Pseudodax moluccanus*. The fossil fish and *P. moluccanus* share a number of unique derived characters. The fossil representative is therefore placed in the Trigonodontinae (syn.: Pseudodacinae), Labridae. According to the ICZN rules the fossil fish has to be designated as *Trigonodon jugleri* (MÜNSTER, 1846). The oldest fossils of this species are from the Early Miocene of Italy and Austria. Most specimens were obtained from the Badenian, Middle Miocene, of the Vienna Basin within the Central Paratethys.

Zusammenfassung

Die als *Trigonodon oweni* schon lange bekannten Gebißzähne und die seit SCHULTZ 1978 als *Asima jugleri* zusammengefaßten Schlundgebißplatten – ursprünglich beschrieben als *Radamas jugleri*, *Taurinichthys Sacheri* und *Stylodus Lebescontei* – sind alles Teile derselben fossilen Fischart, die gemäß den ICZN *Trigonodon jugleri* (MÜNSTER, 1846) heißen muß. Fast alle Merkmale des fossilen Fisches stimmen mit denjenigen des rezenten Meißelzahn-Lippfisches *Pseudodax moluccanus* überein, sodaß auch er zu den Trigonodontinae (syn.: Pseudodacinae), Labridae, zu stellen ist. Die ältesten Vertreter stammen aus dem unteren Miozän Italiens und Österreichs. Die meisten Belege für unsere Untersuchungen stammen aus dem Badenium, Mittel-Miozän, des Wiener Beckens.

Introduction

SISMONDA 1846: 25 first described some large distinctive isolated fossil teeth as *Trigonodon oweni* and found "grandemente analogi ai Tetraodonti". To this day, these teeth

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have been assigned to the Tetraodontiformes (LERICHE 1957, http 2001). In the private collection of Prof.Dr. Helmuth Zapfe, now in possession of the Naturhistorisches Museum Wien, one of us (SCH) recently discovered a complete jaw bone together with one giant tooth and an irregular row of minute teeth behind it (NHMWien 1997z0178/1970): this jaw bone is the first fossil evidence with the teeth *in situ* and, for the first time, makes it possible to determine the status of the numerous isolated teeth described as *Trigonodon oweni* SISMONDA, 1846. The special characters of this jaw, with only one giant tooth in the jaw bone, together with the morphological characters of the tooth (Pl. 1/2a+b), reveals striking similarities with the Recent fish: *Pseudodax moluccanus* (VALENCIENNES, 1840), see Pl. 1/10a-h, 1/11a, and Pl. 2/1-3, especially in Pl. 1/10e-h and 1/11a.

Examination of the skull of *Pseudodax moluccanus* reveals a number of unique features in the form of the lower pharyngeal tooth plate, which are comparable to those of tooth plates that have long been known from Middle Miocene layers as *Radamas jugleri* v.MÜNSTER, 1846, later determined as *Asima jugleri*. Fragments of these lower pharyngeal bones were also described by MICHELOTTI 1861 as *Scarus miocenicus*, by SAUVAGE 1875 as *Taurinichthys Sacheri*, and by BAUZÁ RULLAN 1948 as *Taurinichthys villaltai*.

Approximately 150 years ago the upper pharyngeal tooth plates were found and SAUVAGE 1880 described them as *Stylodus Lebescontei*. A hundred years later, SCHULTZ 1978: 207 ff. recognized that the lower pharyngeal tooth plates (Pl. 1/9) determined as *Asima jugleri* MÜNSTER, 1846, and the upper pharyngeal tooth plates (Pl. 1/3-6), which were determined in literature as *Stylodus Lebescontei* SAUVAGE, 1880 should be united as one species, at that time *Asima jugleri* MÜNSTER, 1846. The links between these forms and *Pseudodax moluccanus* BLK. was already noted by M. LEBESCONTE (see SAUVAGE 1880: 41). Despite this association, SAUVAGE 1880 erected *Stylodus Lebescontei*. Furthermore, it should be noted that BAUZÁ RULLAN 1971: 370, Pl. 29/1-5 also united lower and upper pharyngeals as one species, at that time as *Taurinichthys villaltai*.

Abbreviations:

Jt	Jaw-tooth	Up	Upper pharyngeal tooth plate (s)
Lp	Lower pharyngeal tooth plate (s)	NHMWien	Naturhistorisches Museum Wien, Geol.-Paläont. Abteilung, resp. 1.
TL	Total Length		Zool. Abteilung, Ichthyolog. Sammlung.

Systematics

Family Labridae CUVIER, 1817

Trigonodontinae ARAMBOURG, 1927³
(syn. Pseudodacinae NORMAN, 1957⁴)

Genus *Trigonodon* SISMONDA, 1847

non 1843 *Radamas* – MÜNSTER: 52 (Placoide; Rischelsdorf; Kupferschiefer, Ober-Perm.- Osteodonti incertae sedis, class Chondrichthyes, according to OBRUTSCHEW 1964: 234).

³ published as Trigonodontidae

- Lp 1846 *Radamas* n.g. – MÜNSTER: 11-12 (Pycnodonte / Pycnodontidae).
 Jt 1846 *Trigonodon* – see 1849, 1847, also footnote 4 and 5.
 Jt 1847⁵ *Taurinichthys*. – SISMONDA in MICHELOTTI: 352 (Gymnodontes)
 Lp 1848 *Asima* – GIEBEL: 183-184 (non *Radamas* MÜNSTER, 1843 (Squalidae, Squatinae):
 new name for *Radamas* MÜNSTER, 1846.- Pycnodontes).
 Jt 1849⁶ *Trigonodon* E. SISM. – SISMONDA: 25 (Tetraodonti).
 Jt 1858 *Sargus* – ROUALT: 100 [Sparidae]
 Lp 1861 *Scarus* – MICHELOTTI: 355 (Scaridae).
 Jt 1861 *Trigonodon* E. SISM. – SISMONDA: 22 (Gimnodonti, Ganoidei).
 Lp 1864 *Taurinichthys*, nov. gen. – COCCHI: 88 (Pharyngodopilidae, Labroidi).
 Jt 1864 *Scarus* ? – COSTA: 128-129 [Scaridae].
 Lp 1875 *Taurinichthys* – SAUVAGE: 631 (Phyllodidae).
 Jt 1875 *Sargus* – SAUVAGE: 632 [Sparidae].
 Jt 1879 *Sargus* – BASSANI: 48 (Sparidae).
 Jt 1880 *Sargus* – SAUVAGE: 27 [Sparidae].
 Up 1880 *Styloodus* – SAUVAGE: 41-42 (Odacínés).
 Lp 1890 *Taurinichthys* – SACCO: 296, Nr. 4676 (Ganoidei).
 Lp 1890 *Scarus* – SACCO: 296, Nr. 4684 [Scaridae].
 Jt 1890 *Scarus* – SACCO: 296, Nr. 4689 [Scaridae].
 Jt 1895 *Sargus (Trigonodon)* – BASSANI: 6-10 (Sparidae)
 Jt 1901 *Trigonodon*, SISMONDA – WOODWARD, 4: 531 (Sparidae).
 Lp 1901 *Asima* – WOODWARD, 4: 536-537 (Sparidae).
 Up 1901 *Styloodus* – WOODWARD, 4: 553 (apparently Labroid).
 Up 1901 *Taurinichthys* – WOODWARD, 4: 553 (apparently Labroid).
 Jt 1906 *Trigonodon* – LERICHE: 311 (Sparidae).
 Lp+Up 1906 *Taurinichthys* – LERICHE: 318 (Labridae).
 Lp 1906 *Asima* – SCHUBERT: 692 (Sparidae).
 Jt 1910 *Trigonodon* E. SISMONDA – DE STEFANO: 196 (Sparidae).
 Jt 1923 *Trigonodon* SISMONDA – BROILI & SCHLOSSER: 139 (Sparidae).
 Jt 1927 *Trigonodon* SISMONDA, 1849 – ARAMBOURG: 219 (Trigonodontidae, Nov. fam.,
 Plectognathi)
 Lp 1948 *Taurinichthys* – BAUZÀ RULLÁN: 231 (Indica SAUVAGE las afinidades de los
Taurinichthys, con el género actual *Pseudodax*).

⁴ RANDALL 1981: 100 noted that NORMAN 1957: 339 and 350 introduced the subfamily Pseudacinae –recte Pseudodacinae. ESCHMEYER 1990: 595-596 and 1998: 2729 does not accept NORMAN's synopsis as valid because it is „Technically not an available publication for nomenclatural purposes“. The ICZN (1999): 6 require: „To be published, a work produced before 1986 must have been produced on paper, by a printing method then conventional (such as letterpress, offset printing) or by hectographing or mimeographing.“ Because NORMAN's synopsis was produced at the British Museum in London, is known for example by RANDALL 1981 and 1986, by ESCHMEYER 1990 and 1998, is available also in Vienna etc. we conclude that the distribution of NORMAN's synopsis is sufficient to accept the authorship for Pseudodacinae by NORMAN. Additionally ESCHMEYER 1998 and On-Line 2002 do not indicate the name of the subfamily, he writes: ...“RANDALL 1986: 701 [ref. 5706] in its own subfamily“. Already BLEEKER 1862a: 95 used for his 1861 new established genus *Pseudodax* the systematic position „Pseudodaciformes = Pseudodacina GÜNTH.“, and BLEEKER 1862b: 4 „Pseudodaciformes“. It should be noted, however, that cladistic analyses in the near future will probably change these taxonomic boundaries. The close relationship between *Pseudodax* and the parrotfishes (Scaridae) BELLWOOD (1994) highlighted the need for a revision of these groups.

⁵ Verified by SHERBORN 1932: 6606 and NAEVE 1940: 556: „*Trigonodon* SISMONDA 1847, in MICHELOTTI, Nat. Verh. Hollandsche Maat. Wetensch. te Harlem, (2) 3 (2), 352 – Pisces.“

⁶ On the frontsheet of the reprint in the NHM Vienna, the year 1846 is written, but on the back „Memorie della Reale Accademia delle Scienze di Torino Serie II. Tom. X. pag. 1“ with the date 1849. WOODWARD 1901, 4: 531 quotes 1849. MICHELOTTI 1847: 352 received the name and the description from an unprinted version of SISMONDA's manuscript: „SISMONDA in notâ manuscriptâ mihi traditâ.“ So „1846“ is only written on the reprint and seems to be incorrect.

- Lp 1957 *Taurinichthys* COCCHI – LERICHE: 49 (Labridae).
 Up 1957 *Stylodus* – LERICHE: 49 (Labridae)
 Jt 1957 *Trigonodon* SISMONDA – LERICHE: 50 (Trigonodontidae, Plectognathes).
 Lp+Up 1957 *Scarus* – SIGNOREUX in LERICHE: 50, footnote [Scaridae].
 Lp 1963 *Taurinichthys* – BAUZÀ RULLÀN et al.: 234, Pl. 12 (Ladridae [recte Labridae]).
 Jt 1963 *Trigonodon*, SISMONDA, 1846 – BAUZÀ RULLÀN et al.: 243, Pl. 14/3
 (Trigonodontidae [arranged after Tetraodontoidea])
 Lp 1964 *Taurinichthys* – OBRUTSCHEW: 458 (Labridae).
 Up 1964 *Stylodus* – OBRUTSCHEW: 458 (Labridae).
 Lp+Up 1969 *Scarus* – CAPPETTA: 234-236, Pl. 21/4 (Scaridae).
 non Jt 1969 *Scarus* – CAPPETTA: 234-236, Pl. 21/6 (Scaridae).
 Jt 1971 *Trigonodon* – BAUZÀ RULLÀN: 368, Pl. 27/9+10; 369, Pl. 28/1+2; 383 [arranged
 after *Diodon*, Tetraodontiformes] .
 Lp+Up 1971 *Taurinichthys* – BAUZÀ RULLÀN: 370, Pl. 29/1-5; 394 (afinidades con el género
 actual *Pseudodax*).
 Up 1975 Labridé inc. sed. / Labridé indéterminé – JONET: 215, Pl. 1/16 (Labridae).
 Jt 1975 *Trigonodon* – JONET: 209 (Trigonodontidae).
 Lp 1975 *Scarus miocenicus* MICHELOTTI – JONET: 214 (Scares / Scaridae)
 Lp+Up 1978 *Asima* – SCHULTZ: 207-213, Pl. 1/7a-c, 11a+b, 12a+b, 8-10a+b (? Labridae).
 Lp 1984 *Taurinichthys* – MORNAND: 12 (Labridés / Labridae).
 Up 1984 *Stylodus* – MORNAND: 12 (Labridés / Labridae).
 Jt 1984 *Trigonodon* – MORNAND: 14 (Trigonodontidés, Tetraodontiformes),
 Lp+Up 1998 *Asima* – SCHULTZ: 126, Pl. 57/6-8 (Labridae, Pseudodacinae).
 Jt 1998 *Trigonodon* – SCHULTZ: 126, Pl. 57/10 (Trigonodontidae [Tetraodontiformes]).
 Jt 2002 *Trigonodon* – <http://perso.club-internet.fr/jflhomme/touraine/trigonodon.htm>: 1
 (Trigonodontidés, Tetraodontiformes).
 Lp+Up 2002 *Scarus* [includes *Stylodus* and *Taurinichthys*] –
http://perso.club-internet.fr/jflhomme/touraine/scarus_miocenicus.htm: 1
 (Labridés).
 Up 2002 *Asima* – HIDEN: 4 [Labridae].
 Jt 2002 *Trigonodon* – HIDEN: 4 [Tetraodontidae].

Remarks: To provide a comprehensive overview and to find the correct genus name we listed the synonymy of the fossil genus names: *Trigonodon* is the oldest and therefore the valid genus name for all three different elements of this fish. In the above list, we also indicate the familial designations. Families or other systematic indications in () are exactly written in the paper, those in [] are derived or interpreted by us.

***Trigonodon jugleri* (v. MÜNSTER, 1846)** (Pl. 1, Figs. 1-9)

- Lp 1846 *Radamas Jugleri*, MÜNSTER – MÜNSTER: 11-12; 28, Nr. III/1, Pl. 1/6a-c [reprinted
 in SCHULTZ: Pl. 1/7a-c].
 Jt 1846 *Trigonodon Oweni* E. SISMD. – see SISMONDA 1849 and MICHELOTTI 1847, also
 footnote 4 and 5.
 Jt 1847⁷ *Trigonodon Oweni*. SISMONDA – MICHELOTTI: 352.
 . Lp 1848 *Radamas Jugleri*, MÜNSTER – HÖRNES: 14, Nr. 49.
 . Lp 1848 *Asima Jugleri* – GIEBEL: 184.
 . Jt 1849⁸ *Trigonodon Oweni* E. SISMD. – SISMONDA: 25-26, 85, Pl. 1/14-16.
 Jt 1858 *Sargus Sioni*, sp. nov. – ROUALT: 100.
 . Lp 1861 *Scarus miocenicus*, MICHELOTTI – MICHELOTTI: 355, Pl. 10/3.
 Jt 1861 *Trigonodon Oweni* E. SISMD. – SISMONDA: 22.

⁷ as footnote 5

- . Lp 1864 *Taurinichthys miocenicus* MICHEL. – COCCHI: 87-88, Pl. 6/10, 10a, 10b.
. Jt 1864 *Scarus* ? – COSTA: 128-129, pl. 12/11a, 11b, 11c.
non 1874 *Scarus Baltringensis* n.sp. – PROBST: 282-283, Pl. 3/7.
? 1874 *Scarus Baltringensis* n.sp. – PROBST: 282-283, Pl. 3/8-11.
. Jt 1875 *Sargus Sioni*, M. ROUAULT – SAUVAGE: 632, 642, Pl. 22/3.
. Lp 1875 *Taurinichthys Sacheri*, SAUVG. – SAUVAGE: 631, 642, Pl. 22/20.
. Jt 1879 *Sargus Sioni* ROUAULT – BASSANI: 49-50, Pl. 5/13-14.
. Jt 1880 *Sargus Sioni*. – SAUVAGE: 27.
. Lp 1880 *Taurinichthys Sacheri*, SAUVG. – SAUVAGE: 43, Pl. 2/10-11.
. Up 1880 *Stylodus Lebescontei*, SAUVG. – SAUVAGE: 41-42, Pl. 2/12-12c.
. Lp 1890 *Taurinichthys miocenicus* MICHT. – SACCO: 296, Nr. 4676.
. Lp 1890 *Scarus miocenicus* MICHT. – SACCO: 296, Nr. 4684.
. Jt 1890 *Scarus Oweni* SISMD. (*Trigonodon Oweni* SISMD.) – SACCO: 296, Nr. 4689.
. Jt 1895 *Sargus (Trigonodon) Oweni* E. SISMONDA – BASSANI: 6-10, figs. A, A', A'', B, C and D, pl. 1/3, 3a, 3b.
. Jt 1901 *Trigonodon oweni*, SISMONDA – WOODWARD, 4: 531.
. Lp 1901 [...] indeterminable teeth have also been referred to Sparidae [...] *Asima jugleri* [...] – WOODWARD, 4: 536-537.
. Up 1901 apparently Labroid [...] *Stylodus lebescontei* – WOODWARD, 4: 553.
. Lp 1901 apparently Labroid [...] *Taurinichthys miocenicus* – WOODWARD, 4: 553.
. Lp 1901 apparently Labroid [...] *Taurinichthys sacheri* – WOODWARD, 4: 553.
. Jt 1904 *Trigonodon Oweni* SISMONDA – PRIEM: 291.
. Jt 1906 *Trigonodon Sioni*, ROUAULT, 1858 – LERICHE: 311-314.
Lp+Up 1906 *Taurinichthys Sacheri* SAUVAGE, 1875 – LERICHE: 318-320.
. Lp 1906 *Asima Jugleri* GIEB. – SCHUBERT: 692.
. Jt 1910 *Trigonodon Oweni* SISMONDA – DE STEFANO: 194-198, Pl. 2/16 [Fig. 15: ?- with a long list of additional references, but not controlled by us]
. Jt 1927 *Trigonodon oweni* SISMONDA – ARAMBOURG: 219-221, Fig. 46 A+B, Pl. 12/4-9.
? Jt 1937 *Trigonodon oweni* SISM. – SARRA: 56, Fig. 2 [not a typical tooth].
non Jt 1937 *Trigonodon oweni* SISM. – SARRA: 56, Fig. 3+4 [Fig. 4 in our opinion a tooth of *Sargus jomnitanus* VALENCIENNES].
. Lp 1948 *Taurinichthys Villaltai* n. sp. – BAUZÀ RULLÀN: 231-233, Pl. 12 + 13.
non Jt 1949 *Trigonodon Oweni* SISMONDA, 1849 – BAUZÀ RULLÀN: 214, Pl. 13/1-6.
. Lp 1957 *Taurinichthys miocenicus* MICHELOTTI – LERICHE: 49, 54, Pl. 4/28-29.
. Up 1957 *Stylodus Lebescontei* SAUVAGE – LERICHE: 49-50, 54, Pl. 4/30-31.
Lp+Up 1957 *Scarus miocaenicus* MICHELOTTI, 1861 – SIGNEUX in LERICHE: 50, footnote.
. Jt 1957 *Trigonodon oweni* SISMONDA – LERICHE: 50-51, 54, Pl. 4/32-35.
. Lp 1963 *Taurinichthys villaltai*, BAUZÀ – BAUZÀ RULLÀN et al.: 234-235, Pl. 12.
. Jt 1963 *Trigonodon oweni*, SISMONDA, 1849 – BAUZÀ RULLÀN et al.: 243, Pl. 14/3.
? Jt 1963 *Trigonodon oweni*, SISMONDA, 1849 – BAUZÀ RULLÀN et al.: 243, Pl. 14/4-5.
. Jt 1963 *Trigonodon sioni*, M. ROUAULT, 1858 – BAUZÀ RULLÀN et al.: 243-244, Pl. 14/6-7.
. Up 1969 *Scarus miocaenicus* MICHELOTTI, 1861 – CAPPETTA: 234-236, Pl. 21/4.
. Lp 1969 *Scarus miocaenicus* MICHELOTTI, 1861 – CAPPETTA: 234-236.
non Jt 1969 *Scarus miocaenicus* MICHELOTTI, 1861 – CAPPETTA: 234-236, Pl. 21/6.
. Jt 1971 *Trigonodon oweni* – BAUZÀ RULLÀN: 368, Pl. 27/9+10; 369, Pl. 28/2.
. Jt 1971 *Trigonodon oweni* – BAUZÀ RULLÀN: 369, Pl. 28/1.
. Jt 1971 *Trigonodon oweni* SISMONDA – BAUZÀ RULLÀN: 383.
. Lp 1971 *Taurinichthys villaltai* – BAUZÀ RULLÀN: 370, Pl. 29/1-2.
. Up 1971 *Taurinichthys villaltai* – BAUZÀ RULLÀN: 370, Pl. 29/3-5.
. Lp+Up 1971 *Taurinichthys villaltai* BAUZÀ – BAUZÀ RULLÀN: 394.
. Up 1975 Labridé inc. sed. – JONET: 215, Pl. 1/16.
. Up 1975 Labridé indéterminé – JONET: 227.
. Jt 1975 *Trigonodon elongatus* nov. sp. – JONET: 212-213, 227, Pl. 2/22a+b + 24a+b.
. Jt 1975 *Trigonodon oweni* SISMONDA – JONET: 212, 227, Pl. 2/25.

⁸ as footnote 6

- Lp 1975 *Scarus miocenicus* MICHELOTTI – JONET: 214-215, 228, Pl. 2/33+34.
 . Lp 1978 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 207-213, Pl. 1/7a-c [reprinted from MÜNSTER 1846, Pl. 1/6a-c].
 v. Lp 1978 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 207-213, Pl. 1/11a+b + 12a+b [NHMWien].
 v. Up 1978 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 207-213, Pl. 1/8-10a+b [NHMWien].
 . Lp 1984 *Taurinichthys miocenicus* (MICH.) LERICHE – MORNAND: 12, Fig. "1".
 . Up 1984 *Stylodus lebesconti* SAUVAGE – MORNAND: 12, Fig. "2".
 . Jt 1984 *Trigonodon oweni* SISMONDA – MORNAND: 14, Fig. "3a".
 ? 1992 *Taurinichthys* sp.indet. – SOLT: 496 [not seen by us].
 v. Lp 1998 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 126, Pl. 57/6+7 [NHMWien].
 v. Up 1998 *Asima jugleri* (MÜNSTER, 1846) – SCHULTZ: 126, Pl. 57/8 [NHMWien].
 v. Jt 1998 *Trigonodon oweni* SISMONDA – SCHULTZ: 126, Pl. 57/10 [NHMWien].
 Jt 2002 *Trigonodon oweni* –
<http://perso.club-internet.fr/jflhomme/touraine/trigonodon.htm>: 1, 3 figs.
 Lp+Up 2002 *Scarus miocenicus* [includes *Stylodus* and *Taurinichthys*] –
http://perso.club-internet.fr/jflhomme/touraine/scarus_miocenicus.htm: 1.

Material

from Ottnangian, Early Miocene:

J a w - t e e t h : Prambachkirchen, Upper Austria: ca. 10 jaw-teeth (longest ridge 1.5 cm) (Pl. 1/1; Coll. H. Temmel). – Aussertreffling near Linz, Upper Austria: 1 tooth, strongly worn (Coll. H. Temmel).

L o w e r p h a r y n g e a l : Aussertreffling near Linz, Upper Austria: 1 fragment (Pl. 1/7a+b; Coll. H. Temmel).

from Badenian, Middle Miocene:

J a w t o o t h w i t h b o n e : Devinská Nová Ves (= Neudorf a.d. March), Slovakia: 2 specimens: a left dentary with bone together with a very characteristic tooth, Pl. 1/2a+b, figured also in SCHULTZ 1998: Pl. 57/10, NHMWien 1997z0178/1970, formerly Coll. H. Zapfe. – an indeterminable bone fragment with a tooth, 1857/XIX/34). – Retznei, Styria, Austria: 1 specimen (Coll. G. Wanzenböck).

J a w t e e t h, isolated: Bad Deutsch Altenburg, Lower Austria: 1 tooth (NHMWien 1989/16/5). – Devinská Nová Ves (= Neudorf a.d. March), Slovakia: 39 teeth and 35 tooth fragments (NHMWien 1857/XIX/34; 1939/26; 1957/246; 2002z0190/0001; 2002z0191/0001, leg. E. Kittl 1882). – Kaisersteinbruch, Blauer Bruch, Burgenland, Austria: 99 teeth (32 teeth: Coll. G. Wanzenböck. – 3 teeth: NHMWien 2002z0177/0001, don. A. Kroh. – 18 jaw teeth and 29 fragments of jaw teeth: Museum Mannersdorf. – 1 jaw tooth and 4 fragments: Coll. H. Schutzbier. – 12 fragments of jaw teeth: Coll. H. Schwengersbauer). – Müllendorf, Kreidesteinbruch, Burgenland, Austria: ca. 520 teeth (49 large jaw teeth -ca. 1-1.5 cm long, strongly worn and mostly not complete- and 62 fragments of large teeth, 34 small jaw teeth and ca. 350 fragments, ca. 0.7-1.0 cm long: Coll. H. Temmel. – 21 teeth: Coll. G. Wanzenböck. – 4 teeth, one of them a juvenile one: NHMWien 2002z0176/0001-0004, don. A. Kroh). – Wiesfleck, near Pinkafeld, Burgenland, Austria: 1 tooth and 1 tooth fragment (NHMWien 2002z0072/0001, don. R. Kunz, Wien). – Retznei, Styria, Austria: 2 teeth (NHMWien

2002z0037/0001 +0002, don. A. Kroh). – Lapugy, Romania: 1 tooth (NHMWien 1855/XLIII/1 as *Capitodus truncatus* MÜNST.).

Lower pharyngeal tooth plates: Kaisersteinbruch, Burgenland, Austria: 1 fragment (Coll. G. Wanzenböck). – Müllendorf, Kreidesteinbruch, Burgenland, Austria: 1 lower pharyngeal tooth plate, not quite complete (Pl. 1/8; Coll. H. Zierhofer, now in Coll. G. Wanzenböck), and 9 fragments (7 fragments: Coll. H. Temmel. – 1 fragment: Coll. J. Pingitzer. – 1 fragment: Coll. G. Wanzenböck). – Devinská Nová Ves (=Neudorf a.d. March), Slovakia: 1 complete pharyngeal tooth plate (Pl. 1/9; NHMWien 1979/2119/1, formerly Coll. O. Lienhart – figured specimen in SCHULTZ 1978: Pl. 1/11a+b and in SCHULTZ 1998: Pl. 57/8), and 4 fragments (NHMWien 1857/XIX/33/6 and 1868/VIII/14c – figured specimens in SCHULTZ 1978: Pl. 1/12a+b – and NHMWien 1990/169).

Upper pharyngeal tooth plate: Deutsch-Altenburg, Lower Austria: 1 fragment (NHMWien 1989/16/9). – Kaisersteinbruch, Kreidesteinbruch, Blauer Bruch, Burgenland, Austria: 6 specimens (2 upper pharyngeals: Pl. 1/5a-d; Coll. P. Biermayr. – 2 fragments: Coll. G. Wanzenböck. – 2 small fragments: Coll. Kroh). – Müllendorf, Burgenland: 6 upper pharyngeals (1 fragment and 5 poor fragments: Coll. H. Temmel). – Retznei, Styria, Austria: 1 specimen (Pl. 1/6a+b; Coll. G. Wanzenböck). – Devinská Nová Ves (=Neudorf a.d. March), Slovakia: 6 fragments (Pl. 1/3+4; NHMWien 1857/XIX/33/1-5; p.p. figured specimens in SCHULTZ 1978: Pl. 1/8-10a+b and in SCHULTZ 1998: Pl. 57/6+7. – NHMWien 2002z0120/0005).

Remarks

As *jugleri* MÜNSTER, 1846 was not compared by most later authors, inc. MICHELOTTI, SISMONDA, ROUALT, COCCHI, PROBST, SAUVAGE, BASSANI, SACCO, PRIEM, LERICHE, DE STEFANO, ARAMBOURG, SARRA, BAUZÁ RULLÁN, SIGNEUX, JONET, CAPPETTA, MORNAND, and <http://perso.club> ... 2002, numerous new species were erected, as *oweni* SISMONDA in MICHELOTTI 1847, *sioni* ROUALT 1858, *miocenicus* MICHELOTTI 1861, *sacheri* SAUVAGE 1875, *lebescontei* SAUVAGE 1880, *villaltai* BAUZÁ RULLÁN 1948 and *elongatus* JONET 1975. All are junior synonyms of *jugleri* MÜNSTER, 1846 (see above the lists of synonyms).

Front teeth, differences (*Trigonodon oweni* – *Diplodus jomnitanus*):

The figured specimen in SISMONDA 1846: Pl. 1/14-16 is not a very characteristic one at first sight; only the figure with the section shows some essential characteristics: a tooth with a sharp margin, which becomes very thick at the base of the tooth. With these characters it is possible to distinguish this tooth from most other teeth of Osteichthyes but especially of *Diplodus jomnitanus* (VALENCIENNES), a species with a similar fossil occurrence. Intact teeth with limited abrasion show some additional characters which differ from the teeth of *D. jomnitanus*, which are not to see in fig. 14-16 in SISMONDA 1846: 1) the flanks of a characteristic tooth are curved in *T. oweni*, vertical in *D. jomnitanus*, 2) the front flank of *T. oweni* is much higher than the proximal one, the height at the flanks of *D. jomnitanus* are almost equal, the tooth is much longer than high –e.g. 13 : 9– in *T. oweni*, the teeth are shorter than high –e.g. 11 : 15– in *D. jomnitanus*.

Trigonodon oweni has previously been interpreted as a representative of the extinct family Trigonodontidae of the Tetraodontiformes with an appearance like boxfishes (<http://perso.club-internet.fr/jflhomme/touraine/trigonodon.htm>, 2002).

In the private collection of Prof. Dr. Helmuth Zapfe, now in possession of the Naturhistorisches Museum Wien, recently one of us (SCH) discovered a partly complete left dentary together with the giant tooth and some minute ones at the edge (NHMWien 1997z0178/1970): this partly complete jaw bone is the best fossil evidence of such a bone to-date, and it now makes it possible to place the well known isolated teeth, traditionally described as *Trigonodon oweni* SISMONDA, 1846 with the correct genus name. The unusual form of this dentary, with a single highly modified giant tooth (Pl. 1/2a+b), is shared by only one other species, the Recent fish, *Pseudodax moluccanus* (VALENCIENNES, 1840), see Pl. 1/10a-h and 11a, especially Fig. 10e-h and 11a. The close similarity between the two, with several uniquely derived features makes it possible to place the fossil material in context. *Trigonodon oweni* represents the oral jaw component of an extinct *Pseudodax*-like fish, the pharyngeal bones of which were previously described as *Asima jugleri* (see below). All evidence suggests that *Asima* would have the appearance of a giant *Pseudodax* (see RANDALL in SMITH & HEEMSTRA 1986: Pl. 100 and 102, number 220.50). There is no doubt that *Asima* must be placed like *Pseudodax* in the same subfamily Trigonodontinae (syn.: Pseudodacinae), family Labridae (see ESCHMEYER 1998 and 2002).

It must be noted that in both Recent specimens available to us all the dentaries possess behind the large chiseltooth additionally a small tooth (Pl. 1/10g and 11a), in one dentary additionally two (!) teeth (Pl. 1/10e, f, and h): all these teeth seems to be in a provisional position, with a diagonal orientation and one edge is protruding like a small canine-tooth. Such additional teeth are also present in the fossil material, but only as isolated teeth.

Very similar isolated teeth from the Eocene of Belgium and from Egypt were described as *Trigonodon serratus* (GERVAIS, 1852) and *T. laevis* (PRIEM, 1907). In this paper, we are unable to determine the generic or familial status of these species.

Pharyngeals:

M. LEBESCONTE has already noted the similarities between the upper pharyngeal tooth plates of *Stylodus Lebescontei* and *Pseudodax moluccanus* BLK. (see SAUVAGE 1880: 41). In spite of this knowledge SAUVAGE 1880 used for the lower pharyngeal tooth plate *Taurinichthys* and erected for the upper pharyngeal tooth plate a new genus, *Stylodus*. Finally SCHULTZ 1978: 207 ff. recognized in the very rich teeth collection of Badenian resp. Middle Miocene from Devinská Nova Ves (= Neudorf a.d. March), Slovakia, some lower pharyngeal tooth plates of *Asima jugleri* MÜNSTER, 1846 (Pl. 1/9) and also some fragments of the upper pharyngeal tooth plates (Pl. 1/3-6), which were identified in the literature as *Stylodus Lebescontei* SAUVAGE, 1880. SCHULTZ 1978 compared these with Pl. 2, Fig. 18 in KNER 1860 and concluded that these pharyngeal tooth plates should be united as one species, *Asima jugleri* MÜNSTER, 1846. A similar observation was made by BAUZA RULLAN 1971: 370, Pl. 29/1-5: he gave the lower and the upper pharyngeals the same species name, at that time *Taurinichthys villaltai*.

This material must now be identified as *Trigonodon jugleri* (MÜNSTER, 1846), because the genus name *Trigonodon* is nomenclaturally older than *Asima*; see above the list of synonymies of the genus. The outline of the isolated upper pharyngeals of *Trigonodon jugleri* and of *Pseudodax* are almost identical (Pl. 1/3-6 and 1/11b-d). Although it shares a number of synapomorphies with the parrotfishes (BELLWOOD 1994), including ovoid medial teeth in the lower pharyngeal, *Pseudodax* also possesses a number of unique derived morphological features, including: phyllodont dentition (*sensu* BELLWOOD 1990) in the upper pharyngeals in multiple oblique rows; an ovoid margin of the lower pharyngeal bordered by nodular teeth; mandible with one or two large broad incisiform teeth. All of these features are found in *Trigonodon jugleri*.

Results

The similarity of the jaw tooth and of both pharyngeals of *Trigonodon jugleri* with those of *Pseudodax moluccanus* clearly establishes the strong links between the two taxa. The different sizes of the elements have no taxonomic significance. The different shapes of the tooth plate on the lower pharyngeals, ovoid and tapering anteriorly in *Pseudodax* vs. straight sides and a sharp anterior point in *Trigonodon* (see also Pl. 1/9 and 11e+f) are considered to be adequate characters at this point to maintain generic distinctions: *Trigonodon* SISMONDA, 1847 (incl. syn. *Asima*) and *Pseudodax* BLEEKER, 1861 are separate genera in the Trigonodontinae (syn.: Pseudodacinae), Labridae.

Ecology

Given the similarities of the highly modified jaw teeth and pharyngeals, it is likely that *Trigonodon* shared a broadly similar mode of life as Recent *Pseudodax moluccanus* (Pl. 2/1-3), which lives primarily on coral reefs and associated hard-grounds (1-40 m deep) (LIESKE & MYERS 1994: 226, Pl. 101/11). *Pseudodax* feeds on a broad variety of attached benthic sessile invertebrates and algae. Because the Recent *Pseudodax moluccanus* is widely distributed in tropical to subtropical waters (Red Sea to South Africa, southern Japan, Society Ids, Marquesas and Tuamotu Ids; according to PARENTI & RANDALL 2000: 36. - see also RANDALL 1981: 99-101 and 1986: 700-701; SMITH & SMITH 1963: 40, Pl. 85/E), it is likely that *Trigonodon jugleri* shared a tropical or subtropical distribution. One of the most remarkable features of *Trigonodon* is the great differences in the size when compared to its extant relative. The Recent representative, *Pseudodax*, reaches a total length (TL) of 250 mm. The material examined (193 mm TL, Pl. 1/11) has a tooth length of 2.5 mm. The tooth length of the fossil specimen in the dentary bone measures 16.5 mm. Assuming isometry, this would indicate that the specimen was over 1000 mm TL.

Phylogeny

The new systematic knowledge of *Trigonodon* (including *Asima*) combined with better stratigraphic knowledge about the area of the "colline de Turin" in Italy, and the newly found specimens from the Ottnangian in Upper Austria, provide a clearer indication of their position in the evolution of the Labridae. *Trigonodon jugleri* (Burdigalian/Ottnangian,

Early Miocene – Pliocene) is the oldest record of the Trigonodontinae (syn.: Pseudodacinae) and sits as a putative sister group to the Scaridae (BELLWOOD 1994). The oldest record of the Scaridae is of comparable age: *Calotomus preisli* (Badenian, Middle Miocene; see BELLWOOD & SCHULTZ 1991: 61 ff), cf. Scaridae: *Bolbometopon* (Late Miocene; see BELLWOOD & SCHULTZ 1991: 59). Although molecular evidence points to an Eocene origin for the basal scarid divisions (STREELMAN et al. 2002), it is not until the early or mid Miocene that we see fossils of recognisable trigonodontine / pseudodacine or scarid lineages and genera. Nevertheless, the status of *Trigonodon serratus* (GERVAIS, 1852) and *T. laevis* (PRIEM, 1907) from the Eocene of Belgium and Egypt remain equivocal and if they do represent *Trigonodon* material they would support the early origins of the group (see above in the chapter "remarks", last paragraph).

Distribution

C e n t r a l P a r a t e t h y s :

O t t n a n g i a n , Early Miocene: Austrian Molasse Basin (for details see in chapter material):

Prambachkirchen, Upper Austria (Pl. 1/1). – Aussertreffling near Linz, Upper Austria (Pl. 1/7a+b).

K a r p a t i a n , Early Miocene, Congeria-Rzehakia-bearing sands: ?, Kazár, Hungary (SOLT 1992: 496).

B a d e n i a n , Middle Miocene: Vienna Basin (for details see in chapter material):

Bad Deutsch Altenburg, Lower Austria. – Devinská Nová Ves (= Neudorf a.d. March), Slovakia; (Pl. 1/2a+b, 3+4, 6a-c, and 9); see additionally: MÜNSTER 1846: 11-12, Pl. 1/6a-c; HÖRNES 1848: 14, Nr. 49; SCHUBERT 1906: 692; WOODWARD 1901, 4: 531. – Kaisersteinbruch, Blauer Bruch, Burgenland, Austria (Pl. 1/5a-d). – Müllendorf, Kreidesteinbruch, Burgenland, Austria (Pl. 1/8).

B a d e n i a n , Middle Miocene: Styrian Basin (for details see in chapter material):

Wiesfleck, near Pinkafeld, Burgenland, Austria. – Weissenegg, and Retznei, Styria, Austria (Pl. 1/6a+b).

B a d e n i a n , Middle Miocene: Transylvanian Basin (for details see in chapter material):

Lapugy, Romania.

M e d i t e r r a n e a n a n d A t l a n t i c P r o v i n c e :

B u r d i g a l i a n , Early Miocene (Provengono dall'arenaria serpentinosa / Arenaria terziaria media / Aren. Serpent. Mioc. Med. / terrain miocène): Colline di Torino, Italy (SISMONDA 1846: 25-26, 85, Pl. 1/14-16. – MICHELOTTI 1847: 352. – MICHELOTTI 1861: 355, Pl. 10/3. – SISMONDA 1861: 22. – COCCHI 1864: 87-88, Pl. 6/10, 10a, 10b. – WOODWARD 1901, 4: 553. – DE STEFANO 1910: 195).

S e r r a v a l l i a n ? (Elveziano): Piedmont, Italy (SACCO 1890: 296, Nr. 4676 + 4684 + 4689). – Prov. di Catanzaro and prov. di Cosenza (COSTA 1864: 128-129, pl. 12/11a, 11b,

11c. – BASSANI 1895: 6-10, figs. A, A', A", B, C and D, pl. 1/3, 3a, 3b). – Capo dell'Armi (Reggio Calabria, Italy) (DE STEFANO 1910: 195, Pl. 2/16) and from additional localities not revised by us: Verezzi sulla riviera ligure, Monte Titano, Catanzaro etc., San Bartolomeo near Cagliari (Sardinia), all in Italy (DE STEFANO 1910: 195).

M i d d l e M i o c e n e (Helvetian): Loupian, France (PRIEM 1904: 291. – CAPPETTA 1969: 234-236, Pl. 21/4).

S e r r a v a l l i a n ? (Vindoboniense): Mallorca: Muro (BAUZÀ RULLÀN 1971: 383), Santa Margarita (BAUZÀ RULLÀN 1948: 231-233, Pl. 12+13. – BAUZÀ RULLÀN et al. 1963: 235+243. – BAUZÀ RULLÀN 1971: 383+394), Can Picafort, Sa Porrassa (BAUZÀ RULLÀN 1971: 383. – Mallorca: (BAUZÀ RULLÀN et al. 1963: 244). – Neogen: Spanien (BAUZÀ RULLÀN et al. 1963: 243).

? M i d d l e M i o c e n e (Helvetian): Penedo, Portugal (JONET 1975: 212, 212-213, 214-215, 215, 227, Pl. 1/16, Pl. 2/22a+b, 24a+b, 25, 33, 34).

M i d d l e M i o c e n e (Savignéen)⁹: Touraine, France: Le Quiou and Saint-Juval, Côtes-du-Nord; Gahard, La Chaussérie, and Saint-Grégoire near Rennes, Ille-et-Vilaine; Chazé-Henry, Lasse, Noellet, Pontigné, Maine-et-Loire (SAUVAGE 1875: 631, 632, 642, Pl. 22/3+20. – BASSANI 1879: 49-50, Pl. 5/13-14. – SAUVAGE 1880: 41, 43, Pl. 2/10-11 and 12. – WOODWARD 1901, 4: 553. – LERICHE 1906: 311-314, 318-320 [with long lists of localities, not controlled by us]. – LERICHE 1957: 49-51, 54, Pl. 4/28-35. – <http://perso.club-internet.fr/jflhomme/touraine/trigonodon.htm> (2002): 1, 3 figs. – http://perso.club-internet.fr/jflhomme/touraine/scarus_miocenicus.htm (2002): 1).

M e s s i n i a n (previousley Sahelien): Raz-al-Ain and Planteurs near Oran, Algeria (ARAMBOURG 1927: 219-221, Fig. 46 A+B, Pl. 12/4-9).

P l i o c e n e : Tuscany, Italy (WOODWARD 1901, 4: 531).

?: R e d o n i a n , Early Pliocene¹⁰: Touraine, France (LERICHE 1957: 54).

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⁹ see DEMARCO in STEININGER et al. (1985): 55/Area 309.

¹⁰ as footnote 9.

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Plate 1

- Fig. 1: *Trigonodon jugleri* (v. MÜNSTER, 1846), isolated jaw tooth, inner view; Ottnangian, Early Miocene; Prambachkirchen, Upper Austria. – Coll. H. Temmel. – Natural size.
- Fig. 2: *Trigonodon jugleri* (v. MÜNSTER, 1846), left dentary with bone together with a characteristic tooth and a ridge with minute teeth; Badenian, Middle Miocene, from Devinská Nová Ves (= Neudorf a.d. March), Slovakia. – NHMWien 1997z0178/1970, already figured in SCHULTZ 1998: Pl. 57/10. – Natural size, a -inner view, b - outer view.
- Fig. 3: *Trigonodon jugleri* (v. MÜNSTER, 1846), fragment of upper pharyngeal tooth plate; Badenian, Middle Miocene, from Devinská Nová Ves (= Neudorf a.d. March), Slovakia. – NHMWien 1857/XIX/33/2, already figured in SCHULTZ 1978: Pl. 1/9 and 1998: Pl. 57/6a+b. – Natural size.
- Fig. 4: like Fig. 3, but NHMWien 1857/XIX/33/1, already figured in SCHULTZ 1978: Pl. 1/8 and 1998: Pl. 57/7a+b. – Natural size.
- Fig. 5: *Trigonodon jugleri* (v. MÜNSTER, 1846), right upper pharyngeal tooth plate; Badenian, Middle Miocene, from Kaisersteinbruch, Blauer Bruch, Burgenland. – Coll. P. Biermayr. – a + b - occlusal surface, c + d - basal view, a+ c natural size, b + d - 2x natural size.
- Fig. 6: *Trigonodon jugleri* (v. MÜNSTER, 1846), left upper pharyngeal tooth plate, little worn; Badenian, Middle Miocene, from Retznei, Styria. – Coll. G. Wanzenböck. – a + b - occlusal surface, a - natural size, b – 2,3x natural size.
- Fig. 7: *Trigonodon jugleri* (v. MÜNSTER, 1846), fragment of a lower pharyngeal tooth plate, occlusal surface; Ottnangian, Early Miocene, from Aussertreffling near Linz, Upper Austria. – Coll. H. Temmel. – Natural size, a occlusal surface, b basal view.
- Fig. 8: *Trigonodon jugleri* (v. MÜNSTER, 1846), lower pharyngeal tooth plate; Badenian, Middle Miocene, from Müllendorf, Kreidesteinbruch, Burgenland. – Coll. G. Wanzenböck, formerly Coll. H. Zierhofer. – Natural size.
- Fig. 9: *Trigonodon jugleri* (v. MÜNSTER, 1846), lower pharyngeal tooth plate, using surface; Badenian, Middle Miocene, from Devinská Nová Ves (= Neudorf a.d. March), Slovakia. – NHMWien 1979/2119/1, formerly Coll. O. Lienhart – figured specimen in SCHULTZ 1978: Pl. 1/11a+b and in SCHULTZ 1998: Pl. 57/8. – Natural size.
- Fig. 10: *Pseudodax moluccanus* (VALENCIENNES, 1840), Banda Island. – NHMWien 91.983. – a – left praemaxillary, inner view. – 2x natural size, b – left praemaxillary, outer view. – 2x natural size, c – right praemaxillary, inner view. – 2x natural size, d – right praemaxillary, outer view. – 2x natural size, e – left dentary, inner view. – 2x natural size, f – left dentary, outer view. – 2x natural size, g – right dentary, outer view. – 2x natural size, h – left dentary, inner view; like fig. e, but enlarged: 3,4x natural size.
- Fig. 11: *Pseudodax moluccanus* (VALENCIENNES, 1840), Negros, Philippines, Sulu Sea. – Coll. D.R. Bellwood, Townsville. – 2x natural size, except fig. 10f (157 mm SL, 193 mm TL): a – left praemaxillary, outer view. b – upper pharyngeal tooth plate, right outer view (below is caudal). c – upper pharyngeal tooth plate, using surface (below is caudal). d – upper pharyngeal tooth plate, right inner view (below is caudal). e – lower pharyngeal tooth plate, using surface (below is caudal). f – like fig. e, but 6x natural size.

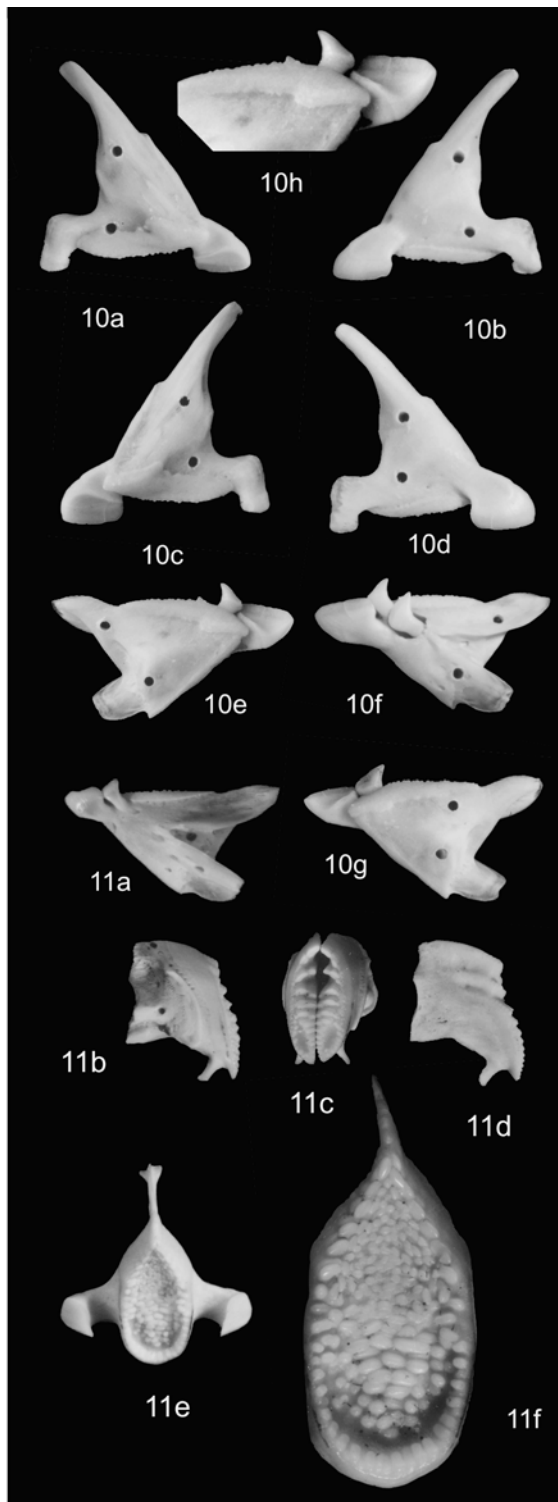
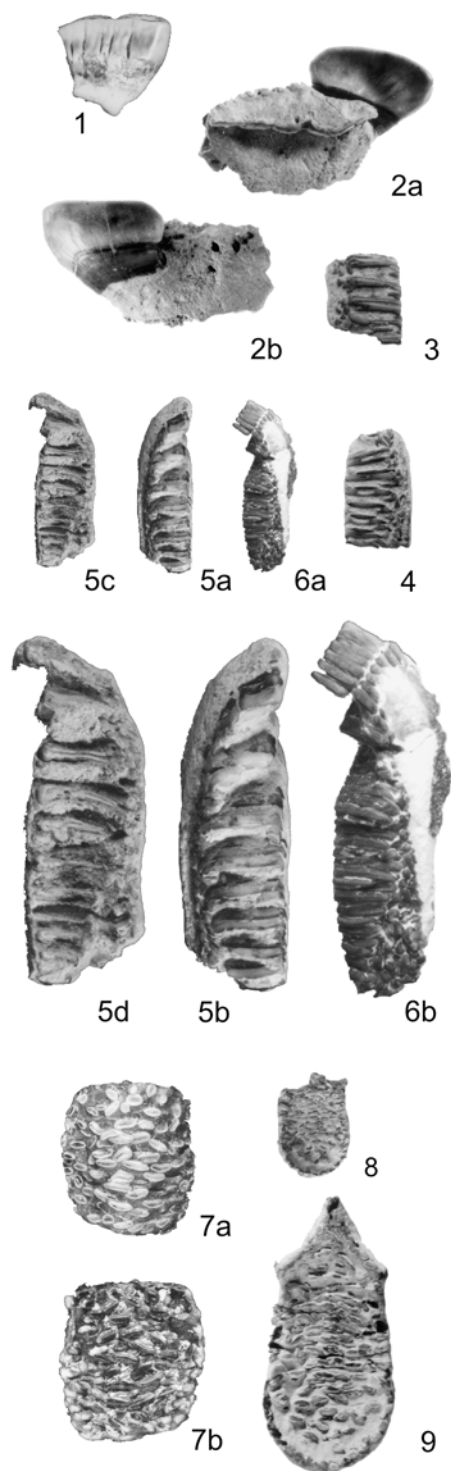


Plate 2

Fig. 1, 2: *Pseudodax moluccanus* (VALENCIENNES, 1840), Cocos-Keeling Islands, S of Sumatra, Indian Ocean: 211 mm SL, 251 mm TL. – Photographs by D.R. Bellwood, Townsville.

Fig. 3: *Pseudodax moluccanus* (VALENCIENNES, 1840); the small fish under it is the Blue-streak Cleaner Wrasse *Labroides dimidiatus* (VALENCIENNES, 1840). – Copyright 2002 by J.E. Randall.



1a



1b



2

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