Available online at www.sciencedirect.com
ScienceDirect
GEOBIOS
Geobios 39 (2006) 491–505
http://france.elsevier.com/direct/GEOBIO/

Evidence for the longest stratigraphic range of a post-Triassic Ichthyosaur: a *Leptonectes tenuirostris* from the Pliensbachian (Lower Jurassic) of Switzerland

Leptonectes tenuirostris du Pliensbachien (Jurassic inférieur) de Suisse : preuve de la plus longue extension stratigraphique chez un Ichthyosaure post-triasique

Michael W. Maisch [a], Achim G. Reisdorf [b,*]

[a] *Institut und Museum für Geologie und Paläontologie, Sigwartstrasse 10, 72076 Tübingen, Germany*
[b] *Universität Basel Geologisch–Paläontologisches Institut, Bernoullistrasse 32, 4056 Basel, Switzerland*

Received 22 May 2003; accepted 27 April 2005
Available online 12 June 2006

Abstract

A three-dimensional well-preserved ichthyosaur skull and parts of the postcranial skeleton are attributed to the species *Leptonectes tenuirostris* (Conybeare, 1822). It was found vertically embedded in Pliensbachian deposits representing three successive biozones (*ibex* to *margaritatus* Zone). The find is dated as early Late Pliensbachian (*margaritatus* Zone) by a rich ammonite and ostracod fauna. It is the first record of the genus *Leptonectes* from Switzerland and from the Late Pliensbachian. It is so far the best preserved and most complete ichthyosaur from this time interval worldwide. With diagnostic specimens known from the Rhaetian (Late Keuper) up to the early Late Pliensbachian (Middle Liassic), *L. tenuirostris* (Conybeare, 1822) has the most extensive stratigraphic range documented for any post-Triassic ichthyosaur so far.

Résumé

Un crâne d'ichthyosaure tridimensionnel avec une partie de son squelette postcrânien a été récemment découvert dans le Pliensbachien du Nord-Ouest de la Suisse. Ce fossile, qui présente un excellent état de préservation, a été attribué à l'espèce *Leptonectes tenuirostris* (Conybeare, 1822). Ce crâne d'ichtyosaure a été trouvé en position verticale, au sein de sédiments recoupant trois biozones successives (de la zone à *ibex* à la zone à *margaritatus*). La présence d'une riche faune d'ammonites et d'ostracodes a permis de dater cet ichtyosaure du début du Pliensbachien supérieur (zone à *margaritatus*). Ce fossile représente la première découverte du genre *Leptonectes* non seulement du Nord de la Suisse mais également du Pliensbachien supérieur. De plus, cet exemplaire est le plus complet et le mieux conservé des ichtyosaures de cet âge connus au monde. Cette découverte, associée aux autres échantillons déjà connus, démontre que *L. tenuirostris* (Conybeare, 1822) était présente du Rhétien (Keuper supérieur) jusqu'au début du Pliensbachien supérieur (Lias moyen) et représente donc l'espèce recouvrant l'intervalle stratigraphique le plus large parmi les ichtyosaures post-triasiques documentés à ce jour.

Zusammenfassung

Ein dreidimensionaler, sehr gut erhaltener Ichthyosaurier-Schädel mit Teilen des postcranialen Skeletts aus dem Pliensbachium der NW-Schweiz wird der Spezies *Leptonectes tenuirostris* (Conybeare, 1822) zugewiesen. Die Ichthyosaurier-Reste waren senkrecht in einer Schichtenfolge eingebettet, die drei aufeinanderfolgende Biozonen (*ibex*- bis *margaritatus*-Zone) umfasst. Der Fund wird anhand der reichhaltigen Ammo-

* Corresponding author.
E-mail address: achim.reisdorf@unibas.ch (A.G. Reisdorf).

0016-6995/$ - see front matter © 2006 Elsevier SAS. All rights reserved.
doi:10.1016/j.geobios.2005.04.005

niten- und Ostracodenfauna in das frühe Spät-Pliensbachium (*margaritatus*-Zone) gestellt. Sowohl für die Schweiz als auch für das Spät-Pliensbachium bedeutet das den Erstnachweis der Gattung *Leptonectes*. Dieser Fund repräsentiert zugleich weltweit den bislang besterhaltenen und umfassendsten Ichthyosaurierrest aus diesem Zeitintervall. Da *L. tenuirostris* (Conybeare, 1822) durch Funde vom Rhät (Spät-Keuper) bis zum frühen Spät-Pliensbachium (Mittel-Lias) belegt ist, besitzt diese Art unter allen post-triassischen Ichthyosauriern die längste stratigraphische Reichweite.

Keywords: Leptonectes tenuirostris; Leptonectidae; Ichthyosauria; Pliensbachian; Liassic; Switzerland

Mots clés : Leptonectes tenuirostris ; Leptonectidae ; Ichthyosauria ; Pliensbachien ; Lias ; Suisse

Schlüsselwörter: Leptonectes tenuirostris; Leptonectidae; Ichthyosauria; Pliensbachium; Lias; Schweiz

1. Introduction

Articulated remains of ichthyosaurs are rarities among the Liassic fossils of Switzerland (e.g. Fraas, 1891: 43; Moesch, 1867; Peyer and Koechlin, 1934; Weidmann, 1981; Table 1). So far, only one almost complete ichthyosaur skeleton was found in Upper Liassic black shales from the Teysachaux mountain (Creux de l'Ours; Posidonia Shale, Lower Toarcian; Von Fischer-Ooster, 1870). It was attributed to *Stenopterygius longifrons* Owen by Von Huene (1939), a species known from coeval strata in UK, France, Belgium and Germany (Owen, 1881; Godefroit, 1993, 1994; Maisch, 1998a; Maisch and Ansorge, 2004). Recently, five additional finds of ichthyosaur remains that can be classified on the generic and specific level have been recorded from the Liassic of Switzerland. They include three skulls from the Posidonia Shale (Lower Toarcium) of the Staffelegg and Asuel (e.g. Streif, 1981; Jordan, 1982; Hostettler, pers. comm. 2005), several skull fragments belonging to one individual of *Ichthyosaurus communis* from the *Arietites* bearing limestones of Frick (Lower Sinemurian; e.g. Rufli-Kornmann, 2001; Reisdorf et al., in press), as well as a specimen from Pliensbachian sediments of Unter Hauenstein described in this paper.

Numerous disarticulated bones, especially isolated vertebrae, indicate that the area of Switzerland belonged to the habitat of ichthyosaurs during the Liassic (Table 1). The rare finds of articulated ichthyosaurs are not explained exclusively by the unfavourable preservation conditions (e.g. Martill, 1985, 1993: Fig. 12), but also by the lack of extended exposures of Liassic rocks. Compared to SW Germany, condensation and tectonics prevented a commercial use of these sediments (e.g. Rickenbach, 1947; Bitterli, 1960; Peters, 1964; Riegraf, 1985: 64; Eckardt et al., 1997; Mumenthaler et al., 1997).

Lower Toarcian black shales all over the world yielded a large number of ichthyosaur skeletons, but the finds in other stratigraphic intervals within the Liassic are only a few (Sander, 2000). Therefore, the find of an ichthyosaur of Late Pliensbachian age has not only regional importance. Generally, Pliensbachian ichthyosaurs are poorly known, and only few more or less diagnostic finds from Germany, Belgium, UK and Canada have been described (Fraas, 1892; Von Huene, 1931; Kuhn, 1939; McGowan, 1978; Godefroit, 1992; Hungerbühler and Sachs, 1996; Maisch and Hungerbühler, 1997; McGowan and Milner, 1999) and only two species are recognised as valid in the last comprehensive overview of ichthyosaur taxonomy (Maisch and Matzke, 2000a), namely *Temnodontosaurus nuertingensis* (Von Huene, 1931) from the Lower Pliensbachian of Southern Germany, based on a fragmentary skull, and *Leptonectes moorei* McGowan and Milner, 1999 from the Lower Pliensbachian of Dorset, based on an incomplete skeleton.

The present specimen represents the first well-preserved articulated ichthyosaur from the Late Pliensbachian to be described and adds a third valid species to the Pliensbachian ichthyosaur fauna, *Leponectes tenuirostris* (Conybeare, 1822). There are no comparable finds from this time interval (*margaritatus* to *spinatum* Zone) known from elsewhere in the world so far. The new specimen, therefore, is of utmost importance, as it narrows the very large gap between the rich ichthyosaur fauna of the Hettangian/Sinemurian and the Early Toarcian.

2. Geological setting

The ichthyosaur skull was found near the village Hauenstein (SO) in an abandoned pit in which Early Aalenian mudstones were quarried (Swiss co-ordinates: 632,900 /248,000; Fig. 1). The outcrop is located in the northern part of the Hauenstein Anticline (Goldschmid, 1965). The topmost beds of the Liassic (Pleydellienbank, Upper Toarcian; sensu Jordan, 1983) form the north-western wall of the pit and dip 40° to SE (158°).

During the operation of the claypit, an incomplete Liassic section was opened; stratigraphically it ranges from the Upper Sinemurian (Obliqua-Schichten; sensu Jordan, 1983) up to the Upper Toarcian (Pleydellienbank; Fig. 2; Rieber, 1987; Meyer and Furrer, 1995). The Liassic deposits in the Hauenstein region are approximately 30 m thick (Jordan, 1983; Reisdorf, 2001).

3. Documentation of the record

As a consequence of clay exploitation, mass movements occurred frequently at the pit walls. In the spring of 1999, such a slide newly exposed ca. 200 m^2 of Middle and Upper Liassic rocks (Swiss co-ordinates 632,880 /248,100). Upper Pliensbachian nodular limestones (Fig. 2, bed 1A) formed the base of the slide, the Posidonia Shale (bed 1B, e.g. Reisdorf, 2001; "Basisschicht"? sensu Kuhn and Etter, 1994; compare Knitter

Table 1
Liassic ichthyosaurs in Switzerland. Symbols and abbreviations are: *) M.H., Middle Hettangian; L.H., Late Hettangian; E.S., Early Sinemurian; E.P., Early Pliensbachian; L.P., Late Pliensbachian; E.T., Early Toarcian; L.T., Late Toarcian. **) CHF, Collection Heid (Frick/AG); CHGJ, Collection Hans G. Jutzi (Schwerzenbach/ZH); CHH, Collection Hans Hartmann (Pratteln/BL); CPV, Collection Peter Vögtli (Diegten/BL); CWB, Collection Werner Brogli (Möhlin/AG); FPJ, collection de la Fondation paléontologique jurassienne (Glovelier/JU); MGL, Musée géologique cantonal Lausanne; MUME, Museo die Fossili di Meride; MzA, Museum zu Allerheiligen Schaffhausen; NATAG, Naturama Aargau Aarau; NMB, Naturhistorisches Museum Basel; NMBE, Naturhistorisches Museum der Bürgergemeinde Bern; NMO, Naturmuseum Olten; NMS, Naturmuseum Solothurn; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich; SMF, Sauriermuseum Frick. ***) co-ordinates after Furrer (1960). ****) The label states that the locality is the Belchen Mountain, where no Liassic rocks exist, the next Liassic rocks occur at the Kilchzimmersattel. ♦) field name. ♦♦) name of strata sensu Wiedenmayer (1963)

Stage	Sub-stage*	Name of strata (*sensu* Jordan 1983)	Finding place	Swiss co-ordinates	Reference	Part of fossil	Repository**	Register number
Toarcian	L.T.	Pleydellienbank	claystone pit Fasiswald (SO)♦	629.100 / 245.100		single vertebrae		
Toarcian	L.T.	Pleydellienbank	claystone pit Staffelegg (AG)♦	647.000 / 254.025		single vertebrae		
Toarcian	L.T.	Pleydellienbank	claystone pit Unter Hauenstein (SO)♦	633.000 / 248.000	e.g. Meyer & Furrer (1995)	a half vertebra	NMBE	NMBE D 2693
Toarcian	L.T.	Pleydellienbank	claystone pit Unter Hauenstein (SO)♦	633.000 / 248.000	e.g. Meyer & Furrer (1995)	one vertebra	NMBE	NMBE D 2692
Toarcian	L.T.	Pleydellienbank	claystone pit Unter Hauenstein (SO)♦	633.000 / 248.000	e.g. Meyer & Furrer (1995)	one vertebra	NMBE	NMBE D 2691
Toarcian	L.T.	Pleydellienbank	claystone pit Unter Hauenstein (SO)♦	633.000 / 248.000	e.g. Meyer & Furrer (1995)	one vertebra	NMBE	NMBE D 2690
Toarcian	L.T.	Pleydellienbank	claystone pit Unter Hauenstein (SO)♦	633.000 / 248.000	e.g. Meyer & Furrer (1995)	one phalanga	NMBE	NMBE D 2689
Toarcian	L.T.	Pleydellienbank	claystone pit Unter Hauenstein (SO)♦	633.000 / 248.000	e.g. Meyer & Furrer (1995)	one vertebra	NMO	NMO 20137
Toarcian	L.T.	Jurensis-Schichten	claystone pit Fasiswald (SO)♦	628.800 / 245.100	pers. comm. Bernhard Hostettler (Glovelier/ JU; 2005)	several vertebrae; dis-articulated	FPJ	
Toarcian	E.T.	Posidonienschiefer	Asuel (JU)	582.900 / 250.000	pers. comm. Bernhard Hostettler (Glovelier/ JU; 2005)	skull	FPJ	
Toarcian	E.T.	Posidonienschiefer	Beznau (AG)	659.500 / 267.000		one vertebra	PIMUZ	PIMUZ A/ III 0998
Toarcian	E.T.	Posidonienschiefer	in the river bed of Betznau river (AG)	659.500 / 267.000	Moesch (1867)	several vertebrae; dis-articulated		
Toarcian	E.T.	Posidonienschiefer	in the river bed of Betznau river (AG)	659.500 / 267.000	e.g. Moesch (1867)	eight vertebrae, ribs; dis-articulated	CHGJ	
Toarcian	E.T.	Posidonienschiefer	Bütz (AG)	649.700 / 265.800		one tooth	PIMUZ	PIMUZ A/ III 1022
Toarcian	E.T.	Posidonienschiefer	Cornol (JU)	579.950 / 249.500	pers. comm. Bernhard Hostettler (Glovelier/ JU; 2003)	one tooth, ribs, single vertebrae; dis-articulated	FPJ	
Toarcian	E.T.	Posidonienschiefer	Creux de l'Ours (FR)♦	565.170 / 154.400***	v. Fischer-Ooster (1870); v. Huene (1939); Furrer (1960); Weidmann (1993); Menkveld-Gfeller (1998)	almost complete skeleton (*Stenopterygius longifrons* Owen)	NMBE	NMBE C 5012
Toarcian	E.T.	Posidonienschiefer	Creux de l'Ours (FR)♦	565.170 / 154.400***	e.g. Weidmann (1993)	ribs from the *Stenopterygius longifrons* Owen (NMBE C 5012)	NMBE	NMBE D 2687
Toarcian	E.T.	Posidonienschiefer	Creux de l'Ours (FR)♦	565.170 / 154.400***	e.g. Weidmann (1993)	ribs from the *Stenopterygius longifrons* Owen (NMBE C 5012)	NMBE	NMBE D 2686
Toarcian	E.T.	Posidonienschiefer	Creux de l'Ours (FR)♦	563.590 / 146.910	Weidmann (1981, 1993); Mettraux (1989)	ribs and three vertebrae; dis-articulated	MGL	MGL 40947 to MGL 40950, MGL 42001 to MGL 42005
Toarcian	E.T.	Posidonienschiefer	Frick (AG)	643.000 / 261.800	Moesch (1867); Peyer & Koechlin (1934)	unspecified remains of ichthyosaurs		
Toarcian	E.T.	Posidonienschiefer	Gansingen (AG)	652.500 / 266.000	Moesch (1867); Peyer & Koechlin (1934)	unspecified remains of ichthyosaurs		
Toarcian	E.T.	Posidonienschiefer	Gansingen (AG)	652.500 / 266.000	Moesch (1867); Peyer & Koechlin (1934)	one vertebra		
Toarcian	E.T.	Posidonienschiefer	Hettenschwil (AG)	657.200 / 269.900	Moesch (1867); Peyer & Koechlin (1934)	unspecified remains of ichthyosaurs		
Toarcian	E.T.	Posidonienschiefer	Hottwil (AG)	654.500 / 266.500	Moesch (1867); Peyer & Koechlin (1934)	unspecified remains of ichthyosaurs		
Toarcian	E.T.	Posidonienschiefer	claystone pit Staffelegg (AG)♦	647.000 / 254.025	e.g. Jordan (1982); Streif (1981)	incomplete skull of an Neoichthyosauria gen et sp. indet.	NATAG	PIMUZ A/ III 0749
Toarcian	E.T.	Posidonienschiefer	claystone pit Staffelegg (AG)♦	647.000 / 254.025		incomplete skull of an Leptonectidae gen. et sp. indet.	PIMUZ	PIMUZ A/ III 0749
Toarcian	E.T.	Posidonienschiefer	Sulz (AG)	649.500 / 265.000	Moesch (1867); Peyer & Koechlin (1934)	spine-rib-fragment	PIMUZ	PIMUZ A/ III 0125
Toarcian	E.T.	Variabilis-Horizont	claystone pit Fasiswald (SO)♦	628.800 / 245.100	pers. comm. Bernhard Hostettler (Glovelier/ JU; 2004)	skull fragment, two vertebrae; dis-articulated	FPJ	
Pliensbachian		Kondensiertes Pliensbachium	claystone pit Fasiswald (SO)♦	628.800 / 245.100	pers. comm. Bernhard Hostettler (Glovelier/ JU; 2004)	several vertebrae; dis-articulated	FPJ	
Pliensbachian	L.P.	Kondensiertes Pliensbachium	claystone pit Unter Hauenstein (SO)♦	632.880 / 248.100	this paper	skull, postcranial skeleton and two phalangae (*Leptonectes tenuirostris*, Conybeare, 1822)	NMO	NMO 26575
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)♦	633.400 / 247.050		one vertebra	NMO	NMO 20136

Stage	Sub-stage*	Name of strata (*sensu* Jordan 1983)	Finding place	Swiss co-ordinates	Reference	Part of fossil	Repository**	Register number
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		bone fragment indet.	NMO	NMO 20135
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one rib	NMO	NMO 20134
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		bone fragment indet.	NMO	NMO 20133
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one phalanga	NMO	NMO 20132
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one vertebra	NMO	NMO 20131
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one vertebra	NMO	NMO 20130
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		bone fragment indet.	NMO	NMO 20129
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one rib	NMO	NMO 20128
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one vertebra	NMO	NMO 20127
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		bone fragment indet.	NMO	NMO 20126
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		one rib	NMO	NMO 20125
Pliensbachian	? E.P.	Kondensiertes Pliensbachium	claystone pit Erlimoos (SO)◆	633.400 / 247.050		bone fragment indet.	NMO	NMO 20124
? Pliens-bachian	?	?	Hemmiken (BL)	260.100 / 635.100	pers. comm. Thomas Bolinger (Olsberg/ AG; 2004)	several vertebrae; dis-articulated		
Pliensbachian	?	?	Kleinzinki-brunnen (BL)◆	617.000 / 262.500	Peyer & Koechlin (1934)	one vertebra	NMB	L.D. 26
Sinemurian	E.S.	Arietenkalk	Beggingen (SH)	682.125 / 291.525	Früh (1962)	articulated spine (caudalia)	MzA	NAT 910
Sinemurian	E.S.	Arietenkalk	Beggingen (SH)	682.125 / 291.525		eight vertebrae (caudalia; ? same individual described by Früh 1962)	PIMUZ	PIMUZ A/ III 0494
Sinemurian	? E.S.	? Arietenkalk	Beggingen (SH)	682.125 / 291.525		bone fragments (four pieces)	PIMUZ	PIMUZ A/ III 0836
Sinemurian	E.S.	Arietenkalk	claystone pit Frick (AG)	643.000 / 261.900	Maisch et al. (subm.), e.g. Hartmann (1999), Rufli-Kornmann (2001)	incomplete skull of an *Ichthyosaurus communis* Conybeare, 1822	SMF	SMF 46
Sinemurian	E.S.	Arietenkalk	claystone pit Frick (AG)	643.000 / 261.900	e.g. Meyer & Furrer (1995) Kindlimann (1990), Sander (1990)	vertebrae and ribs; dis-articulated	SMF	
Sinemurian	E.S.	Arietenkalk	claystone pit Frick (AG)	643.000 / 261.900	e.g. Meyer & Furrer (1995) Kindlimann (1990), Sander (1990)	several vertebrae; dis-articulated	NATAG	
Sinemurian	? E.S.	? Arietenkalk	Hallau (SH)	676.000 / 284.400		one vertebra	NMB	L.D. 39
Sinemurian	E.S.	Arietenkalk	Ittenthal (AG)	646.800 / 263.300	Moesch (1867); Peyer & Koechlin (1934)	unspecified remains of ichthyosaurs		
Sinemurian	E.S.	Arietenkalk	Kanton Basel (BS)	?		skull fragment (*Temnodontosaurus* sp.)	NMB	L.D. 35/36
Sinemurian	E.S.	Arietenkalk	Olsberg (AG)	626.800 / 263.150	Moesch (1867); Peyer & Koechlin (1934)	one vertebra		
Sinemurian	E.S.	Arietenkalk	Schupfart (AG)	639.950 / 263.400		one phalanga	CWB	
? Sinemurian	?	(Broccatello)◆◆	Cave di Arzo (TI)	717.300 / 082.100	Renesto et al. (2002)	one incomplete vertebra (? Leptopterygiidae)	MUME	MUME 133
Hettangian	L.H.	Eisenooidreiche Folge	claystone pit Frick (AG)	643.000 / 261.900	Maisch et al. (subm.)	several vertebrae and ribs; dis-articulated	CHH	
Hettangian	L.H.	Eisenooidreiche Folge	claystone pit Frick (AG)	643.000 / 261.900	Maisch et al. (subm.)	several vertebrae and ribs; dis-articulated	CPV	
Hettangian	M.H.	Insektenmergel	Schambelen	659.400 / 257.000	Heer (1865), Moesch (1867)	one tooth		
?	?	?	Breitenmatt (AG)◆	654.025 / 265.375	pers. comm. Beat Lüdi (Strengelbach/ AG; 2003)	one vertebra	NMO	NMO 26577
?	?	?	Densbüren (AG)	646.300 / 256.100		one vertebra	NMBE	NMBE D 2694
?	?	?	Kanton Basel (BS)	?		one tooth	NMB	L.D. 31
?	?	?	Kilchzimmer-sattel (SO)****◆	? 627.300 / 246.150		one vertebra	NMS	NMS 9230
?	?	?	Lausen (BL)	624.000 / 258.500		three vertebrae	NATAG	
?	?	?	Reben v. München-stein (BL)◆	614.000 / 262.600		one vertebra (Neoichthyosauria gen. et sp. indet.)	GPIB	GPIB R 11
?	?	?	Wolberg (AG)◆	641.000 / 262.200	Peyer & Koechlin (1934)	three vertebrae; dis-articulated	CHF	

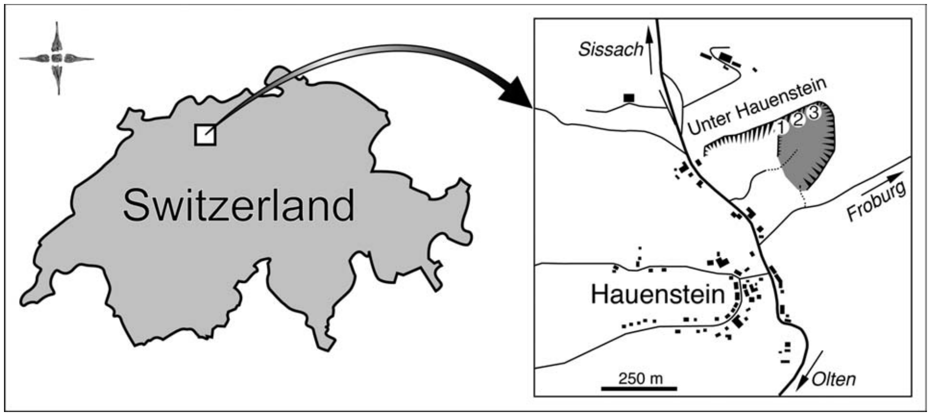


Fig. 1. Location of the claypit at Unter Hauenstein. Numbers 1–3 refer to three Liassic sections (1, Swiss co-ordinates: 632,800 /248,000; 2, 632,850 /248,050; 3, 632,880 /248,100). **1**. Liassic section 1 (Rieber, 1987; collection Rieber, Paläontologisches Institut und Museum der Universität Zürich); **2**. Liassic section 2 (measured by the co-author, ammonite material stored in the Naturmuseum Olten; catalogue numbers: NMO 8778 to NMO 8832); **3**. Liassic section 3 (measured by the co-author, H.-R. Rüegg, W. Tschudin, H. Hartmann, ammonite material stored in the Naturmuseum Olten; catalogue numbers: NMO 8699 to NMO 8777; NMO 8833-8964).

and Ohmert, 1983: 237, 242; Knitter and Ohmert, 1986: 166–168) served as gliding horizon.

At this place, C.A. Meyer (Basel) discovered a limestone nodule (17 cm long, 16 cm high, 12 cm wide), wherein a part of the postcranial skeleton of an ichthyosaur is preserved. Later —independently of the previous find—skull bones (e.g. a sclerotical ring), ribs, and two phalanges of the same individual were found at the same place (bed 1A) in September 1999 by A.G. Reisdorf (Basel).

During an excavation campaign, a team of the Geologisch–Paläontologisches Institut Basel discovered the vertically embedded skull of the ichthyosaur described in this paper. The skull is surrounded by three beds, representing three successive ammonite zones (*ibex* Zone up to *margaritatus* Zone; Fig. 2). Between November 2001 and December 2002, the specimen was prepared (Geowissenschaftliches Atelier Gebrüder Imhof; Trimbach/SO). Since January 2003, the finds are stored in the collection of the Naturmuseum Olten (NMO): the ichthyosaur remains (NMO 26575), the host sediment (NMO 26575), and the accompanying fauna (ammonites, nautilids, bivalves, brachiopods, NMO 8699-8832). In June 2003, a team from the Geologisch–Paläontologisches Institut Basel started a second excavation to obtain additional reliable biostratigraphic data (ammonoids and ostracods; NMO 8833-8964, NMO 8699-8718). To analyse the emplacement process of the ichthyosaur and to decipher the history of the sediment accumulation and post-depositional compaction, the ichnofabrics were analysed by Wetzel and Reisdorf (in press).

4. Systematic palaeontology

Order ICHTHYOSAURIA De Blainville, 1835.
HUENEOSAURIA Maisch and Matzke, 2000a.
LONGIPINNATI Von Huene, 1948.
MERRIAMOSAURIA Motani, 1999.
PARVIPELVIA Motani, 1999.
NEOICHTHYOSAURIA Sander, 2000.
Family LEPTONECTIDAE Maisch, 1998b.
Genus ***Leptonectes*** McGowan, 1996.
Type-species: *Ichthyosaurus tenuirostris* Conybeare, 1822.

Leptonectes tenuirostris (Conybeare, 1822) McGowan, 1996.

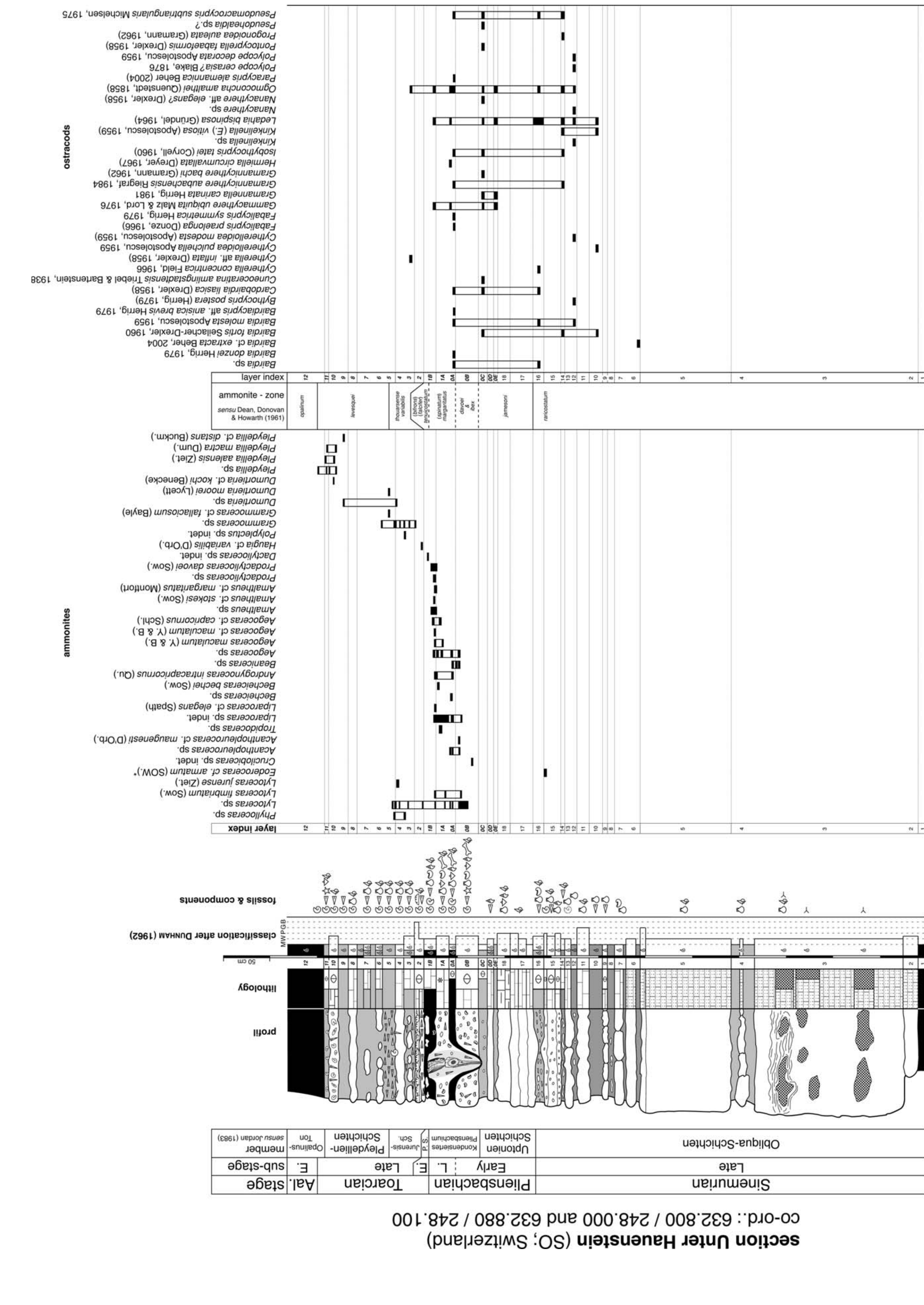
Distribution: Rhaetian to Lower Sinemurian, Southern UK, Lower Sinemurian, Southern Germany, ? Lower Pliensbachian, Belgium, Upper Pliensbachian, Switzerland.

Additional species included in the genus: *Leptonectes solei* (McGowan, 1993) McGowan, 1996, *L. moorei* McGowan and Milner, 1999.

Description: The skull is three-dimensionally preserved (Fig. 3). The snout region is almost complete. Much of the left half of the skull roof is missing (Fig. 4). The postorbital region is strongly damaged and incomplete on the right side but moderately well-preserved on the left side. Preservation of the individual bones and teeth is moderately good. The bone surface has in many places suffered both from erosion and mechanical damage.

The skull as a whole is characterised by a strikingly elongate and narrow snout and dominated by the enormous orbits. These typical ichthyosaur features are almost over-exaggerated in the present specimen.

The length of the left orbit is 115 mm, its maximum height is 85 mm. The preorbital length of the skull is 247 mm, the prenarial length (length of the rostrum) is 186 mm, the length of the premaxillary segment of the upper jaw is 181 mm. All measurements were taken on the left side of the specimen, which is best preserved. As the tip of the premaxillary rostrum is missing, preorbital, premaxillary and rostral length must originally have been somewhat larger. Presumably, judging from the completely preserved mandible, the anteriormost 8 mm are missing. The left mandibular ramus is complete anteriorly and almost complete posteriorly. Its length as preserved is 370 mm, the original length can not have been more than 400 mm. If one takes this estimated value, the orbital ratio of the skull (as defined by McGowan 1974, 1976) is 0.28, the prenarial ratio (with an estimated value of the original prenarial length


section Unter Hauenstein (SO; Switzerland)
co-ord.: 632.800 / 248.000 and 632.880 / 248.100
stage
sub-stage
member sensu Jordan (1983)
Sinemurian
Pliensbachian
Toarcian
Aal.
Late
Early
L.
E.
Obliqua-Schichten
Uptonien Schichten
Pliensbachium Kondensierles
Jurensis-Sch.
Pleydellien-Schichten
Opalinus-Ton
profil
lithology
classification after Dunham (1962)
fossils & components
50 cm
Reisdorf (1999/2005), *) Rieber (1997)
layer index
ammonites
Phylloceras sp.
Lytoceras sp.
Lytoceras fimbriatum (Sow.)
Lytoceras jurense (Ziet.)
Eoderoceras cf. armatum (SOW.)*
Crucilobiceras sp. indet.
Acanthopleuroceras sp.
Acanthopleuroceras cf. maugenesti (D'Orb.)
Tropidoceras sp.
Liparoceras sp. indet.
Liparoceras cf. elegans (Spath)
Becheiceras sp.
Becheiceras bechei (Sow.)
Androgynoceras intracapricornus (Qu.)
Beaniceras sp.
Aegoceras sp.
Aegoceras maculatum (Y. & B.)
Aegoceras cf. maculatum (Y. & B.)
Aegoceras cf. capricornus (Schl.)
Amaltheus sp.
Amaltheus cf. stokesi (Sow.)
Amaltheus cf. margaritatus (Montfort)
Prodactylioceras sp.
Prodactylioceras davoei (Sow.)
Dactylioceras sp. indet.
Haugia cf. variabilis (D'Orb.)
Polyplectus sp. indet.
Grammoceras sp.
Grammoceras cf. fallaciosum (Bayle)
Dumortieria sp.
Dumortieria moorei (Lycett)
Dumortieria cf. kochi (Benecke)
Pleydellia sp.
Pleydellia aalensis (Ziet.)
Pleydellia mactra (Dum.)
Pleydellia cf. distans (Buckm.)
ammonite - zone sensu Dean, Donovan & Howarth (1961)
raricostatum
jamesoni
davoei & ibex
(spinatum) margaritatus
(bifrons) (falcifer) tenuicostatum
thouarsense variabilis
levesquei
opalinum
ostracods
Bairdia sp.
Bairdia donzei Herrig, 1979
Bairdia cf. extracta Beher, 2004
Bairdia fortis Seilacher-Drexler, 1960
Bairdia molesta Apostolescu, 1959
Bairdiacypris aff. anisica brevis Herrig, 1979
Bythocypris postera (Herrig, 1979)
Cardobairdia liasica (Drexler, 1958)
Cuneoceratina amlingstadtensis Triebel & Bartenstein, 1938
Cytherella concentrica Field, 1966
Cytherella aff. inflata (Drexler, 1958)
Cytherelloidea pulchella Apostolescu, 1959
Cytherelloidea modesta (Apostolescu, 1959)
Fabalicypris praelonga (Donze, 1966)
Fabalicypris symmetrica Herrig, 1979
Gammacythere ubiquita Malz & Lord, 1976
Gramannella carinata Herrig, 1981
Gramannicythere aubachensis Riegraf, 1984
Gramannicythere bachi (Gramann, 1962)
Hermiella circumvallata (Dreyer, 1967)
Isobythocypris tatei (Coryell, 1960)
Kinkelinella sp.
Kinkelinella (E.) vitiosa (Apostolescu, 1959)
Ledahia bispinosa (Gründel, 1964)
Nanacythere sp.
Nanacythere aff. elegans? (Drexler, 1958)
Ogmoconcha amalthei (Quenstedt, 1858)
Paracypris alemannica Beher (2004)
Polycope cerasia? Blake, 1876
Polycope decorata Apostolescu, 1959
Pontocyprella fabaeformis (Drexler, 1958)
Progonoidea auleata (Gramann, 1962)
Pseudohealdia sp.?
Pseudomacrocypris subtriangularis Michelsen, 1975

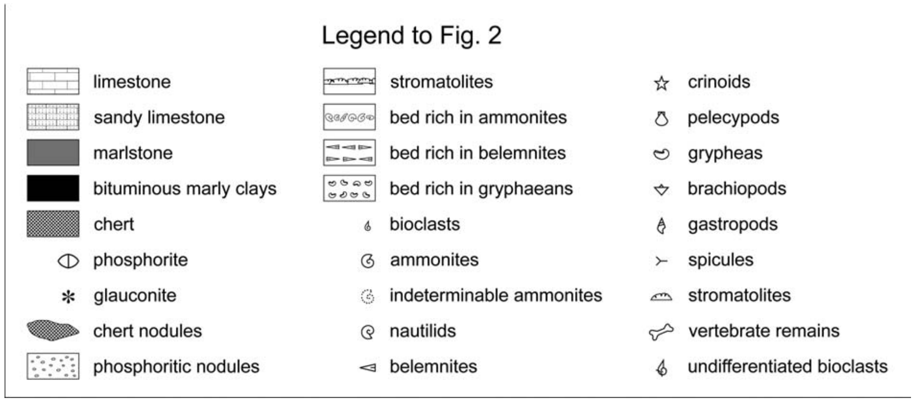


Fig. 2. Detailed section of the Liassic at the location Unterer Hauenstein (section 1: layers 1 to 18; section 3: layers 0E to 12, in *italics*); the beds hosting ichthyosaur are marked. The biostratigraphic subdivision of sections 1 and 3 is based on ammonite and ostracod records; ammonoid zones in parentheses were not discovered in the Unter Hauenstein outcrop.

of 192 mm, assuming that there was no overbite, i.e. no elongation of the upper jaw beyond the anterior end of the mandible) is 0.48, the preorbital (snout) ratio is 0.64 (assuming an original preorbital length of 255 mm), the premaxillary ratio (assuming a premaxillary length of 189 mm) is 0.47.

The external naris is a moderately large opening, being about 45 mm in length and 12 mm in height. It is of elongate, low triangular shape with straight and posteriorly diverging dorsal and ventral margins. Its borders are formed by the premaxilla, lacrimal, nasal and, unusually, the prefrontal.

The orbits are very large and of elliptical shape. They are bordered by the lacrimals, jugals, postorbitals, postfrontals and prefrontals. The right sclerotic ring is largely well-preserved in articulation. The ventral half of the right one is disarticulated, whereas the dorsal half remains in articulation but has fallen inside the empty orbital cavity during decomposition (Fig. 3). The external diameter of the left sclerotic ring is about 96 mm. The internal diameter is 43 mm anteroposteriorly and 33 mm dorsoventrally. If compared to the completely three-dimensional specimen described by Maisch and Matzke (2003), these measurements indicate a considerable dorsoventral deformation of the sclerotic ring and, therefore, the entire skull. That the sclerotic ring is deformed is also indicated by the medially deflected parts of the anterior sclerotic plates that have been squashed and now lie almost in the same level as the rest of the sclerotic ring. There are at least 16 sclerotic plates.

The temporal fenestra is a small opening which is slightly elongated anterolaterally–posteromedially, being 35 mm in length and 30 mm in maximum width. It is bordered by the postfrontal anterolaterally, the supratemporal posterolaterally and posteriorly and the parietal anteromedially and medially. The position and size of the foramen parietale can not be determined.

The premaxillary rostrum misses its tip. The both premaxillaries are quite well-preserved, particularly on the left side. The premaxilla is a low, long elongate and narrow bone which bears most of the upper dentition. At least 29 teeth can be recognised in the right premaxilla, the total number probably ranges between 35 and 40, extrapolated from the density of the teeth in complete segments of the upper tooth row in the entire premaxilla. The lateral surface of each premaxilla shows a well-developed fossa praemaxillaris which extends from the anterior preserved end of the snout backwards to the anterior narial margin, starting as a narrow, well-marked groove and widening into a rather shallow trough posteriorly.

About 72 mm behind the preserved tip of the snout, the premaxillaries are medially separated by the nasals. Posteriorly, each premaxilla contacts the maxilla ventrally and the nasal dorsally. The premaxilla forms the entire anterior and most of the ventral border of the external naris. The subnarial process of the premaxilla completely excludes the maxilla from the external naris. It extends 31 mm from the anterior narial margin backwards on the left side, the naris itself being 45 mm in length.

The supranarial process of the premaxilla is not preserved on either side.

The maxilla is a very low, narrow and short splint of bone. It extends only about 5 mm anterior to the external naris on the left side. Its ventral border is almost straight. The element reaches its greatest height at the level of the posterior narial margin, forming a dorsally convex suture with the lacrimal. There are remnants of at least 12 teeth in the right maxilla. The original number might have been at least 15, as the tooth row is evidently incompletely preserved. The posteroventral margin of the maxilla forms a slightly laterally extending ledge.

The nasals are extensive elements which form the dorsal roof of the snout posteromedial to the premaxillaries. The right nasal is seen to extend far onto the skull roof, reaching above the middle of the orbit. From the level of the posterior half of the naris to slightly behind the anterior orbital margin, the nasals are depressed, forming a conspicuous internasal excavation which posteriorly leads into a deep, narrow groove that extends up to mid-orbital length, i.e. as far as the skull roof is preserved. There is no indication of an internasal foramen. Further anteriorly, the dorsal surface of the nasals is transversely convex. The posterolateral portion of the skull roof component of the nasal is also markedly convex, forming an ele-

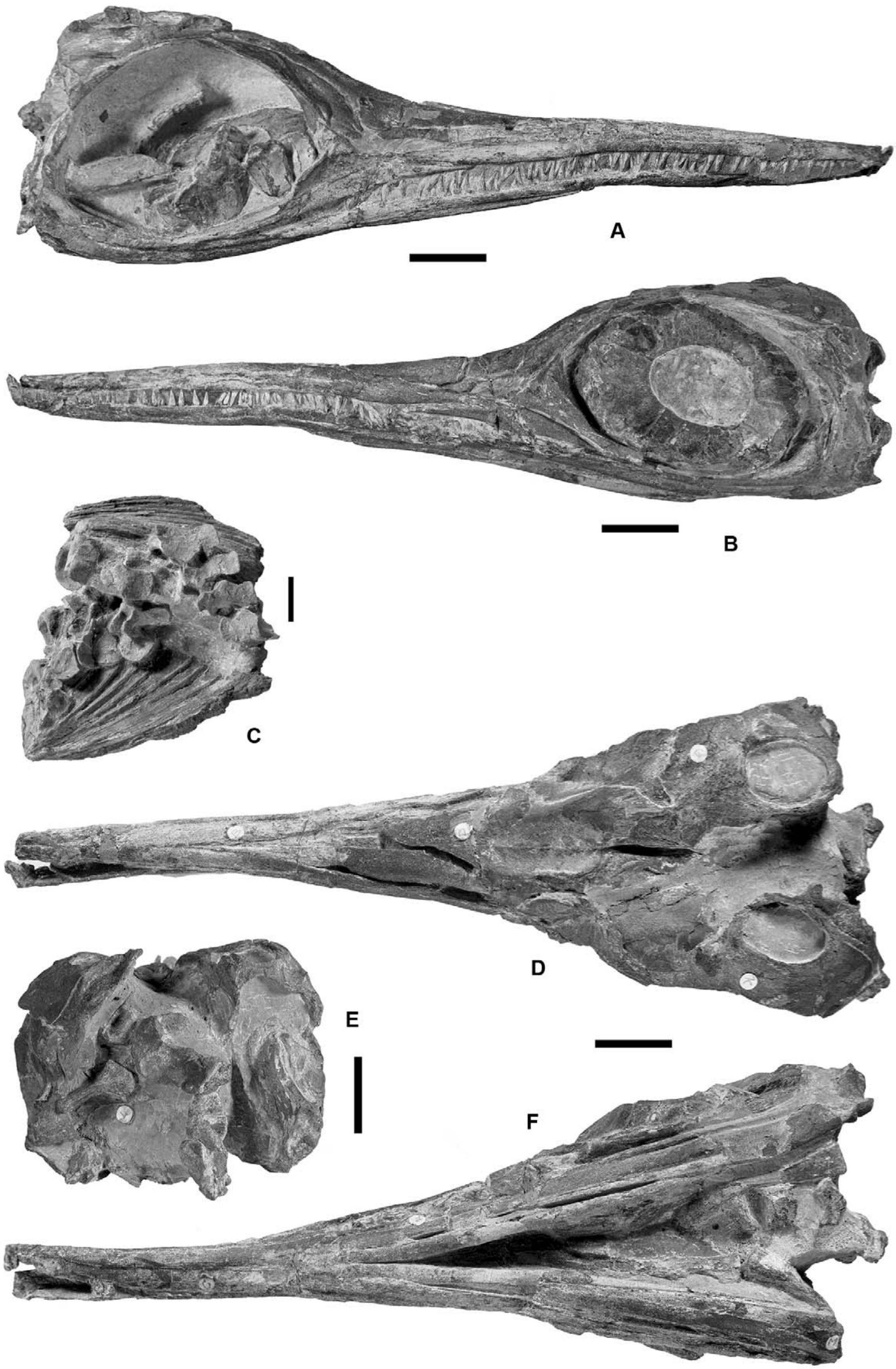


Fig. 3. Skull and partial postcranium of *Leptonectes tenuirostris* (Conybeare, 1822) (register number: NMO 26575) from the Upper Pliensbachian (*margaritatus* Zone) of Unter Hauenstein, NW Switzerland. **A**. Skull in left lateral view, note the partial disarticulation of the sclerotic ring. **B**. Skull in right lateral view with the sclerotic ring well articulated. **C**. Part of the thoracal vertebral column. **D**. Skull in dorsal view, showing the small temporal fenestrae. **E**. Skull in posterior view. **F**. Skull in ventral view. Scale bars equals 30 mm.

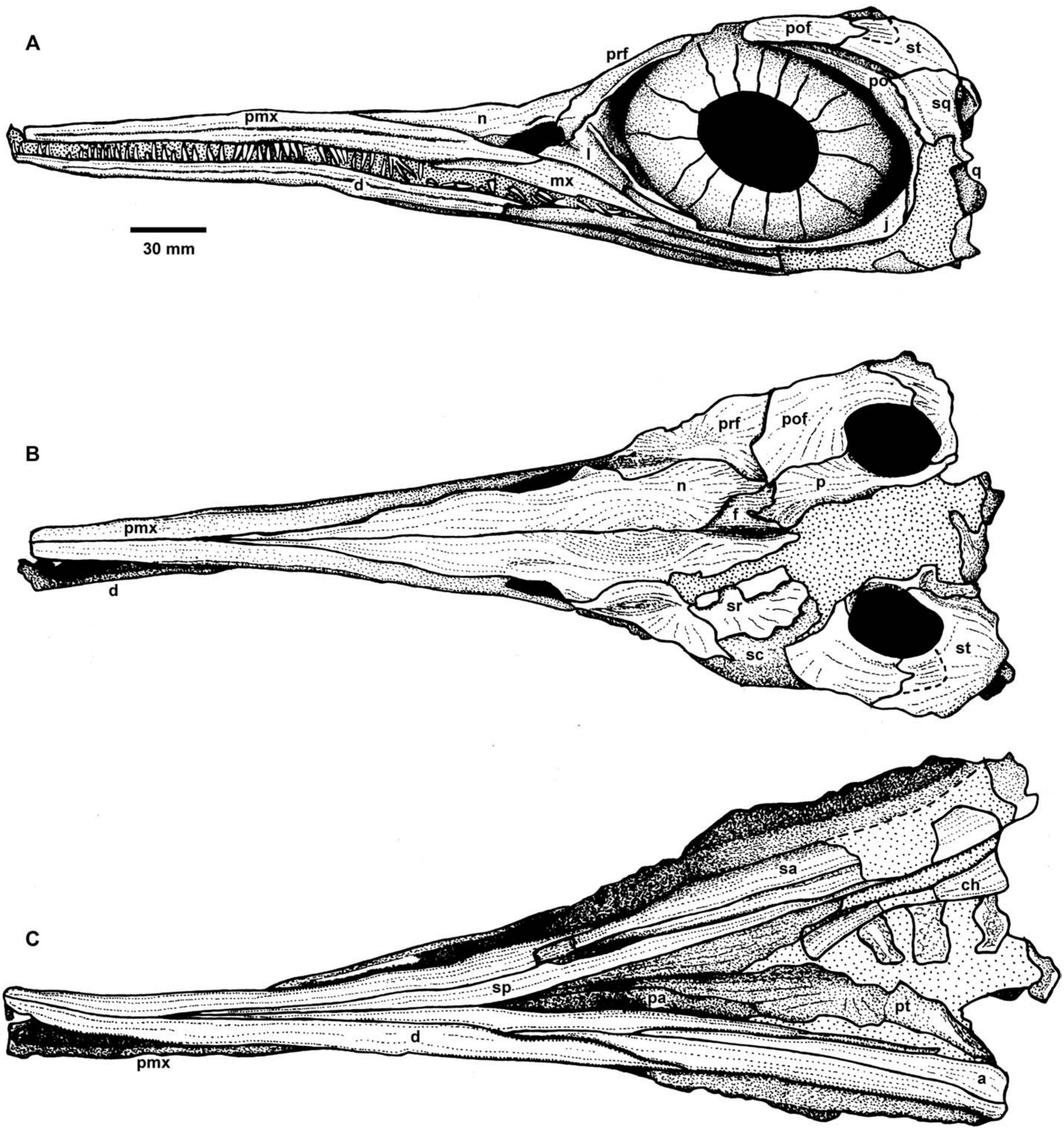


Fig. 4. Skull of *Leptonectes tenuirostris* (Conybeare, 1822) (register number: NMO 26575) from the Upper Pliensbachian (*margaritatus* Zone) of the Unterer Hauenstein, NW Switzerland in **A**: left lateral, **B**: dorsal and **C**: ventral view. Abbreviations: a: angular; ch: ceratohyal; d: dentary; f: frontal; j: jugal; l: lacrimal; mx: maxilla; n: nasal; p: parietal; pa: palatine; pmx: premaxilla; po: postorbital; pof: postfrontal; prf: prefrontal; pt: pterygoid; q: quadrate; sa: surangular; sc: sclerotic ring; sp: splenial; sq: squamosal; sr: imprints of the underside of the skull roof; st: supratemporal. Scale bar equals 30 mm.

vated rim around the excavatio internasalis. Both nasals show a laterally extending wing-like process along the dorsal margin of the external naris, better preserved on the right side. It is similar to but not as conspicuous as that described by Maisch and Matzke (2003) for a specimen of *L.* cf. *tenuirostris* from the Lower Lias of Lyme Regis. Posterior to the external naris, the nasal forms a ventrally concave suture with the prefrontal. Posteriorly, a point-contact with the postfrontal is established, but posteromedially the parietal is apparently not reached. Whether the nasal really contacted the parietal externally is hard to tell, as most of the bone surface of the posterior half of the skull roof is strongly damaged or not yet prepared. Considering the usually high degree of overlap of the individual skull bones of ichthyosaurs (e.g. Sollas, 1916), the sutural relationships displayed by superficially damaged skulls have to be viewed with caution when compared to well-preserved specimens.

The nasals are clearly separated from the posterior narial margin by the lacrimal and prefrontal. This might be the original state or a small posteroventral process of the nasal might be missing from the specimen. In the skull described by Maisch and Matzke (2003) the prefrontal also closely approaches the posterior narial margin separated only by a very narrow zone of contact between the nasal and lacrimal.

Little remains of the right frontal. It was, at least externally, a very small element, contacting the nasal anterolaterally, possibly the prefrontal laterally (below the nasal) and the parietal posterolaterally. There is no evidence for contact with the postfrontal.

The right parietal is a large element which extends far anterior to the small temporal fenestra, of which it forms the anteromedial and medial borders. Anterolaterally it contacts the frontal, laterally the postfrontal and posterolaterally the supratemporal. The posteroventral, occipital flange of the parietal is largely preserved on the left side. It is set off from the dorsal surface of the bone by a distinct, pronounced ridge.

The lacrimal is well-preserved on both sides. It forms the posteroventral and the ventral half of the posterior border of the external naris. Dorsally it contacts the prefrontal, ventrally the jugal and maxilla and anteroventrally the premaxilla. The external anteroventral margin of the orbit, which is also formed by the lacrimal, is reinforced by means of a strongly developed laterally protruding bony shelf, which is well visible on both sides of the specimen. This ridge is also found, although slightly less markedly developed, in *L.* cf. *tenuirostris* described by Maisch and Matzke (2003). Medial to this shelf the posterior surface of the lacrimal is deeply concave.

The jugal is a low, narrow bar of bone which forms most of the ventral margin of the orbit. It is markedly compressed dorsoventrally. Anteriorly it does not extend beyond the anterior orbital margin, in fact it ends markedly posterior to that level. The posterior contact with the postorbital is visible on the left side. The postorbital ramus of the jugal extends at least one third of the orbital height upwards and covers the postorbital anteriorly.

The postorbital is better preserved on the left side. It forms most of the posterior orbital margin. Anterodorsally it develops a thin, transversely expanded lamella which covers the postfrontal ventrally and extends almost to mid-orbital level. It is not visible whether an internal contact to the prefrontal was established, but the two elements were certainly not widely separated.

The prefrontal is an extensive plate of bone which forms the anterior half of the dorsal orbital margin and also sends a lamella downwards which takes part in the formation of the anterodorsal margin of the orbit. There is a marked depression on the dorsal surface of the bone, slightly dorsomedial to the ventral contact with the lacrimal. A similar feature was described by Maisch and Matzke (2003) in *L.* cf. *tenuirostris*. The medial suture to the nasal is almost straight in its posterior two thirds, but convex further anteriorly. Posteriorly the prefrontal contacts the postfrontal, by which it is overlapped in a suture which runs obliquely in anteromedial–posterolateral direction.

The postfrontal forms the posterior half of the dorsal orbital margin externally but, as pointed out above, is underlapped for most, if not all, of this distance by the postorbital. It also forms the anterolateral margin of the temporal fenestra, whereas the lateral margin is, externally, largely formed by the supratemporal, which is, however, overlapped by the postfrontal externally. A rather straight suture with the parietal extends from the anterior margin of the temporal fenestra forwards. There seems to be only a point-contact with the frontal and a very short one with the nasal.

The supratemporal forms most of the lateral margin of the temporal fenestra as well as most of the posterior margin. It contacts the parietal medially and the postfrontal anterolaterally. It is a high, short bone which closely approaches the dorsal orbital margin. The descending occipital flange is only partially preserved on both sides. It still shows sutural contact to the ascending lamina of the pterygoid on the right side.

The left squamosal is a thin but extensive plate of bone of triangular shape. It covers the posterior lamina of the postorbital. Its ventral contact with the quadratojugal is not seen, as this element is not recognisably preserved on either side.

The left quadrate is almost preserved in articulation, but largely covered by the squamosal laterally and the supratemporal and stapes posteromedially. It has a deeply concave lateral margin, which must have formed part of an extensive quadrate foramen. The ascending plate is quite delicate, only three to four mm wide along the lateral margin at maximum, with the entire bone being more than 50 mm high.

The left stapes is preserved between the remnants of a cervical vertebra and the left quadrate, being supported ventrally by the left pterygoid. It is thus remaining in a more or less natural position. Its proximal end is 17 mm wide whereas the distal end is only 5 mm wide and almost not expanded at all as compared to the narrow and slender shaft.

Too little is preserved of the other postorbital and occipital skull elements to merit further description.

Of the palate, both pterygoids and part of the right palatine are quite well exposed. The pterygoid has a rather wide anterior ramus, which extends far forward at least to the level of the anterior end of the external naris as a narrow strip of bone. There is no postpalatinal process of the pterygoid. The palatine extends posteriorly along the lateral pterygoid margin up to the anterior rim of the subtemporal fenestra. The medial margins of both pterygoids seem to enclose only a rather small interpterygoid vacuity. These palatal features are very reminiscent of *Eurhinosaurus longirostris* (Maisch and Matzke, 2000a), in which the large interpterygoid vacuities which are otherwise ubiquitous among derived ichthyosaurs are almost entirely reduced. The secondary reduction of the interpterygoid vacuity can therefore be postulated as a fifth potential leptonectid synapomorphy, apart from those listed by Maisch (1998b); and Maisch and Matzke (2000a). In contrast to *Leptonectes,* the vomer extends very far posteriorly in *Eurhinosaurus*, however

(Maisch and Matzke, 2000a). That nothing of the vomer is seen in the present specimen therefore constitutes a potential important difference in the construction of the palate between the two leptonectid genera. The posterior portion of the pterygoid is characterised by an unusually extensive ascending lamina, which forms a tight sutural contact with the supratemporal. This very large ascending flange is also found in *E. longirostris*, where the contact with the supratemporal is particularly tight, and in *L.* cf. *tenuirostris* (Maisch and Matzke, 2003).

The mandibular elements are only seen in lateral and ventral view. The dentary is the largest of the mandibular bones, extending from the tip of the lower jaw to the first quarter of the orbit. Ventromedially it contacts the splenials, posteroventrally the angular and surangular. Each dentary bears a conspicuous fossa dentalis, which extends from the tip of the snout, where it is a hardly recognisable, narrow, shallow groove to the level of the external naris. It is deepest, widest and most strongly developed at about half the length of the dentary. There are about 25 teeth visible in the left dentary. Probably there were originally at least 40–50 dentary teeth.

The splenials are very extensive elements. They start about 75 mm posterior to the tip of the mandible, medially separating the dentaries. They form the larger part of the mandibular symphysis, which extends for about 165 mm. The two lower jaw rami diverge, being first only separated by a very narrow cleft which widens increasingly. At about mid-orbital level the two lower jaw rami are 40 mm apart, whereas at the posterior end of the mandible the distance is less than 80 mm. The posterior termination of the splenial is situated only about 20 mm in front of the end of the (slightly incomplete) lower jaw ramus on the right side.

The right angular is largely preserved, only its posteriormost, retroarticular portion is missing. It forms only a very narrow zone at the lower margin of the external lateral side of the mandible. At the posteriormost preserved end it slightly widens dorsally. Anteriorly it ends at the level of the posterior third of the external naris.

The surangular forms most of the external surface of the posterior third of the mandible. Its lateral surface is markedly convex. A deep and well-defined fossa surangularis extends from the posterior termination of the dentary backwards to the preserved posterior end of the mandible. Dorsal to it the surangular forms a marked ridge, which even slightly overhangs the fossa.

The teeth of the specimen are all quite similar in shape and morphology, regardless of their position in the jaws. They are all very narrow, pointed and slender with more or less straight crowns. The anteriormost teeth are, however, slightly smaller, with crowns of 4–5 mm in length, whereas the posterior dentary and maxillary teeth can have crowns of 5–6.5 mm in length. The widest crowns only measure 2 mm in diameter across their bases. The cross section of the tooth crowns is rounded, there are no carinae. The enamel, as far as it is preserved, is macroscopically smooth and does also not show any ridges at examination with a hand lens (magnification × 10), a typical, autapomorphic feature of the Leptonectidae.

The postcranium is mostly represented by an articulated portion of the posterior thoracal vertebral column (Fig. 3). A string of seven centra is preserved in natural articulation. A second series includes at least three vertebrae and a fourth which is incompletely prepared, they are also well articulated. In addition there are remains of at least three completely disarticulated centra.

All vertebrae which allow for identification of the rib facets are clearly from the posterior thoracal region. The rib facets are clearly subdivided into separate para- and diapophyses, which are situated low on the lateral vertebral surface. Their exact outline and position is unclear, due to damage to the bone surface. Nevertheless the parapophyses occupy a marginal position touching both the ventral and anterior rim of the vertebral centrum, whereas the diapophysis is clearly separated from the anterior margin and positioned at about mid-length of the centrum.

In addition to the centra there are remains of numerous thoracal neural arches. They possess low and rectangular neural spines and undivided and weakly developed pre- and post-zygapophyses.

The thoracal ribs of both sides of the body have retained their natural position to a remarkable extent, in contrast to the more dislocated vertebral elements. With a single exception only parts of the rib-shafts are preserved which are broken both anteriorly and posteriorly. One single well-preserved proximal end of a rib, the posteriormost preserved on the right side of the specimen, clearly shows two facets for articulation with the centrum, but is not distinctly subdivided into two articulatory heads.

Two complete and one fragmentary fin elements are preserved in articulation. The complete ones are ascribed to the first digit, as they have clearly defined notches along their anterior margins. They are too small to represent the radius, which is usually notched in *L. tenuirostris* (McGowan, 1974, 1989) whereas the rest of the phalanges of the forefin are rounded. Given that the radius was also notched as usually in leptonectids, It must thus be assumed, that the specimen had at least three notches along the leading edge of the forefin. A further difference to typical *L. tenuirostris* is that the phalanges that are not rounded, but angular and apparently have formed a tightly fitting polygonal pattern, at least in the proximal part of the fin.

5. Discussion and comparison with other specimens

The Swiss skull is clearly identifiable as a member of the ichthyosaur family Leptonectidae by the possession of the following diagnostic autapomorphies (Maisch, 1998b; Maisch and Matzke, 2000a): very large orbit, extremely slender and narrow, elongate snout, very small temporal fenestrae, teeth without a distinct surface sculpturing of the enamel.

The family Leptonectidae currently comprises two genera, *Leptonectes* McGowan, 1996 and *Eurhinosaurus* Abel, 1909.

Eurhinosaurus is characterised by the possession of a distinct overbite, i.e. an elongation of the upper jaw beyond the anterior end of the mandible. A slight overbite is also found as a variation in some of the English specimens of *L. tenuirostris* (McGowan, 1989), it is, however, never nearly as marked as in *Eurhinosaurus*. The Lower Liassic species *E. costini* (McGowan, 1986) from UK is characterised by a snout length which slightly exceeds the length of the entire mandible, which is never the case in *L. tenuirostris*. In the upper Liassic *E. longirostris* (Owen and Jaeger in Von Jaeger, 1856) the snout length exceeds the mandibular length by a factor of more than 1.5. Even though the Swiss specimen lacks the tip of the snout, it has a complete and well-developed mandible and there are probably only a few mm missing at the anterior end of the upper jaw. It is completely inconceivable that there was any marked overbite, and therefore the specimen not can be referred to *Eurhinosaurus*.

The genus *Leptonectes* currently comprises three valid species, *L. tenuirostris* (Conybeare, 1822), the type species, which is known from the uppermost Rhaetian to Lower Sinemurian of UK (McGowan, 1974, 1989) and the Lower Sinemurian of Southern Germany (Von Huene, 1922; Maisch, 1999), *L. solei* (McGowan, 1993) from the Lower to Upper Sinemurian of UK and *L. moorei* (McGowan and Milner, 1999) from the Lower Pliensbachian of UK.

L. solei is distinguished from the Swiss specimen by its much larger size (skull length exceeds 1000 mm) and much smaller orbit (orbital ratio 0.15 in the holotype). Judging from the skull alone, there is a slight possibility that *L. solei* represents only extremely large individuals of *L. tenuirostris*, but as there are also qualitative differences in the postcranial skeleton, such as the presacral vertebral counts and shape of the pelvic elements between the two species (McGowan, 1993), *L. solei* must be accepted as a valid taxon.

L. moorei, is stratigraphically closest to the Swiss specimen and differs by its very short snout from all other known leptonectids, which are usually characterised by extremely elongated rostra. The type and a single known specimen approaches the Swiss skull in entire length, which is only 328 mm (McGowan and Milner, 1999). The orbital diameter of 107.2 mm is also close to that observed in the Swiss specimen. However, snout length in *L. moorei* is only 194 mm compared to estimated 255 mm for the Swiss specimen. The snout ratio of *L. moorei* therefore is only 0.57, whereas the orbital ratio is 0.31, as compared to 0.64 and 0.28 in the Swiss specimen. However, the Swiss specimen is intermediate both in total size and regarding all relevant skull ratios between *L. moorei* and typical *L. tenuirostris*. Consequently, it is a possibility—which should not be ignored—that *L. moorei* is in fact only a juvenile *L. tenuirostris*, and that there was a considerable positive allometric growth of the snout and anterior end of the maxilla, and a negative allometry of the orbit in this species. However, additional material is required to resolve this question, and also the type of *L. moorei* needs to be described in more detail to make a qualitative osteological comparison between the nominal species of *Leptonectes* possible.

The skull measurements and ratios of the Swiss specimen, as compared to those given by McGowan (1974, 1989, 1993, 1996) for English specimens of *L. tenuirostris*, indicate a comparatively larger orbit and shorter snout in the present specimen than it is typical for *L. tenuirostris*. In fact the specimen slightly falls out of the most recent specific diagnosis provided by McGowan (1989). McGowan (1989: p. 415) states that the orbital ratio in *L. tenuirostris* is always lower than 0.25. He provides measurements for seven individuals (McGowan, 1996: pp. 442) which range between 0.18 and 0.24. In the Swiss specimen the orbital ratio is 0.28. The prenarial ratio in *L. tenuirostris* is typically larger than 0.56 (McGowan, 1989) with a range from 0.57 to 0.62 (McGowan, 1996, based on six specimens), compared to only 0.48 in the Swiss specimen. The preorbital (snout) ratio, typically larger than 0.70 (McGowan, 1989) and ranging between 0.71 and 0.76 (McGowan, 1996, based on seven specimens) is only 0.64 in the Swiss skull. Finally, the premaxillary ratio, usually larger than 0.48 in *L. tenuirostris* (McGowan, 1989) with a range between 0.47 and 0.54 (McGowan, 1996, based on five specimens) is 0.47 in the Swiss specimen and thus, the only one which falls into the range of variation known from English specimens of *L. tenuirostris*.

Reasons for these observed discrepancies are that the orbit is relatively larger, whereas the snout and the anterior extent of the maxilla are relatively shorter in the Swiss specimen.

However, the entire skull length of the Swiss specimen was only about 380 mm. The specimens from the English Lower Jurassic are usually considerably larger. McGowan (1993) listed nine specimens presumably including those which were used for the measurements provided in his 1996 paper (at least the measurements and ratios correspond and do not fall outside the range reported by McGowan, 1996). The range of skull lengths observed in these specimens are 530–950 mm, the average skull length is 631 mm, that is more than one third larger than the Swiss specimen.

It therefore appears plausible that the observed differences are due to ontogenetic variation rather than specific differences, particularly as there are no conspicuous osteological differences between the Swiss skull and the English specimens. It has long been known that the orbit shows a considerable negative allometry during ontogenetic growth in many ichthyosaurs. This has been documented for several taxa, and a positive allometry for the maxilla has also been documented (see e.g. McGowan, 1973, 1994) for several Jurassic ichthyosaurs. The data presented by McGowan (1996) do not indicate any specific allometric trends in the English specimens. These were, however, judging from their comparatively much larger skulls, probably all adults in which no clear allometries might be expected to be observable anymore.

Osteologically, as seen from the above description, the Swiss specimen matches in most observable aspects *L. tenuirostris* and, particularly, the specimen recently described by Maisch and Matzke (2003) as *L.* cf. *tenuirostris* from the Lower Lias of Lyme Regis. The slight differences encountered—extent of the prefrontal towards the naris, larger extent of the postfrontal, occurrence of notches in the forefin—might, if not merely individual or ontogenetic variations, be interpreted as the result of anagenetic morphological changes during the long time period which separates the Swiss specimen from the much older articulated skeletons from UK. It can not be completely ruled out, of course, that the Swiss specimen represents a distinct taxon. Nevertheless there is too little evidence in shape of potentially diagnostic morphological characters to differentiate the Swiss specimen from *L. tenuirostris*. Therefore based on the presently available data, the Swiss specimen can only be referred to *L. tenuirostris* (Conybeare, 1822), representing one of the smallest and most juvenile specimens of this taxon hitherto described.

One specimen which needs to be discussed in the present context is the incomplete skull of *Ichthyosaurus numismalis* from unspecified Lower Pliensbachian strata (Lias gamma) of Kirchheim/Teck in Württemberg (deposited in the Staatliches Museum für Naturkunde, Stuttgart; SMNS 8501). It was referred to the genus *Leptopterygius* by Von Huene (1922) (found to be preoccupied and replaced by the name *Leptonectes* by McGowan, 1996) who pointed out the close resemblance to *L. tenuirostris*, which was also hinted at in the original description by Fraas (1892).

The specimen, which only comprises the posterior portion of the prenarial snout region and the corresponding segment of the mandible, belongs to a considerably larger individual than the Swiss specimen. The slender, elongate, completely unsculptured teeth are very reminiscent of those of *Leptonectes* and *Eurhinosaurus*. They show concentric thickenings of the enamel, which can also be observed in specimens of *E. longirostris* (pers. obs.). The maxilla extends considerably further anterior to the naris than in the Swiss specimen, as it is, however, also expectable for such a large specimen. The maxilla is very low and does not reach the external naris. The subnarial and supranarial processes of the premaxilla are extensive. The premaxilla is underlain by the lacrimal even beyond the anterior margin of the external naris, as it was recently observed by Maisch and Matzke in *I. communis* (Maisch and Matzke, 2000b), a feature which is therefore not characteristic of that species but probably quite widespread among basal neoichthyosaurs.

Osteologically a perfect agreement with other specimens of *L. tenuirostris* is found, and nothing speaks against a referral of *L. numismalis* to that species. Fraas (1892) only recognised the specimen as a new species because of its different stratigraphic occurrence (in the Lower Pliensbachian “Numismalismergel”, named after the terebratulid brachiopod *Cincta numismalis*). With the discovery of the Swiss specimen of *L. tenuirostris* in the Upper Pliensbachian this doubtful argument has been entirely invalidated. *I. numismalis* Fraas, 1892 is therefore herewith referred to *L. tenuirostris* (Conybeare, 1822) as a junior subjective synonym.

6. Conclusions

The specimen of *L. tenuirostris* described above is a very remarkable find for a variety of reasons. First, it is one of the best preserved and most complete three-dimensionally preserved skulls of the ichthyosaur family Leptonectidae and reveals a wealth of additional detail on the osteology of the cranial skeleton of these basal neoichthyosaurs.

Furthermore, it is the first record of the genus and species from Switzerland. In fact, only few specimens of leptonectids have ever been discovered outside UK in strata older than the Lower Toarcian, and of these the Swiss specimen is certainly the best and most completely preserved one.

The geological age of the Hauenstein skull, which was found in Upper Pliensbachian strata that can be assigned to the *margaritatus* Zone, is of particular interest. Not only is it the first substantial ichthyosaur find from the Pliensbachian of Switzerland, but also one of the few diagnostic Pliensbachian ichthyosaur specimens worldwide. It is the only well-preserved, diagnostic ichthyosaur skull specimen from the Upper Pliensbachian known so far from anywhere in the world.

The species *L. tenuirostris* has its first occurrence in beds of Rhaetian age (pre-*planorbis* beds) of Southern UK (McGowan, 1974, 1989). The stratigraphically youngest record so far, the specific assignment of which remains doubtful, was a partial forefin from the Lower Pliensbachian of Belgium (Godefroit, 1992). The new specimen clearly demonstrates that the stratigraphic range of *L. tenuirostris* includes most of the Pliensbachian. With specimens now known from the Uppermost Triassic to the *margaritatus* Zone, *L. tenirostris* is the most long-lived of all post-Triassic ichthyosaur species. It is only rivalled by the Triassic form *Phalarodon nordenskioeldii* in this respect, which extends from the Spathian to the Upper Ladinian. As the taxonomy of this species is still in need of further clarification, its very long range must, however, be viewed with caution.

The Swiss specimen of *L. tenuirostris* is also unusual because of its small size and skull proportions which disagree with larger specimens of the same species, but can be explained by a positive allometric growth of the snout and a negative allometric growth of the eyes during ontogeny, phenomena which have been documented in other ichthyosaur taxa the ontogeny of which is better known. Extrapolation of the ontogenetic trends observed in *L. tenuirostris* makes it appear likely, that some species of the genus which are currently recognised as valid, such as *L. moorei* from the Lower Pliensbachian of UK, could be just based on ontogenetic variation, but a clarification of this problem remains outside the scope of this study.

Acknowledgements

S. Boll, I. Groebke, Ch.A. Meyer, H.-R. Rüegg, B. Thüring and W. Tschudin (Geologisch–Paläontologisches Institut, Basel) excavated the ichthyosaur specimen. The PCO Olten AG as well as the Kanton Solothurn gave the permission for excavation. The Lotterie-Fonds des Kantons Solothurn and the Naturmuseum Olten financially supported the preparation. That was arranged by P. Jordan (Solothurn), P.F. Flückiger (Olten) and Ch.A. Meyer (Basel) and carried out by the Geowissenschaftliches Atelier Gebrüder Imhof (Trimbach). R. Schlatter (Leipzig) kindly identified the ammonoids and E. Beher (Heidelberg) prepared and identified the ostracods. W. Gerber (Tübingen) photographed the material. The manuscript benefited from the critical comments of P. Dèzes (Basel), C. Klug

(Zürich), D. Korn (Berlin), K. Waite (Basel) and A. Wetzel (Basel). The thoughtful reviews by N. Bardet (Paris) and J.-M. Mazin (Lyon) helped much to improve the manuscript. This study was financially supported by the Schweizerischer Nationalfonds zur Förderung der wissenschaftlichen Forschung (project Nos. 2000-56640.99 to A. Wetzel) and Freiwillige Akademische Gesellschaft (Basel). Numerous colleagues helped searching information on ichthyosaur remains from Switzerland: J. Ayer (Neuchâtel), J.-P. Berger (Fribourg), D. Bernoulli (Basel), T. Bolinger (Olsberg), W. Brinkmann (Zürich), W. Brogli (Möhlin), T. Bürgin (St. Gallen), B.C. Neuhaus (Fribourg), P. Dèzes (Basel), A. Fasel (Fribourg), P. Favre (Liestal), M. Felber (Mórbio Inferiore), M. Feldmann (Glarus), R.F. Foelix (Aarau), H. Furrer (Zürich), H. Geisser (Thurgau), E. Gerber (Fribourg), K. Haldimann (Basel), H. Hartmann (Pratteln), S. Hinsken (Basel), E. Hofstetter (Bellikon), B. Hostettler (Glovelier), B. Hotz (Luzern), B. Imhof (Olten), T. Imhof (Olten), M.S. Jacquat (La Chaux-de-Fonds), M. Jäger (Dotternhausen), H.G. Jutzi (Schwerzenbach), F. Lörcher (Dotternhausen), B. Lüdi (Strengelbach); R. Marchant (Lausanne), U. Menkveld-Gfeller (Bern), R. Müller (Näfels), E. Müller-Merz (Solothurn), Ch. Obrist (Stein), J.-C. Praz (Sion), M. Rümbeli (Frick), H.-J. Siber (Aathal), C. Spörli (Wettingen), J. Stirnimann (Buchrain), R. Stockar (Lugano), I. Stoessel-Sittig (Schaffhausen), A. Tintori (Milano), P. Vögtli (Dietgen), M. Weick (Basel), M. Weidmann (Jongny) and K. Wettstein (Frick). All these contributions are gratefully acknowledged.

References

Abel, O., 1909. Cetaceenstudien. 1. Mitteilung: Das Skelett von *Eurhinodelphis cocheteuxi* aus dem Obermiozän von Antwerpen. Sitzungsberichte der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 118, 241–253.

Bitterli, P., 1960. Bituminous “Posidonienschiefer” of Mount Terri, Jura mountains. Bulletin der Vereinigung Schweizerische Petroleum-Geologen und Ingenieur(e) 26, 41–48.

De Blainville, H.M.D., 1835. Description de quelques espèces de la Californie, précédée de l’analyse d’un système général d’érpétologie et d’amphibiologie. Nouvelles Archives du Muséum d’Histoire Naturelle de Paris 4, 236–296.

Conybeare, W.D., 1822. Additional notes on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. Transactions of the Geological Society of London 1 (2), 103–123.

Eckardt, P., Labhart, T.P., Arnold, A., Gerber, M., Rück, P., Baumer, A., 1997. Festgesteine für Bauzwecke. In: Die mineralischen Rohstoffe der Schweiz (Ed. by Schweizerische Geotechnische Kommission). Schweizerische Geotechnische Kommission, Zürich, pp. 169–296.

von Fischer-Ooster, C., 1870. Über *Ichthyosaurus tenuirostris* (Conybeare) aus den Liasschichten am westlichen Fusse des Moléson in den Freiburger Alpen. In: Ooster, W.A., Von Fischer-Ooster, C. (Eds.), Protozoë Helvetica. H. Georg, Basel and Geneva, Bd. II, pp. 73–84.

Fraas, E., 1891. Die Ichthyosaurier der süddeutschen Trias- und Jura-Ablagerungen. Laupp, Tübingen 1–81.

Fraas, E., 1892. *Ichthyosaurus numismalis*. Jahreshefte des Vereins für Vaterlandische Naturkunde in Württemberg, Stuttgart 48, 22–31 (Stuttgart).

Furrer, H., 1960. Der Ichthyosaurus von Teysachaux. Mitteilungen der Naturforschenden Gesellschaft Bern, NF 18, 75–80.

Godefroit, P., 1992. Présence de *Leptopterygius tenuirostris* (Reptilia, Ichthyosauria) dans le Lias moyen de Lorraine belge. Bulletin de l’Institut Royal des Sciences Naturelles de Belgique 62, 163–170.

Godefroit, P., 1993. The skull of *Stenopterygius longifrons* (Owen, 1881). Revue de Paléobiologie 7, 67–84.

Godefroit, P., 1994. Les reptiles marins du Toarcien (Jurassique inférieur) belgo-luxembourgois. Mémoires pour servir à l’explication des cartes géologiques et minières de la Belgique 39, 1–98.

Goldschmid, H.O., 1965. Die Geologie des Faltenjura zwischen Olten und Unterem Hauenstein. Tätigkeitsbericht der Naturforschenden Gesellschaft Baselland 24, 15–91.

Von Huene, F., 1922. Die Ichthyosaurier des Lias und ihre Zusammenhänge. Gebrüder Borntraeger, Berlin 1–114.

Von Huene, F., 1931. Neue Ichthyosaurier aus Württemberg. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abhandlungen 65, 305–320.

Von Huene, F., 1939. Ein ganzes Ichthyosaurier-Skelett aus den westschweizerischen Voralpen. Mitteilungen der Naturforschenden Gesellschaft Bern 1939, 1–14.

Von Huene, F., 1948. Short review of the lower tetrapods. In: Du Toit, A. (Ed.), Royal Society of South Africa. Special Publications Robert Broom Commemorative Volume, Cape Town, pp. 65–106.

Hungerbühler, A., Sachs, S., 1996. Ein großer Ichthyosaurier aus dem Pliensbachium von Bielefeld. Neue Einblicke in die Ichthyosaurier des Mittleren Lias und das Gebiß von *Temnodontosaurus*. Bericht des Naturwissenschaftlichen Vereins Bielefeld und Umgegend, Bielefeld 37, 15–52.

Von Jaeger, G.F., 1856. Über eine neue Spezies von Ichthyosauren (*Ichthyosaurus longirostris* Owen et Jäger) nebst Bemerkungen über die übrigen in der Liasformation Württembergs aufgefundenen Reptilien. Nova Acta Academiae caesareae Leopoldino-Carolinae germanicae naturae curiosorum. Halle 25, 937–967.

Jordan, P., 1982. Der Lias zwischen Unterem Hauenstein und Schinznach (Solothurner und Aargauer Faltenjura). M.Sc. Thesis, University of Zürich (unpublished).

Jordan, P., 1983. Zur Stratigraphie des Lias zwischen Unterem Hauenstein und Schinznach (Solothurner und Aargauer Faltenjura). Eclogae geologicae Helvetiae 76, 355–379.

Knitter, H., Ohmert, W., 1983. Das Toarcium der Schwärze bei Badenweiler (Oberrheingebiet S Freiburg). Jahreshefte des Geologischen Landesamtes Baden-Württemberg 25, 233–281.

Knitter, H., Ohmert, W., 1986. Zur Pliensbachium/Toarcium-Grenze im Oberrheingebiet. Jahreshefte des Geologischen Landesamtes Baden-Würtemberg 28, 161–172.

Kuhn, O., 1939. Ein Ichthyosaurier aus dem oberen Lias gamma von Fallstein im nördlichen Harzvorland. Nova Acta Academiae caesareae Leopoldino-Carolinae N.F. Halle 7, 135–138.

Kuhn, O., Etter, W., 1994. Der Posidonienschiefer der Nordschweiz: Lithostratigraphie, Biostratigraphie und Fazies. Eclogae geologicae Helvetiae 87, 113–138.

Maisch, M.W., 1998a. Kurze Übersicht der Ichthyosaurier des Posidonienschiefers mit Bemerkungen zur Taxionomie der Stenopterygiidae und Temnodontosauridae. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 209, 401–431.

Maisch, M.W., 1998b. A new ichthyosaur genus from the Posidonia Shale (Lower Toarcian, Jurassic) of Holzmaden, SW-Germany with comments on the phylogeny of post-Triassic ichthyosaurs. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 209, 47–78.

Maisch, M.W., 1999. Leptonectiden und Temnodontosauriden aus dem Alpha-Ölschiefer (Sinemurium) von Baden-Württemberg (SW-Deutschland). Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1999 (8), 490–512.

Maisch, M.W., Ansorge, J., 2004. The Liassic ichthyosaur *Stenopterygius* cf. *S. quadriscissus* from the Lower Toarcian of Dobbertin (Northeastern Germany) and some considerations on Lower Toarcian marine reptile palaeobiogeography. Paläontologische Zeitschrift 78, 161–171.

Maisch, M.W., Hungerbühler, A., 1997. Revision of *Temnodontosaurus nuertingensis* (von Huene, 1931), a large ichthyosaur from the Lower Pliensbachian (Lower Jurassic) of Nürtingen, South Western Germany. Stuttgarter Beiträge zur Naturkunde B248, 1–11.

Maisch, M.W., Matzke, A.T., 2000a. The Ichthyosauria. Stuttgarter Beiträge zur Naturkunde B298, 1–159.

Maisch, M.W., Matzke, A.T., 2000b. New data on the cranial osteology of *Ichthyosaurus communis* Conybeare, 1822 (Ichthyosauria, Lower Jurassic). Geologica et Palaeontologica 34, 137–143.

Maisch, M.W., Matzke, A.T., 2003. The cranial osteology of the ichthyosaur *Leptonectes* cf. *tenuirostris* from the Lower Jurassic of England. Journal of Vertebrate Paleontology 23, 116–127.

Reisdorf, A.G., Maisch, M.W., Wetzel, A., in press. A huge Sinemurian Ichthyosaurus skull and its lithostratigraphic framework in northern Switzerland. Eclogae geologicae Helvetiae.

Martill, D.M., 1993. Soupy substrates: a medium for the exceptional preservation of Ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. Kaupia-Darmstädter Beiträge zur Naturgeschichte 2, 77–97.

Martill, D.M., 1985. The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. Philosophical Transactions of the Royal Society. London B 311, 155–166.

McGowan, C., 1973. Differential growth in three ichthyosaurs: *Ichthyosaurus communis*, *I. breviceps* and *Stenopterygius quadriscissus* (Reptilia, Ichthyosauria). Life Sciences Contributions, Royal Ontario Museum 93, 1–21.

McGowan, C., 1974. A revision of the latipinnate ichthyosaurs of the Lower Jurassic of England (Reptilia: Ichthyosauria). Life Sciences Contributions, Royal Ontario Museum 100, 1–30.

McGowan, C., 1976. The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. Canadian Journal of Earth Science 13, 668–683.

McGowan, C., 1978. Further evidence for the wide geographical distribution of ichthyosaur taxa (Reptilia: Ichthyosauria). Journal of Paleontology 52, 1155–1162.

McGowan, C., 1986. A putative ancestor for the swordfish-like ichthyosaur *Eurhinosaurus*. Nature 322, 454–455.

McGowan, C., 1989. *Leptopterygius tenuirostris* and other long-snouted ichthyosaurs from the English Lower Lias. Palaeontology 32, 409–427.

McGowan, C., 1993. A new species of large, long-snouted ichthyosaur from the English lower Lias. Canadian Journal of Earth Science 30, 1197–1204.

McGowan, C., 1994. *Temnodontosaurus risor* is a juvenile of *T. platyodon* (Reptilia: Ichthyosauria). Journal of Vertebrate Paleontology 14, 472–479.

McGowan, C., 1996. The taxonomic status of *Leptopterygius* Huene, 1922 (Reptilia, Ichthyosauria). Canadian Journal of Earth Science 33, 439–443.

McGowan, C., Milner, A.C., 1999. A new Pliensbachian ichthyosaur from Dorset, England. Palaeontology 42, 761–768.

Meyer, C.A., Furrer, H., 1995. Taphonomie und paläoökologische Rekonstruktionen: Beispiele aus dem Mesozoikum des Jura. Eclogae geologicae Helvetiae 88, 711–720.

Moesch, C., 1867. Der Aargauer Jura und die nördlichen Gebiete des Kantons Zürich. Beiträge zur Geologischern Karte Schweiz 4, 1–319.

Motani, R., 1999. Phylogeny of the Ichthyopterygia. Journal of Vertebrate Paleontology 19, 473–496.

Mumenthaler, T., Meyer, C., Sigg, J., 1997. Rohstoffe für die Ziegelindustrie. In: Die mineralischen Rohstoffe der Schweiz (Ed. by Schweizerische Geotechnische Kommission). Schweizerische Geotechnische Kommission, Zürich, pp. 23–63.

Owen, R., 1881. Monograph on the fossil Reptilia of the Liassic Formations. Part 3. Ichthyopterygia. Monograph of the Palaeontographical Society London 35, 83–134.

Peters, T.J., 1964. Tonmineralogische Untersuchungen an einem Keuper-Lias-Profil im Schweizer Jura (Frick). Schweizerische Mineralogische und Petrographische Mitteilungen 44, 1–30.

Peyer, B., Koechlin, E., 1934. Ein Saurierwirbel aus dem Terrain à chailles von Grellingen (Berner Jura). Verhandlungen der Naturforschenden Gesellschaft in Basel 45, 68–77.

Reisdorf, A., 2001. Neue Lias-Profile entlang der Transitgasleitung der TRG 3: Wirbligen (BL) und Titterten (BL). In: Schmaedecke, M., Jordan, P.G. (Eds.), Ein Schnitt durch den Jura. Geologische und archäologische Aufschlüsse beim Bau der Transitgasleitung TRG 3. Archäologie und Museum, Berichte aus Archäologie und Kantonsmuseum Baselland. Liestal, pp. 43–48.

Rickenbach, E., 1947. Die Vorkommen von bituminösen Schiefern. Beiträge zur Geologie der Schweiz, Geotechnische Serie 26, 44–54.

Rieber, H., 1987. Lias und Dogger der Tongrube Unter Hauenstein der Portlandcementwerke AG Olten. In: Gygi, R., Rieber, H. (Eds.), Der Jura in der Nordschweiz DUGW. Stratigraphische Kommission, Subkommission für Jura-Stratigraphie. Exkursionsführer, pp. 73–77.

Riegraf, W., 1985. Mikrofauna, Biostratigraphie und Fazies im unterem Toarcium Südwestdeutschlands und Vergleiche mit benachbarten Gebieten. Tübinger Mikropaläontologische Mitteilungen 3, 1–232.

Rufli-Kornmann, S., 2001. Ein Jahrzehnt Sauriermuseum—Frick feierte. Basler Zeitung, Basel.

Sander, P.M., 2000. Ichthyosauria: their diversity, distribution and phylogeny. Paläontologische Zeitschrift 74, 1–35.

Sollas, W.J., 1916. The skull of *Ichthyosaurus* studied in serial sections. Philosophical Transactions of the Royal Society. London B 208, 63–126.

Streif, K., 24 Juni 1981. Bezirksschülerin fand Schädelfragmente eines Fischsauriers. Badener Tagblatt, Baden 43.

Weidmann, M., 1981. Un Ichtyosaure dans le Lias supérieur des Préalpes médianes vaudoises. Bulletin de la Société Vaudoise des Sciences Naturelles 75, 165–170.

Wetzel, A., Reisdorf, A.G., in press. Ichnofabrics elucidate the accumulation history of an condensed interval containing a vertically emplaced ichthysaur skull. In: Bromley et al. (Eds.), Ichnology at the Crossroads: A Multidimensional Approach to the Science of Organism–Substrate Interactions. SEPM Special Publication.

Wiedenmayer, F., 1963. Obere Trias bis mittlerer Lias zwischen Saltrio und Tremona (Lombardische Alpen). Die Wechselbeziehungen zwischen Stratigraphie, Sedimentologie und syngenetischer Tektonik. Eclogae geologicae Helvetiae 56, 529–640.