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Revision of the Bivalvia from the Upper Jurassic Reuchenette Formation, Northwest Switzerland—Ostreoidea

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Abstract

The current work is the first part of a taxonomic revision of the highly diverse Kimmeridgian bivalve fauna of the Reuchenette Formation of northwestern Switzerland (Canton Jura). It provides a taxonomic, paleoecologic and bibliographic review of the eight oyster species characterizing the northern Helvetic shelf: *Circunula* **n. gen.** *cotyledon* (Contejean, 1859) (Gryphaeidae, ?Pycnodonteinae), *Nanogyra* (*Nanogyra*) *nana* (J. Sowerby, 1822), *Nanogyra* (*Palaeogyra*) *reniformis* (Goldfuss, 1833), *Nanogyra* (*Palaeogyra*) *virgula* (Deshayes, 1831) (Gryphaeidae, Exogyrinae), *Helvetostrea* **n. gen.** *sequana* (Thurmann & Etallon, 1862) (Flemingostreidae, Crassostreinae), *Praeexogyra dubiensis* (Contejean, 1859), *Praeexogyra monsbeliardensis* (Contejean, 1859) (Flemingostreidae, Liostreinae), and *Actinostreon gregareum* (J. Sowerby, 1815) (Arctostreidae, Palaeolophinae).
The paper proposes two new genera: *Circunula* and *Helvetostrea*. *Palaeogyra* Mirkamalov, 1963, is considered a subgenus of *Nanogyra* Beurlen, 1958. Lectotypes are designated for six species: *C. cotyledon*, *Praeexogyra acuminata*, *P. dubiensis*, *P. monsbeliardensis*, *H. caprina*, *H. sequana*. The figured types of *H. oxfordiana* (Rollier, 1917) and *N. auricularis* (Münster in Goldfuss, 1833) are considered holotypes by monotypy. All types are refigured in drawings and/or photographs.

Early phases of shell ontogeny in general and the generic characters of *Praeexogyra* are revisited. Larval shells or their internal moulds are shown for six species: *N. nana*, *N. reniformis*, *N. virgula*, *N.* cf. *auricularis*, *Praeexogyra* cf. *sandalinoides* (de Loriol, 1901), and *Actinostreon marshii* (J. Sowerby, 1814). All of them are "*Crassostrea*"-like suggesting a planktic-planktotrophic mode of development. *Circunula* **n. gen.** shows a relatively high incidence of prosogyry (up to *ca.* 20% of studied specimens) during very early postlarval development. To a lesser extent, prosogyry has also been ob-

served in species of *Catinula, Praeexogyra* and *Pernostrea*. Chomata are typical of early ontogenetic stages of *Circunula* **n. gen.**, but they disappear during later growth stages.

Circunula **n. gen.** *cotyledon* is a typical early settler on hardgrounds but occurs also in subtidal soft-bottom environments attached to large shells. *Nanogyra* (*N.*) *nana* attached itself to all kinds of biogenous hard and soft substrates including algal stems and thalli. It is regularly found in calm to moderately energetic shallow marine paleoenvironments. *Nanogyra* (*P.*) *reniformis* frequently settled on the interior of empty bivalve shells. *Nanogyra* (*P.*) *virgula* was esentially a secondary soft-bottom dweller of shallow marine marls and lime muds. The species is often found concentrated in widely distributed (par)autochthonous lumachelles ("virgula marls" of authors) in the Upper Oxfordian, Upper Kimmeridgian and Tithonian. *Praeexogyra dubiensis* and *P. monsbeliardensis* occur in marly, shallow marine paleoenvironments. *Praeexogyra dubiensis* appears to have preferred attachment to small objects in a moderately energetic facies. In the study area it is also associated with algal meadows. *Praeexogyra monsbeliardensis* was preferentially gregarious in somewhat deeper and calmer paleoenvironments. The strongly chambered and probably fast growing *Helvetostrea* **n. gen.** *sequana* was adapted to moderate to high energetic shallow marine, marly habitats. It is frequently associated with corals and forms ostreoliths or small oyster buildups. *Actinostreon gregareum* usually lived gregariously but was also able to attach itself to algae on soft substrates. The species is known from calm marly to higher energetic coralline paleoenvironments.

Key words: taxonomy, paleoecology, revision, historical review, *Circunula* **n. gen.**, *Helvetostrea* **n. gen.**, Kimmeridgian

Introduction

The Swiss and adjacent French Jura Mountain Chain represents a historical region for Jurassic paleontological and geological research as is well reflected by publications of Agassiz (1840, 1842–1845), Contejean (1859), J.-B. Greppin (1870), É. Greppin (1893), Etallon (1860, 1862, 1863), de Loriol (1886–1888, 1892, 1895, 1896, 1897), Rollier (1911–1917), Thurmann (1832, 1836, 1837, 1849, 1851, 1852a, b, 1857), and Thurmann & Etallon (1861–1864). Studies in the Ajoie region of the Swiss Canton Jura are invariably linked to Jules Thurmann (1805–1855), who worked as a professor for mathematics and natural sciences at the college in Porrentruy (Ajoie, Canton Jura) and from 1837 to 1843 as headmaster of the "École Cantonale de Porrentruy". His contributions include the first consistent subdivision of the Jurassic strata of northwestern Switzerland with detailed lists of their characteristic fossils in the surroundings of his hometown Porrentruy. He also introduced the name "Kimméridgien" as a stage of his "Groupe Portlandien" (Thurmann 1832) following the English "Kimmeridge Clay" and French "Marnes kimmeridiennes". His probably most famous work, the well-illustrated "Lethea Bruntrutana", however, was finished and published posthumously by M. A. Etallon in three volumes (see Thurmann & Etallon 1861–1864). Charles Contejean (1859), who worked on the Upper Jurassic in the adjoining region of Montbéliard, Département Doubs, of the French Jura, adopted many of the manuscript names used by Thurmann and Thurmann & Etallon.

Unfortunately, a part of the studied material including several types figured in Thurmann and Etallon (1861–1864) became lost in the course of time, inhibiting a thorough review of the old bivalve collections. In the past decade, however, constructional work on the Transjurane highway in the Swiss Canton Jura uncovered numerous fossil-rich temporary outcrops of Oxfordian to Kimmeridgian age (157 to 152 Ma; see Gradstein *et al.* 2004). Since then, the research group "Paléontologie A 16" (PAL A16) and collaborating scientists unearthed many thousand invertebrate specimens (mainly bivalves, gastropods, cephalopods, brachiopods, corals, echinoderms) as well as large numbers of vertebrate remains, including two disarticulated skeletons and isolated bones and teeth of crocodiles, 90 more or less complete carapaces of large turtles (Anquetin *et al*. 2014; Billon-Bruyat 2005a; Püntener *et al*. 2014), a non-pterodactyloid pterosaur (Billon-Bruyat 2005b), fishes, and numerous spectacular dinosaur track sites (Marty *et al.* 2007; Marty 2008).

So far, the main focus of the research group lay on the discovery and investigation of the vertebrate faunas and dinosaur track sites (Marty 2008), ammonite biostratigraphy (Comment *et al*. 2011), and on invertebrate paleoecology, including initial studies of bivalves (Ayer *et al*. 2008; Heinze 2007; Hicks 2006; Koppka 2009, 2010; Richardt 2006). The project of the present author foresees a comprehensive taxonomic revision of the bivalve fauna which represents the most abundant group comprising *ca.* 100 species represented by some ten thousand specimens) (see Koppka 2010 for a preliminary list of taxa).

This study deals with the Ostreoidea. Oysters represent a taxonomically challenging group owing to their notorious phenotypic plasticity combined with a relative sparseness of unique specific and generic characters, high

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APPENDIX

Tables 1–8: Species measurements.
Abbreviations. No. = inventory number; H = height, L = length, I = inflation or maximal upturning of the ventral margin; MC = Musée Cuvier Montbéliard; LT = lectotype; PL = paralectotype; 2V = bivalved specimen; LV = left valve; RV = right valve; o = opisthogyrate; p = prosogyrate orientation of the umbo (um.); Litho = lithology; ext. = exterior (lateral), int. = interior; Lst. = limestone; B. M. = Banné Marls; L. Virgula Marl = "Lower Virgula Marl" (bed 4500).

TABLE 1. *Circunula* **n. gen.** *cotyledon* (Contejean, 1859).

No.	shell	H	L	I	H/L	I/L	um.	attached to	Litho./facies
MC 27E105 LT	2V	5.2	4.3	1.1	1.21	0.26	o	*Trichites* ext.	Rang Marls
MC 27E105a PL	LV	2.6	3.1	0.4	0.84	0.13	o	*Circunula* (LT)	Rang Marls
MC 27E104 PL	RV	3.9	3.3	0.7	1.18	0.21	p?	unknown	Rang Marls
MC 27E108 PL	LV	7.5	6.2	1.8	1.21	0.29	o	hardground	Natica Lst.
VTT001-1196	2V	3.0	3.1	0.8	0.97	0.26	p	external mould	Banné Marls
VTT001-1546	RV	3.4	2.8	0.45	1.21	0.16	o	unknown	Banné Marls
VTT001-1615	2V	2.6	2.6	1.2	1.00	0.46	p	*Isognomon*	Banné Marls
VTT001-3215	2V	2.65	2.35	0.8	1.13	0.34	p	*Isognomon*	Banné Marls
VTT001-3238	2V	2.6	2.7	1.0	0.96	0.37	p	*Costigervillia*	Banné Marls
VTT001-3248	LV	3.0	2.7	1.35	1.11	0.5	o	*Costigervillia*	Banné Marls
VTT001-3262	2V	3.25	3.1	0.7	1.05	0.23	o	*Ceratomya*	Banné Marls
VTT006-112	RV	5.9	6.6	0.9	0.89	0.14	o	unknown	Banné Marls
VTT006-863	RV	4.9	5.1	0.6	0.96	0.12	o	*Isognomon*	bed 70, B. M.
CRA001-25	LV	3.7	3.9	1.1	0.95	0.28	o	*Isognomon*	Banné Marls
CHS009-4	LV	5.1	5.3	0.3	0.96	0.06	o	hardground	base Banné M.
SCR002-1049	LV	6.7	6.3	0.8	1.06	0.13	o	hardground	layer 2000
SCR003-1599	LV	5.8	6	0.95	0.97	0.16	o?	hardground	layer 2000
ALO009-1-I	LV	1.4	1.1	0.1	1.27	0.09	o	*Trichites* int.	Banné Marls
ALO009-1-II	LV	1.4	1.2	0.1	1.27	0.08	p	*Trichites* int.	Banné Marls
ALO009-1-III	LV	3.2	3.3	0.15	0.97	0.05	o	*Trichites* int.	Banné Marls
ALO009-1-IV	LV	1.75	1.6	0.12	1.1	0.08	p	*Trichites* int.	Banné Marls
ALO009-1-V	LV	1.1	1.3	0.1	0.85	0.09	o	*Trichites* int.	Banné Marls