

ZOOTAXA

3927

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

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Table of contents

Abstract	3
Introduction	4
Material	5
Methods	6
Bibliography	7
Taxonomy	14
Classification outline	14
Order Ostreida Féruccac, 1822	15
Superfamily Ostreoidea Rafinesque, 1815	15
Family Gryphaeidae Vialov, 1936	15
Subfamily ?Pycnodontinae Stenzel, 1959	15
Genus <i>Circunula</i> new genus	15
<i>Circunula</i> n. gen. <i>cotyledon</i> (Contejean, 1859)	16
Subfamily Exogyrinae Vialov, 1936	22
Tribe Nanogyrini Malchus, 1990	22
Genus <i>Nanogyra</i> Beurlen, 1958	22
Subgenus <i>Nanogyra</i> (<i>Nanogyra</i>) Beurlen, 1958	22
<i>Nanogyra</i> (<i>Nanogyra</i>) <i>nana</i> (J. Sowerby, 1822)	22
Subgenus <i>Nanogyra</i> (<i>Palaeogyra</i>) Mirkamalov, 1963	29
<i>Nanogyra</i> (<i>Palaeogyra</i>) <i>reniformis</i> (Goldfuss, 1833)	29
<i>Nanogyra</i> (<i>Palaeogyra</i>) <i>virgula</i> (Deshayes, 1831)	32
Family Flemingostreidae Stenzel, 1971	36
Subfamily Crassostreinae Scarlato & Starobogatov, 1979	36
Genus <i>Helvetostrea</i> new genus	36
<i>Helvetostrea</i> n. gen. <i>sequana</i> (Thurmann & Etallon, 1862)	36
Subfamily Liostreinae Vialov, 1983	42
Genus <i>Praeexogyra</i> Charles & Maubeuge, 1953	42
<i>Praeexogyra dubiensis</i> (Contejean, 1859)	44
<i>Praeexogyra monsbeliardensis</i> (Contejean, 1859)	46
Family Arctostreidae Vialov, 1983	49
Subfamily Palaeolophinae Malchus, 1990	49
Genus <i>Actinostreon</i> Bayle, 1878	49
<i>Actinostreon gregareum</i> (J. Sowerby, 1815)	50
Acknowledgements	56
References	57
APPENDIX	70

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, ?Pycnodontinae), *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 essentially 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 “Kimmeridgien” 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 “Letheia 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

incidence of convergence (Malchus 1998, 2008; this study), and long species durations. In addition, Jurassic oysters most likely developed via planktonic larvae (Malchus 1995; Malchus & Sartori 2013; this study) resulting in a wide dispersal potential. Given these characteristics, the taxonomic revision of the Ajoie oysters takes a wide geographic approach embracing the interconnected facies belts of the Trans-European Late Jurassic carbonate platform systems (see Geologic setting, below). The study also includes extensive bibliographic research and provides numerous complete citations of monographs issued in many parts (as was typical of many important works of the 19th century), and a number of transliterations of Russian titles, which are not readily available from the current literature.

Material

“Paléontologie A16” (PAL A16) (Switzerland). Most of the examined material (8 species, with more than 4200 specimens) was collected during the excavations and prospection works of the PAL A16 research and is stored in Porrentruy, Switzerland. The best preserved and diverse oyster fauna is found in the Banné Marls (*cymodoce* Zone, Lower Kimmeridgian), of the locality Vâ Tche Tchâ near Courtedoux. Additional material comes from the boundary of the *mutabilis/eudoxus* Zones (Upper Kimmeridgian) around 30 m above the Banné Marls in the Courtedoux area.

Samples of the PAL A16 collection are coded alphanumerically, consisting of three letters for the municipality, three letters for the site, sampling year, and sample number (e.g., CTD-SCR009-1234 refers to Courtedoux – Sur Combe Ronde – 2009 – no.1234). Sample numbers may refer to more than one specimen.

“Jurassica” (Switzerland). “Jurassica” is the former Musée jurassien des Sciences Naturelles (MJSN) in Porrentruy, Switzerland, which originally hosted the types and topotypes of Thurmann & Etallon’s (1861–1864) “*Lethea bruntrutana*”. However, most of this material seems to be lost. Specimens of *Nanogyra* (*Palaeogyra*) *virgula* (Deshayes, 1831) from the “Lower Virgula Marl” of the Banné hill are figured herein (MJSN S294/1–11, Pl. 8.7–8; Pl. 9.1–8).

Musée Cuvier (MC) (France). The present material was compared with type material of Contejean (1859) from the Oxfordian and Kimmeridgian collected near Montbéliard, France, and currently hosted in the Musée Cuvier: *Ostrea cotyledon* Contejean, 1859 (MC-27-E-105, lectotype designated, Fig. 5.1–4 and paralectotypes MC 27E-105a, MC 27E-104, Fig. 5.4–7), and the Oxfordian *O. dubiensis* Contejean, 1859 (MC-27-E-112, lectotype designated and refigured, Fig. 17.1–7; paralectotypes MC-27-E-114, 116, see Pl. 15.1–2) and *O. monsbeliardensis* Contejean, 1859 (MC-27-E-141, lectotype designated and refigured, Fig. 19.1–5; paralectotypes, see Pl. 14.1a,b and Fig. 18.1–3). The museum also contains material from the collection Scheurer which was available for comparison and preparation.

Eidgenössische Technische Hochschule (ETH) (Switzerland). Additional species of *Helvetostrea* n. gen. from the Oxfordian were described by Rollier (1917). Photos of the type material were only available for *Ostrea caprina* Rollier, 1917 (refigured on Fig. 16.2–5) (ETH Zürich, lectotype designated Ve.S. 4563, refigured in Fig. 16.1, 6). For *Ostrea oxfordiana* Rollier, 1917, the original drawings are refigured (Fig. 16.7–9).

Staatliches Museum für Naturkunde Stuttgart (SMNS) (Germany). Middle Jurassic (Bathonian) specimens of *Catinula knorri* (Voltz, 1828) (SMNS 67691/1–5, Pl. 3.6, Pl. 4.2–3, 5–6), and Lower Jurassic (Hettangian) *Nanogyra auricularis* (Münster in Goldfuss, 1833)(b) (SMNS 67694/1, Pl. 10.2a–d).

Fondation paléontologique jurassienne (FPJ), Glovelier (Switzerland). One specimen of *Praeexogyra monsbeliardensis* (Contejean, 1859) from the Upper Jurassic (Kimmeridgian, FPJ Glov. 5.2.98 MB/3-60, Pl. 13.3) and a right valve of the rare species *Nanogyra* (*N.*) *rivelensis* (de Loriol, 1904) (de Loriol 1902–1904) from the Swiss Oxfordian (FPJ 750, Fig. 11.7–8) were made available by the “Fondation paléontologique jurassienne” (FPJ) in Glovelier (Switzerland), and as far as figured herein, will be stored in the “Naturhistorisches Museum Bern” (NMBE).

Personal collections. Material from the author’s personal collection is stored at the “Institut für Geographie und Geologie” of the Ernst-Moritz-Arndt University in Greifswald (Germany) (GG 382/1–5). It includes ?*Praeexogyra sandalinoides* (de Loriol, 1901) from the Callovian of Northern Germany (GG 382-1–2, Pl. 15.3a,b, 4a,b) and ?*P. aff. sandalina* (Goldfuss, 1833)(b) juvenile shell, GG 382-3, Pl. 6.5; GG 382-4, Pl. 10.3–4); *Actinostreon marshii* (J. Sowerby, 1814) from the Callovian (Middle Jurassic) of Lithuania, with one juvenile

specimen with preserved prodissoconch (GG 382-5, Pl. 19.4a–c, Fig. 9.4); and an adult specimen from the Rotkyte-collection of the Geological Institut in Vilnius (Nr. 2402, Pl. 19.3a,b).

Methods

Sample selection, treatment, and imaging. All size classes were considered in search of both invariant and ontogenetically changing shell characters. In a number of cases this included shells of 10 mm size or less which were cleaned by chemical treatment (see below). Shell microstructures of larger specimens were studied in thin sections, and spat that was occasionally found attached to larger shells was examined using a scanning electron microscope.

Sample preparation and imaging of microstructures and spat was carried out by N. Malchus at the Institut Català de Paleontologia Miquel Crusafont, in Bellaterra, Catalunya (Spain) (preparation and optical microscopy), and scanning electron microscopy (SEM) at the Central Microscopic survey of the Universitat Autònoma de Barcelona. Microstructures were examined with a Leica polarization microscope (DM2500P), equipped with a Leica DFC490 digital camera. For macrophotographic imaging, carried out at the PAL 16 facilities, specimens were whitened with ammonium chloride. Digital images were taken with a Nikon D300, MicroNikkor 60 mm, flash Elinchrom in collaboration with B. Migy (PAL A16). Detailed scientific illustrations were prepared by P. Roeschli (PAL A16) in cooperation with the author with discussion and explication of taxonomic important details (e.g., resilifer, chomata, adductor muscle imprints).

This study uses the geographic coordinate system WGS 84 (World Geodetic System), which is the reference coordinate system used by GPS. However, note that the original geographic descriptions of type localities were often imprecise in the 19th century.

Scanning electron microscopy. Juvenile samples of several specimens of *Nanogyra* (*N.*) *nana* (J. Sowerby, 1822), *Nanogyra* (*Palaeogyra*) *virgula* (Deshayes, 1831) and, for comparison, a RV of *Nanogyra* (*N.*) cf. *auricularis* (Münster in Goldfuss, 1833)(b) (for meaning of lower case letters see below, “Bibliography”) were studied with SEM to observe the ontogenetic development. The aragonitic prodissoconchs of the material from the Reuchenette Formation were not preserved, but the maximum size of imprints from the larval shells could be measured of some species.

Thin-sectioning. Specimens of larger species, *Circumula cotyledon*, *Helvetostrea sequana*, *Praeexogyra monsbeliardensis* and *Actinostreon gregareum* were chosen to examine shell microstructures. Shells were cut approximately in a dorsal-ventral direction, polished (grain size 800), mounted on a standard glass slide and then polished (grain size 1200) to ca. 45 µm thickness. Specimens were cleaned in a series of alcohol (70, 96 and 99%) for 45 seconds each, and then bathed in a solution of Histo-Clear I (15 minutes) and II (15 minutes). The slides were covered with DPX mounting medium and a cover slide. Shell microstructures were interpreted on the basis of Carter (1990), Malchus (1990), and Siewert (1972).

Etching. Mechanical preparation of fragile shells is problematic. However, the calcitic oyster shells are relatively resistant to chemical treatment by potassium hydroxide (KOH). Hence, small chippings of KOH were placed around the shell to soften the sediment matrix. After several hours the chemical reaction produces a caustic, gelatinous slime that is water-soluble for a short time after which it becomes insoluble and almost impossible to remove. The moist slime was brushed off under flowing water using a plastic brush and the process was repeated several times. After each etching step, the reaction was interrupted by leaving the fossil in a water bath for several hours. After final brush-cleaning, specimens were bathed in water for at least three days to stop the reaction. Otherwise the KOH within the shell fissures or voids is likely to destroy the shell, a process that may continue for years. The method provides a great potential to discover details of calcitic bivalve shells if the matrix is a marl and marly limestone; it is inadequate for pure limestones, however.

Terminology, abbreviations and synonymy list symbols. The morphological and microstructure terminology is adopted from Carter (1990), Carter *et al.* (2012), Malchus (1990), and Stenzel (1971). The following abbreviations are used in the text and Table 1:

CCF: complex cross foliated shell microstructure.

H: shell height.

hc: hollow shell chambers.

I: shell inflation (convexity).

L: shell length.

LV: left valve.

PAM: posterior adductor muscle scar.

RF: regular foliated shell microstructure.

RV: right valve.

SP: simple prismatic, outermost shell layer, better developed in RV, often absent in LV.

Symbols used in synonymy lists:

*: marks the type species.

v (vidi): refers to material the author has studied personally.

n (non): indicates material that is here regarded as incorrectly attributed to a given species.

?: indicates doubts concerning the determination of a species or generic assignment.

Bibliography

The most important bibliographic source for the present project was the Mesozoic Bivalve Catalogue “Bivmes” housed at the “Fachgruppe Paläoumwelt, Geozentrum Nordbayern” of the University of Erlangen-Nürnberg. The author used the catalogue during a two weeks research visit to Erlangen in 2010. “Bivmes” was compiled by Prof. F. T. Fürsich and Dr. W. Werner over several decades. It consists of a non-digitized, alphabetically sorted card-file catalogue of nearly all figured Jurassic bivalves available from several thousand publications. Each file card is dedicated to a single species in its original spelling, with copies of the figured specimens, citation of pages and figures (checked for correctness), stratigraphy, age, brief geographic remarks, and references to revisions. For transliterations of cyrillic letters see under references “Cyrillan alphabet (2014)”.

A number of older reference works published over a longer time span are here cited as cumulative references. They are currently difficult to get hold of and are thought to provide a better means to pin down and find original taxonomic references. In order to avoid lengthy authorship citations, however, the following list shows the abbreviated forms as used in the text followed by the cumulative reference (as cited in the references). Subdivisions into a, b , c (etc.) have been introduced here and are not authoritative.

Goldfuss, 1833(b)—see Goldfuss (1826–1844).

J. Sowerby, 1814 [1815, 1816, 1819, 1822, respectively]—see Sowerby, J. (1812–1822).

J. de C. Sowerby, 1824 [1825, 1840a,b, respectively]—see Sowerby, J. de C. (1822–1846).

Münster in Goldfuss, 1833(b)—see Goldfuss (1826–1844).

Quenstedt 1851(b)—see Quenstedt (1851–1852).

Quenstedt 1857(b)—see Quenstedt (1856–1857).

Quenstedt 1884—see Quenstedt (1882–1885).

Roemer 1835 [1836, respectively]—see Roemer, F.A. (1835–1839).

Rollier 1915 [1917, respectively]—see Rollier (1911–1917).

Thurman & Etallon 1861 [1862, 1864, respect.)]—see Thurmann & Etallon (1861–1864).

Thurmann in Thurmann & Etallon—see Thurmann & Etallon (1861–1864).

Geologic setting. Kimmeridgian paleogeography, climate and environment. At the time when the sediments of the Upper Jurassic Reuchenette Formation were deposited, the Earth’s climate was several degrees warmer than today. Polar ice caps were small or lacking (Price 1999; Brigaud *et al.* 2008; see also Lécuyer *et al.* 2003; Malchus & Steuber 2002). Western Europe was largely covered by a shallow epicontinental sea bounded in the South by the Tethys Ocean and the Valais and Briançonnais troughs (Fig. 1). South-central Western Europe lay in a subtropical climate belt around 27° northern paleolatitude (Frakes *et al.* 1992; Thierry *et al.* 2000) favouring the establishment of a broad, structurally complex system of carbonate platforms that extended from the southeastern Paris Basin to the Ligurian Tethys in the South (Marty 2008) and into the southern German Jura sea to the East (Fig. 1).

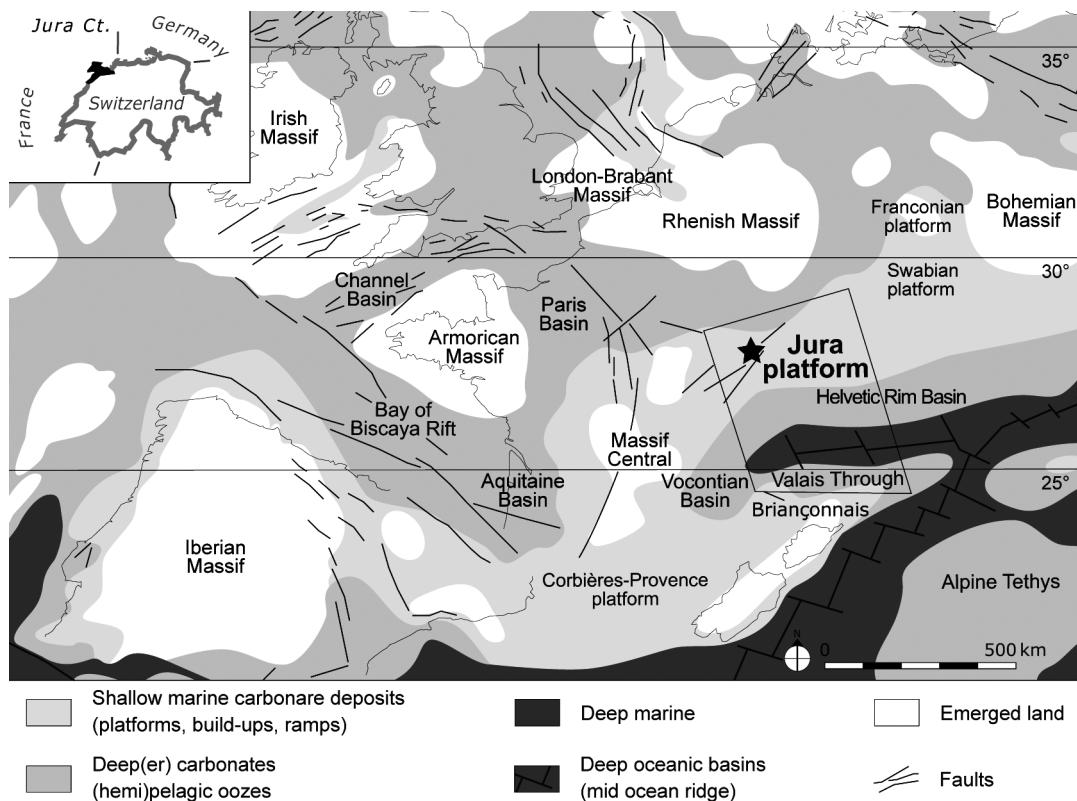


FIGURE 1. Paleogeography of the Jura carbonate platform in the Kimmeridgian (Upper Jurassic). Modified after Marty (2008); Thierry *et al.* (2000) and Thierry & Barrier *et al.* (2000).

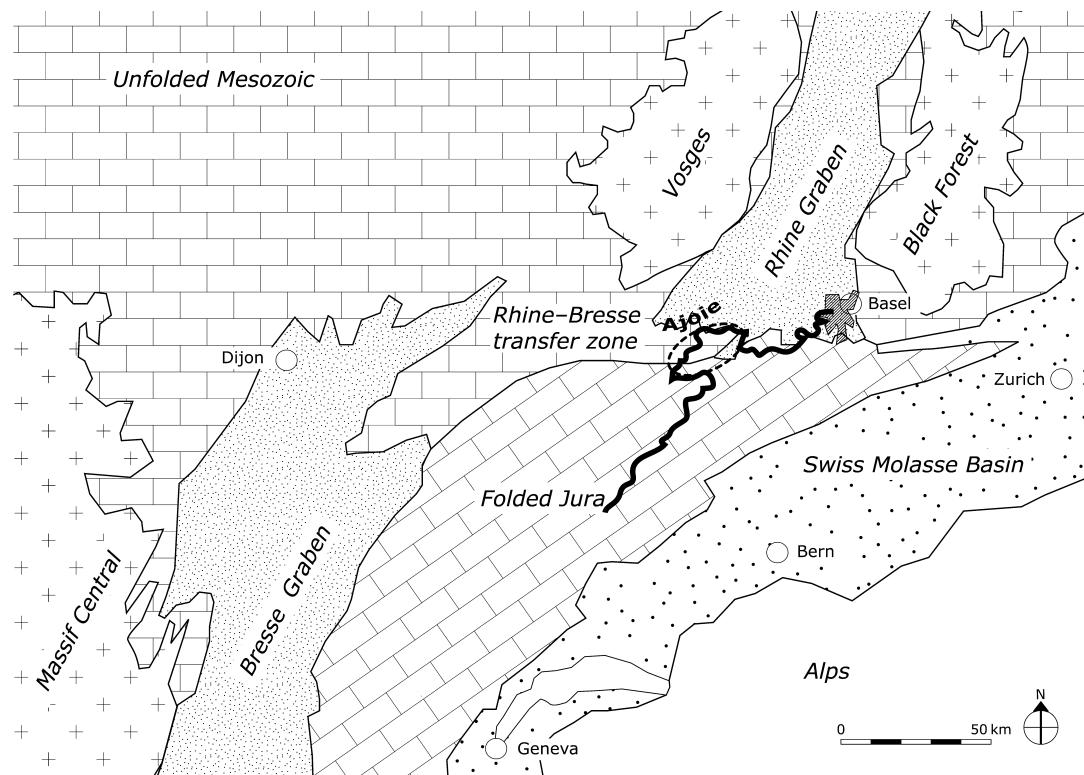


FIGURE 2. Geological setting of the Jura arc and the position of the Ajoie, Northwest Switzerland. Modified after Braillard (2006b) and Marty (2008).

The study area of the Ajoie region was located close to the northern central rim of a carbonate platform and ramp system. Owing to its paleogeographic position, the environment hosted a rich invertebrate fauna dominated by bivalves, associated corals, gastropods, echinoderms (Thurmann & Etallon 1861–1864; Waite *et al.* 2008), and vertebrates (turtles and marine crocodiles) (Anquetin *et al.* 2014; Billon-Bruyat 2005a; Marty & Billon-Bruyat 2004). The invertebrate fauna, especially the ammonites, show signs of tropical Tethyan as well as Boreal influences (Colombié & Ramail 2007, Jank *et al.* 2000a–c). The predominantly shallow-water limestones and marls were less suited for ammonites and local ammonite faunas show a strong provincialism which has so far hampered a complete biostratigraphic correlation with Kimmeridgian successions in France and Germany (*cf.* Colombié 2002; Colombié & Ramail 2007; Comment *et al.* 2011; Gygi 2000a,b; Jank *et al.* 2006a,b,c; Marty & Hug 2004; Strasser 2007). Due to the shallow water environment, the sedimentary history reflects also minor sea level fluctuations which led to the formation of hardgrounds (Waite *et al.* 2010; see also Fig. 4), the preferred settling ground of some of the oyster species described here, and supratidal flats some of which with dinosaur tracks (Marty *et al.* 2003, 2007; Marty 2008).

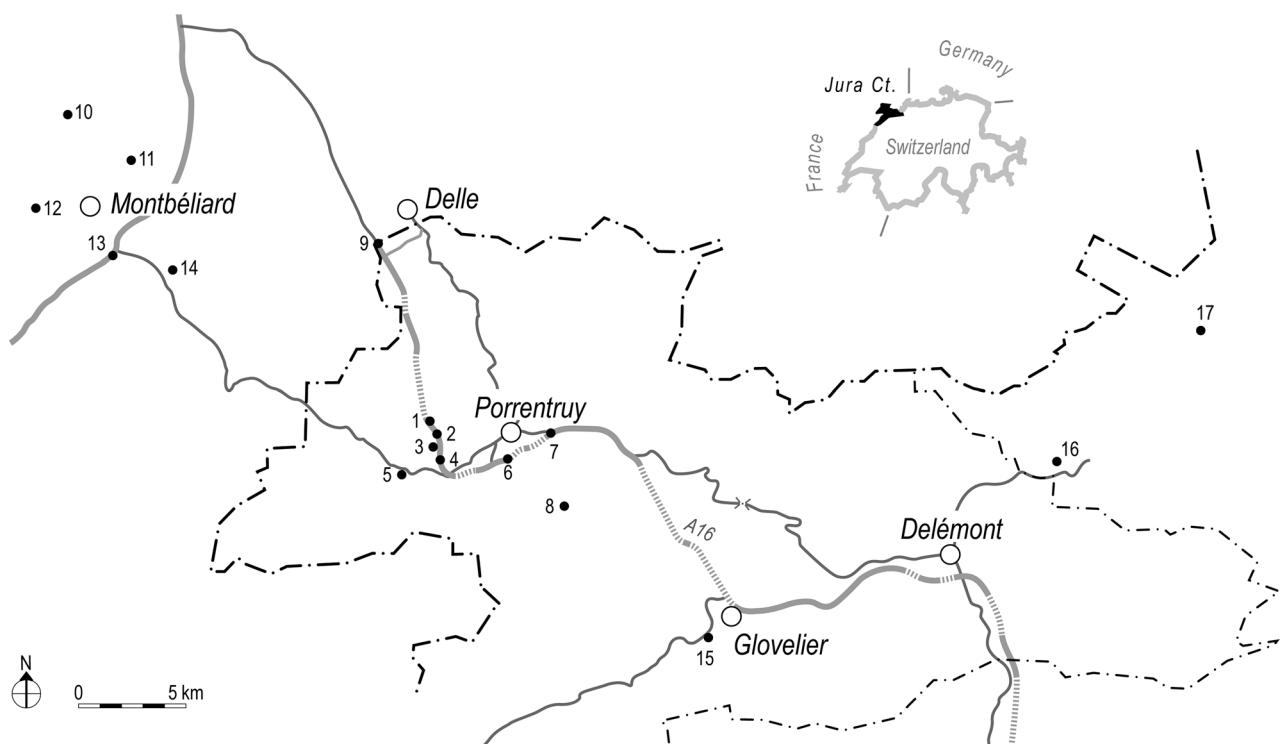


FIGURE 3. Map of locations in northwestern Switzerland and adjacent areas in France (region of Montbéliard). 1–9. Excavation sites of the Paleontologie A16 on the Transjurane highway (A 16) and nearby situated outcrops (Ajoie, Canton Jura, Switzerland): 1, Courtedoux–Vâ Tche Tchâ (CTD-VTT); 2, Courtedoux–Bois de Sylleux (CTD-BSY); 3, Courtedoux–Tchâfouè (CTD-TCH); 4, Courtedoux–Sur Combe Ronde (CTD-SCR); 5, Chevenez–La Scierie (CHE-CHS); 6, Porrentruy–Tunnel du Banné (POR-TLB, same position as the Banné hill); 7, Porrentruy–Cras d’Hermont (POR-CRA); 8, Courgenay–Alombre aux Vaches (CGN-ALO); 9, Boncourt–Queue au Loup (BON-QLP). 10–14. Localities of Contejean (1859) in the area of Montbéliard (Franche-Comté, France): 10, Bussurel close to Héricourt (Department Haute-Saône); 11, Beauregard near Châtenois-les-Forges (Department Territoire de Belfort); 12, Rôce in Sainte-Suzanne, Montbéliard (department Doubs); 13, Arbovans (Department Doubs); 14, La Baume in Audincourt (Department Doubs). 15–17. Swiss localities for compared material: 15, Glovelier (Canton Jura); 16, Liesberg, clay pit Andil (Canton of Basel-Country); 17, Blauen (Canton of Basel-Country).

Post-Jurassic development. The uppermost Kimmeridgian of the Reuchenette Formation was originally overlain by Tithonian sediments of the Twannbach Formation (Tithonian; type region north of the lake Biel; Thalmann 1966), which was mostly eroded during Cretaceous and Early Tertiary times (Jank 2006c). Owing to a commencing uplift and gentle, overall northward tilting of south-central Europe, the northern platform and its Mesozoic base began to break up into blocks separated by primarily SW-NE directed faults. This process was reinforced during the Oligocene when extensional tectonics along the Mediterranean-Mjösen continental rift zone

gave rise to the Rhine and Bresse Graben systems (Braillard 2006; Milanovsky 1972). The process was accompanied by N-S directed compression in the area, which forced the folding of the Folded Jura (“Jura plissé”) until Late Miocene (Braillard 2006a).

The plateau of the Ajoie is located at the eastern end of the Rhine-Bresse transfer zone, with the Vosges Mountains and the Upper Rhine Graben in the North and the Folded Jura Mountains of the district of Franches Montagnes to the South (Fig. 2). The Ajoie belongs almost entirely to the Tabular Jura and consists of slabs of subhorizontal Jurassic strata, separated by narrow dislocated belts as a result of Tertiary tectonics (Marty *et al.* 2007; Trümpy 1980). Parts of the Folded Jura (Mont Terri anticline) are over-thrust onto the Tabular Jura (Tschopp 1960) of the Ajoie region.

Today the Ajoie has a relatively flat morphology (mean elevation *ca.* 500 m) with characteristic dry valleys generated by fluvial erosion and karstic dissolution along faults (Braillard 2006a,b).

Litho- and biostratigraphy of the Reuchenette Formation. The Upper Jurassic in the study area is approximately 400m thick, the upper 180m of which belong to the Reuchenette Formation (Schneider 1960; Thalmann 1966; Tschopp 1960; Hantzpergue, pers. comm. 2014) of Early–Late Kimmeridgian age. Comment *et al.* (2011) provide the most recent review of formal stratigraphic subdivisions (Colombié & Ramail 2007; Gygi 1990, 1995, 2000a,b; Jank *et al.* 2006a–c; Marty 2008; Marty & Hug 2004; Strasser 2007; Waite *et al.* 2010).

Vabenau Member. The Vabenau Member is the lowermost stratigraphic unit of the Reuchenette Formation (Comment *et al.* 2011) dominated by light-coloured limestones of *ca.* 50 m thickness. It is more or less equivalent to the “Hypoptérocerien” of Thurmann (1852a) and “Hypostrombien” of Thurmann & Etallon (1861). A hardground known from several sections separates the Vabenau from the overlying Banné Member indicating a period of erosion (Fig. 4A).

Jank *et al.* (2006a–c) divided the member into “Thalassinoides Limestones”, “Nautilid Beds” (“Nautilidenschichten”) and “Lower Grey and White Limestones”. The ichnogenus *Thalassinoides* is usually related to burrowing activities of decapod crustaceans just below the sediment-water interface which become abundant from the Jurassic onwards. The Nautilid Beds contain large specimens of *Paracenoceras* sp. Rare co-occurring ammonites determined as *Lithacospinctes cf. janus* (Choffat) and *Physodoceras circumspinosum* (Oppel) suggest a Late Oxfordian (*planula* Zone, *galar* Subzone) or, more likely, an Early Kimmeridgian age (*rupellense* or *baylei* Zone) (Jank *et al.* 2006a,b; G. Schweigert 2010, pers. comm.). After recent work on ostracods (Schudack *et al.* 2013) and on ammonites, together with a correlation with the region Montbéliard by Hantzpergue (pers. comm. 2014), the unit belongs in the basal *cymodoce* Zone *sensu gallico* (Fig. 4A).

The pure limestone units of the Vabenau Member usually contain few bivalves, whereas the marly limestone intercalations in the Nautilid Beds are highly fossiliferous. This fauna (fossil lists in Schneider 1960, p. 9; Thurmann & Etallon 1861, p. 56) is similar to associations found in the Banné Marls. Among the bivalves only two oyster species, *Actinostreon gregareum* (J. Sowerby, 1815) and *Nanogyra nana* have been found in the “Nautilid Beds” and basal “Lower Grey and White Limestones” (Fig. 4A). The oyster *Gryphaea (Bilobissa) ermontiana* (Thurmann & Etallon, 1862) was described from this level, but no additional material was rediscovered until now. For taxonomic information see comparisons under *Helvetostrea n. gen. sequana* (Thurmann & Etallon, 1862).

Banné Member. The Banné Member (Gygi 2000a,b), named after the small hill Banné southeast of Porrentruy, is a widespread transgressive marl unit that reaches its maximum thickness of 12 m in the Porrentruy region (Fig. 4B, layers 70 to 1690). It is topped by the “Nerinean Limestones” (Jank *et al.* 2006a–c) of the Courtedoux Member without an apparent hiatus (Fig. 4B, layer 1700).

The marls near Courtedoux yielded some poorly preserved internal moulds of the ammonite genera *Rasenia*, *Rasenoides* and *Prorasenia* of the *cymodoce* Zone indicating an Early Kimmeridgian age (Comment *et al.* 2011; Jank *et al.* 2006a,b). The marls are also known in southwestern Switzerland in the Vallée de Joux (Canton Vaud, see Aubert 1943) and can be correlated with the French “Marnes de Rang” (Chevallier 1986, p. 145, fig. 61) which are distributed at least over 180 km in a NE–SW direction between Montbéliard (Franche-Comté) and Nantua (Rhône-Alpes).

Historically, the Banné Marls have been given numerous informal names such as “Marnes kimméridgiennes ou du Banné” (Marcou 1848, p. 104), “Marnes à ptérocerès” (Contejean 1859; Contini & Hantzpergue 1973), “Zone ptérocerienne” (Thurmann 1852a) or “Zone strombienne” (Thurmann & Etallon 1861–1864). These latter terms refer to the characteristic stromboid gastropod *Harpagodes thiriae* (Contejean, 1859), previously assigned to *Strombus* or *Pterocera* (sometimes misspelled as *Pteroceras*). This spiny gastropod is very common in the Banné Marls and a characteristic fossil in the Lower Kimmeridgian.

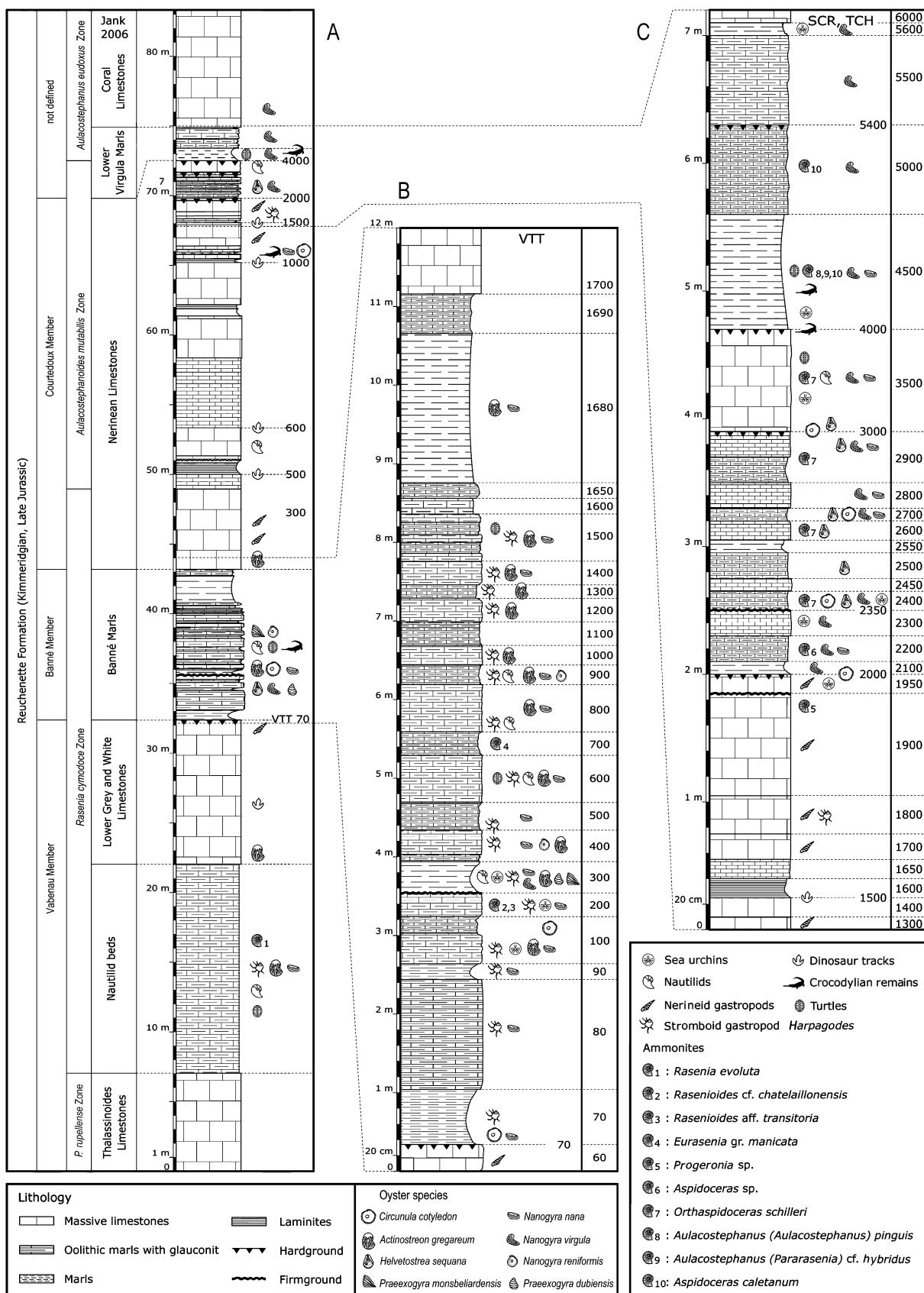


FIGURE 4. Litho- and biostratigraphy of the observed parts of the Reuchenette Formation in the Ajoie, with distribution of oysters and characteristic fossils. A. Synthetic section. B. Detailed section of the Banné Member in Vâ Tche Tchâ (VTT), Lower Kimmeridgian. C. Detailed section of the upper part of the Courtedoux Member and “Lower Virgula Marl”; based on Tchâfouè (TCH) and Sur Combe Ronde (SCR), Upper Kimmeridgian (note separate bed numeration for VTT and SCR/TCH).

The Banné Member contains the highest diversity of bivalve taxa (*ca.* 80 species) in the study area including all oysters described here.

Courtedoux Member. The Courtedoux Member (Comment *et al.* 2011)—“Epiptérocérien” of Thurmann (1852a) and “Epistrombien” of Thurmann & Etallon (1861)—consists for most of its succession of limestones with mass accumulations of nerineoidean gastropods (*Cossmannea*, *Ptygmatis*, *Cryptoplacus*) that are intercalated with sublaminated limestones with dinosaur tracks (Marty 2008). Overall, the member reaches approximately 30–35 m in thickness.

The “Nerinean Limestones” of Jank *et al.* (2006a–c) are equivalent to the entire Courtedoux Member, and the limestones yielding nerineoidean gastropods correspond closely with the “Calcaires à *Corbis*” of Contejean (1859) in the Montbéliard region (France). Both are characterized by the frequent occurrence of the lucinid bivalve *Fimbria subclathrata* (Buvignier, 1843) (= *Corbis* of the old literature) and rare finds of the stromboid gastropod *Harpagodes* (own observations in Sur Combe Ronde, layers 1800–1950). This unit is cut off by a limonitic hardground (Fig. 4A, C, layer 2000) with signs of paleokarstic weathering and deep borings of the ichnogenus *Trypanites* suggesting a transgression onto a former land surface (Cole & Palmer 1999; Waite, 2008; Waite *et al.* 2010).

The Nerinean Limestones in their strict sense probably represent a shallow, lagoonal to high-energy tidal flat facies which is almost barren of ammonites and oysters, except for *Actinostreon* at the base and few *Nanogyra* (*N.*) *nana* in its top. However, the uppermost portion between layers 1900 and 1950 (Fig. 4C) contained a specimen of the ammonite *Progeronia* sp. (Hantzpergue, pers. comm. 2014) indicative of the Lower Kimmeridgian *cymodoce* Zone (Scherzinger & Schweigert, pers. comm. 2011) as the “Calcaires à *Corbis*” in Montbéliard (Contini & Hantzpergue 1973, p. 144) or, more likely, the Upper Kimmeridgian *mutabilis* Zone (= *acanthicum* Zone) (Comment *et al.* 2011; Jank *et al.* 2006a–c; Hantzpergue, pers. comm. 2014).

The hardground layer 2000 itself is colonized by large *Circunula* **n. gen.** *cotyledon*, *Nanogyra* (*P.*) *virgula*, and cemented *Eopecten velatus* (Goldfuss, 1833)(b); this fauna actually belongs to the following transgressive unit. The final *ca.* 3 m of the Courtedoux Member—“Hypovirgulien inférieur” sensu Thurmann & Etallon (1861–1864) or “Calcaires à *Mactres*” sensu Contejean (1859)—consist of marls and marly limestones up to hardground layer 3000 with *Gastrochaenolites* borings. Several incursions of ammonites of the *Orthaspidoceras lallierianum-schilleri* group define the *lallierianum* Subzone (layers 2100–3500) of the upper *mutabilis* Zone (Fig. 4C, and ammonite legend).

The bivalve fauna of these horizons is diverse (particularly horizons 2300 and 3500) and is represented by numerous infaunal heterodont species and epifaunal oysters including mass accumulations of *Nanogyra* (*P.*) *virgula* (layer 2100) and the main appearance of *Helvetostrea* **n. gen.** *sequana* (layers 2400–2900, Fig. 4C). The dominance of *N. (P.) virgula* (Deshayes, 1831) was recognized previously; the term “Virgulien” in the original sense of Thurmann (1852, p. 216–217) refers to the shift from *N. nana* towards *N. (P.) virgula* as the most abundant oyster. Other bivalves belong to *Ceratomyopsis*, *Myophorella*, *Gervillella*, *Stegoconcha*, *Trichites*, *Myopholas*, *Pleuromya* among others (layers 2400, 2700, 2900). Another hardground (layer 3000) with *Circunula* **n. gen.** *cotyledon* and *Gastrochaenolites* borings is followed by limestones of the “*schilleri* horizon” (layer 3500) containing numerous *Orthaspidoceras schilleri*. These limestones are truncated by hardground layer 4000.

The marly units are open marine platform sediments with the highest abundance of ammonites in the Reuchenette Formation, nearly all belonging to the genus *Orthaspidoceras*.

“Lower Virgula Marl”. In the Ajoie region the Courtedoux Member is overlain by the “Lower Virgula Member” (sensu Strasser 2007, Fig. 2A) (= “Lower Virgula Marl” of Comment *et al.* 2011; and “Northern Virgula Marls” of Jank *et al.* 2006c). It contains a 1 m-thick brown marl rich in *Nanogyra* (*P.*) *virgula* (= “Virgula Marl” in the strict sense) and the overlying *ca.* 2.5–4 m thick massive limestones up to layer 7000 (present observations), which are also characterized by this oyster.

The Ajoie Virgula Beds belong to the *Aulacostephanus* (*Pararasenia*) *hybridus* horizon of the middle *eudoxus* Zone, but the ammonite co-occurs with *Aspidoceras caletanum* (Oppel), the index species of the following subzone (Hantzpergue 1989; Comment *et al.* 2011) (Fig. 4C). The “Lower Virgula Marl” can be correlated with the French “Calcaires et Marnes à Virgules inférieurs” of Contejean (1859) and parts of the “Hypovirgulien” sensu Thurmann & Etallon (1861–1864).

Nanogyra (*P.*) *virgula* is the dominant oyster species; *Nanogyra* (*N.*) *nana* co-occurs in much lower quantities. These marls also contain many more or less complete carapaces of turtles, numerous remains of crocodylians, and large branches of the wood *Protocupressinoxylon purbeckensis* Francis (Billon-Bruyat 2005a; Philippe *et al.* 2010).

Uppermost Reuchenette Formation. The lower Virgula Beds are followed by the yellowish to white “Coral Limestones” of Jank *et al.* (2006a–c). One single specimen of *Aulacostephanus eudoxus* (from the quarry Chevenez La Combe) is known from these beds. The relatively diverse fauna is characterized by several genera of mostly recrystallized corals. At Sur Combe Ronde, small specimens of *Actinostreon cf. gregareum* (J. Sowerby) occur with some abundance. This is the first record of this oyster genus above the Banné Marls. Other characteristic bivalves belong to *Spondylopecten*, *Ctenolima*, *Lithophaga*, *Barbatia*, and *Trigonia*. The rhynchonellid brachiopod *Torquirhynchia cf. speciosa* (Münster, 1839) appears to be restricted to this part of the whole section.

The coral-rich interval is overlain by more than 30 m of the poorly fossiliferous “Upper Grey and White Limestones” sensu Jank *et al.* (2006a–c). It is topped by the “Oyster Limestone” of Jank *et al.* (2006c). This marly sedimentary sequence which occurs *ca.* 50 m above the Lower Virgula Marl and which is well known from the quarry “Chevenez-La Combe” (Jank *et al.* 2006c for a section; fig. 5) was not exposed on the Transjurane highway. For that reason only sparse data about the fossil content are available. Some specimens of the ammonite *Aspidoceras caletanum* (Oppel, 1863) are known from the “Oyster Limestone” (= “Upper Virgula Marl” sensu Comment *et al.* 2011; “Zone Virgulienne” of Thurmann & Etallon 1861), indicating rapid sedimentation (Jank *et al.* 2006). This horizon contains the oysters *Nanogyra (P.) virgula* and *N. (N.) nana*.

The highest strata (“Epivirgulien” sensu Thurmann & Etallon 1861) of the Reuchenette Formation are nearly completely eroded in the Ajoie. Only a small area near Chevenez yielded two finds of *Aulacostephanus contejeani* (Thurmann & Etallon) and *Gravesia gigas* (Zieten), ammonites which indicating higher strata around the Kimmeridgian/Tithonian boundary (Comment *et al.* 2011; Hantzpergue, pers comm. 2014).

Taxonomy

Classification outline

Molecular phylogenetics seems to be the only method capable of providing some invariant anchor points to oyster systematics which necessarily needs to be interwoven with morphological data from both living and fossil taxa. Hence, the starting point for the current classification scheme is based on the most comprehensive molecular analyses currently available and complemented by the paleontological approach of Carter *et al.* (2011) (see Bieler *et al.* 2010 for an alternative view).

According to the genetic data of Giribet & Distel (2003, fig. 3.5) and Ó Foighil & Taylor (2000, figs. 2–5), Lophinae oysters appear either as a sister taxon to, or some species also nested within, Ostreinae rather than being basal to them. Hence, the two subfamilies form a crown group which is here synonymized with the Family Ostreidae.

Crassostreinae essentially form a sister taxon to this “restricted” family Ostreidae, and either a *Saccostrea* or a *Crassostrea* species appears at the base. Consistent in all analyses, Recent Gryphaeidae form the sister taxon of Ostreidae plus Crassostreinae, and the superfamily of Recent Ostreoidea appears very robustly as a monophylum: Gryphaeidae (Crassostreinae (Ostreinae, Lophinae)).

In the present context, these genetic results suggest that Mesozoic *Lopha*-like oysters, here represented by the Jurassic genus *Actinostreon*, are convergent to Recent Lophinae justifying the placement of these Mesozoic taxa outside Lophinae and outside Ostreidae, that is, in Arctostreidae Vialov, 1983 (Carter *et al.* 2011, p. 8; Malchus 1990) (see Hautmann 2001, for a contrasting view). In addition, as a consequence of excluding Crassostreinae from Ostreidae, this subfamily is included in the Family Flemingostreidae Stenzel, 1971 (Carter *et al.* 2011).

Indirectly, the genetic results also suggest that brooding evolved only once in Recent oysters, converting this character in a potential autapomorphy of the stem species of Ostreidae (see Ó Foighil & Taylor 2000, for anatomical arguments). The time when this happened cannot be ultimately fixed. However, current evidence from fossil larval shells hints towards the Tertiary (Eocene, Miocene) (Malchus & Sartori 2013, p. 78, 84, 86). All pertinent results from the present study are consistent with this view [e.g., Pl. 9.10c–e, Pl. 10.1–2 (*Nanogyra*), Pl. 6.5, 10.3a (*Praeexogyra*), Pl. 19.4a–d (*Actinostreon*)]. As of today, it appears therefore likely that none of the Jurassic *Ostrea*- or *Crassostrea*-like taxa belongs to the Ostreidae as defined above.

TABLE 1. Main shell features for the eight oyster species from the Swiss Reuchenette Formation. “Convex-concave” RV refers to the nomenclature of Malchus (1990) (see also Malchus & Aberhan 1998). Microstructure data refer to the left valve (LV) except for *Actinostreon* (LV+RV). The outermost simple prismatic (SP) or cross foliated (CF) shell layer are probably eroded in some species. Abbreviations see under “Methods: Terminology”.

Species	LV outline	LV convexity	LV sculpture	RV convexity	RV sculpture	Resilifer	Posterior	Chomata	Microstructure
<i>Circumla</i> n. gen.	round	low, ventral margin	dorsally with	weakly	faint radial	curved	round	only in	SP, RF, CCF
<i>cotyledon</i>	upturned	radial furrows	inflated	threads				juveniles	
<i>Nanogryra</i> (N.)	oval	capacious	smooth	convex-	commarginal	exogyrate	dorsally	absent	SP, RF
<i>nana</i>				concave	growth crests	biconcave			
<i>Nanogryra</i> (<i>P.</i>)	kidney	weakly inflated	smooth	flat, weakly	smooth, faint	exogyrate	round	present	RF, lenses?
<i>reniformis</i>				convex	radial threads				
<i>Nanogryra</i> (<i>P.</i>)	comma	capacious	numerous radial	convex-	faint radial	exogyrate	oval	present	RF, lamellar
<i>virgula</i>	drop	capacious	riblets	concave	threads			lenses	
<i>Praeexogyra</i>			commarginal	flat, ventrally	ventrally faint	trigonal,			
<i>dubiensis</i>			growth lines,	concave	radial threads	oblique	biconcave	absent	SP, RF
<i>Praeexogyra</i>	kidney	capacious	weak swellings	commarginal	faint radial	trigonal,	high-oval	absent	RF, CF
<i>monsbeliardensis</i>			swellings	concave	threads	oblique			
<i>Helveticostrea</i> n.	trapezoid,	capacious, thick	irregular growth	flat	unknown	ostreoid,			
gen. <i>sequama</i>	tube-like	shelled	squamae			massive		absent	RF, CCF, large
						bourelts		chambers	
<i>Actinostreon</i>	broadly	convex	plicae (5–35)	convex	plicae (5–35)	weakly	round,	present	RF, CCF,
<i>greagareum</i>	crescentic					convex	dorsally flat to		hollow
						(RV),	weakly		chambers (both
						massive	concave		valves)
							bourelts		

These "cornerstones" apart, the evolution of Jurassic oysters, especially the phylogenetic relationships between *Circunula* n. gen., *Helvetostrea* n. gen., *Praeexogyra*, and *Nanogyra* described herein and the true origin of *Liostrea*, *Catinula*, *Praeexogyra*, and *Crassostrea* remain a puzzle. Therefore, the presently proposed classification is necessarily tentative.

Important morphological features. Classical characters examined in this approach are shell shape, external ornament, phenotypic variation, coiling, muscle-scar shape and position, chomata, microstructure (e.g. Aqrabawi 1993; Carter & Malchus in Carter *et al.* 2011; Hautmann 2001; Malchus 1990, 1998; Stenzel 1971), and as far as possible the larval shell (Malchus 1995, 2000, 2004a; Malchus & Sartori 2013). For comparison of characteristic shell features of the Reuchenette oysters see Table 1.

It was found, however, that many of the postlarval characters, which are generally accepted as diagnostic at various taxonomic levels, can vary with age (size). Although strongly limited by taphonomy and diagenesis, the present approach thus tried to include even the smallest specimens of each species to capture information on their earliest shell stage characters. Some relevant examples are briefly circumscribed:

Coiling—Early postlarval growth in oysters is almost intrinsically anterior-directed helicoidal thus producing an opisthogyrate, or at least opisthocline umbo. This appears to be due to a delayed offset of the larval coiling tendency (Malchus 2000, p. 308, text-figs. 1–4; 2004a, p. 99, characters E to I; 2004b, p. 1546, text-figs. 3b, 8). However, offset and even radical changes in coiling direction may occur very early after metamorphosis. This is, for example, the case in an unusually large number of individuals of *Circunula* n. gen. *cotyledon* which are prosogyrate in early postlarval life. Another example is *Actinostreon gregareum* which is actually strongly exogyroid in earliest postlarval life (Pl. 16.6; Pl. 18.1b,c; Pl. 19.4a–d). But this potentially important feature is rarely preserved because the juvenile umbo becomes easily eroded. Generally speaking, later growth phases are mostly characterized by gradual changes in the degree of coiling rather than by radical re-orientation. Gradual changes may also be diagnostic, as discussed here for various species of *Nanogyra*. Coiling and changes of coiling direction also affect the orientation and width of the ligament area which are thus not independent diagnostic features (Malchus 2000, 2004a,b). These characters are often better visible in the free right valve (Fig. 9) than in the attached and often xenomorphic left valve.

Chomata—Malchus (1998) already mentioned that these denticle-like shell margin features of still unknown provenience (Malchus & Sartori 2013) may disappear during ontogeny. It is again *Circunula* n. gen. *cotyledon* providing a case in point where the character is deemed to be species (or genus) specific. Chomata also seem to leave antimarginal riblets on the shell exterior, at least in *Nanogyra* (*Palaeogyra*). Hence, the presence/absence of an apparently independent external ornamental feature may actually be linked to the onset/offset of an internal shell feature.

Posterior adductor scar—Juvenile imprints may have a different shape, orientation and position compared with their adult pendants. The posterior adductor of juvenile *Actinostreon gregareum*, for instance, leaves an “elongated” imprint (Pl. 18.3b) whereas that of the adult is round (Pl. 16.5b, 6a; Pl. 17.1b,c, 3b,c). In addition, the posterior border of the juvenile imprint corresponds to the ventral side of the adult adductor scar. It appears plausible to assume that this ontogenetic change largely corresponds to a rotational growth of the soft parts.

Order Ostreida Féruccac, 1822

Superfamily Ostreoidea Rafinesque, 1815

Family Gryphaeidae Vialov, 1936

Subfamily ?Pycnodonteinae Stenzel, 1959

Genus *Circunula* new genus

Type species. *Ostrea cotyledon* Contejean, 1859; lectotype (see under species); Lower Kimmeridgian, France and Switzerland.

Diagnosis. Strongly inequivalve and thin-shelled. Left valve (LV) weak capacious, with upturned ventral margin, right valve (RV) usually dorsally convex and ventrally concave, margins upturned. Outline circular or

suborbicular to oval, rarely subquadrate or subtriangular. Attachment area large (almost entire LV). Both valves smooth with fine concentric growth lines, RV with weak antimarginal riblets and occasionally with radial grooves and commarginal pustules. Antimarginal riblets or grooves restricted to attachment area of LV (rarely observable). Left valve lacks umbonal cavity. Posterior adductor scar posterodorsal, round (gryphaeate), deeply inserted. Juveniles with well-developed chomata on dorsal margin, lacking in later growth phases. Ontogenetic change of hinge morphology from triangular-ostreate to prosodetic twisted with a narrow, ventrally projected posterior bourrelet.

Microstructure of RV with outer shell layer of slightly reclined prisms, middle shell layer complex cross-foliated and thin low-angle (probably) regularly foliated structures; chambering absent; microstructure of LV not seen.

Etymology. Word combination derived from Latin *circulus* (= circle line), because of the characteristic round shape, and affix *-nula*, adopted from *Catinula*. The gender is female.

Remarks. The common oversight, especially in the older literature, of both chomata and coiling preferences of Jurassic oysters during early ontogenetic growth phases hampers comparisons with other taxa and evaluation of their taxon specificity, e.g., flexible coiling may be species-specific. However, none of the morphologically similar Jurassic genera as *Liostrea* (Liostreinae, Flemingostreidae), *Catinula*, *Deltoideum* and *Pernostrea* (Gryphaeinae, Gryphaeidae) develops chomata at any growth stage. This trait is considered generic, therefore, which warrants the separation of *Circunula n. gen.* from the taxa just mentioned. Furthermore, the other taxa do not share the preferred circular shape of *Circunula*. For example, *Pernostrea* has a spatulate outline, *Deltoideum* a strong pointed umbo associated with a concave posterodorsal margin, and *Liostrea*, which is also dorsally pointed, lacks radial riblets on its right valve. For species level comparisons see under *C. cotyledon*.

The phylogenetic position of the new genus is unclear, however. The presently tentative association with Pycnodonteinae is based on phenotypic similarities, including chomata, of *Circunula n. gen.* and small, largely attached pycnodonteine oysters (*Phygraea* Vialov, 1936, and *Labrostrea* Vialov, 1945) from the Upper Cretaceous (Nestler 1965; Cooper 1992). There is presently no evidence of a vesicular shell structure in *Circunula*, however.

Circunula n. gen. cotyledon (Contejean, 1859)

Figs. 5–8; Pls. 1–2; Pl. 3.1–5; Pl. 4.1, 4

- ? 1837 *Ostrea multiformis*, nobis. var. *orbicularis* Koch & Dunker: p. 45, pl. 5, fig. 11n (only).
- v * 1859 *Ostrea cotyledon*, Ctj. Contejean: p. 319, pl. 24, fig. 15–17.
- v 1861 *Ostrea cotyledon*, Ctj.—Thurmann & Etallon: p. 45, 53, 55, 56, 61, 66.
- 1862 *Ostrea cotyledon*, Ctj.—Etallon: p. 442.
- 1862 *Ostrea cotyledon*, Ctj.—Thurmann & Etallon: p. 271, pl. 39, fig. 2.
- 1867 *Ostrea cotyledon*, Ctj.—Greppin, J.-B.: p. 92.
- 1867 *Ostrea cotyledon*, Ctj.—Moesch: p. 200.
- 1870 *Ostrea cotyledon*, Ctj.—Greppin, J.-B.: p. 82, 104.
- 1872 *Ostrea cotyledon* Contejean—de Loriol, Royer & Tombeck: p. 406, pl. 24, fig. 2.
- 1880 *Ostrea cotyledon* Contej.—Struckmann: p. 62.
- 1882 *Ostrea multiformis* Dunk. et Koch—Alth: p. 296 (114), pl. 27 (10), fig. 20.
- 1890 *Ostrea cotyledon*, Ctj.—Mathey: p. 17.
- 1905 *Ostrea cotyledon* Contejean—Schmidt: p. 159.
- 1917 *Ostrea cotyledon* Contej.—Rollier: p. 590.
- 1963 *Liostrea cotyledon* Contej.—Pčelinčev & Lysenko: p. 133.
- 1971 *Liostrea cotyledon*—Pugaczewska: p. 198.
- v 1973 *Ostrea cotyledon* Ctj.—Contini & Hantzpergue: p. 175.
- v 2006 *Liostrea cotyledon*—Hicks: p. 36.
- v 2006 *Liostrea cotyledon* (Contejean 1859)—Richardt: p. 9, 18.

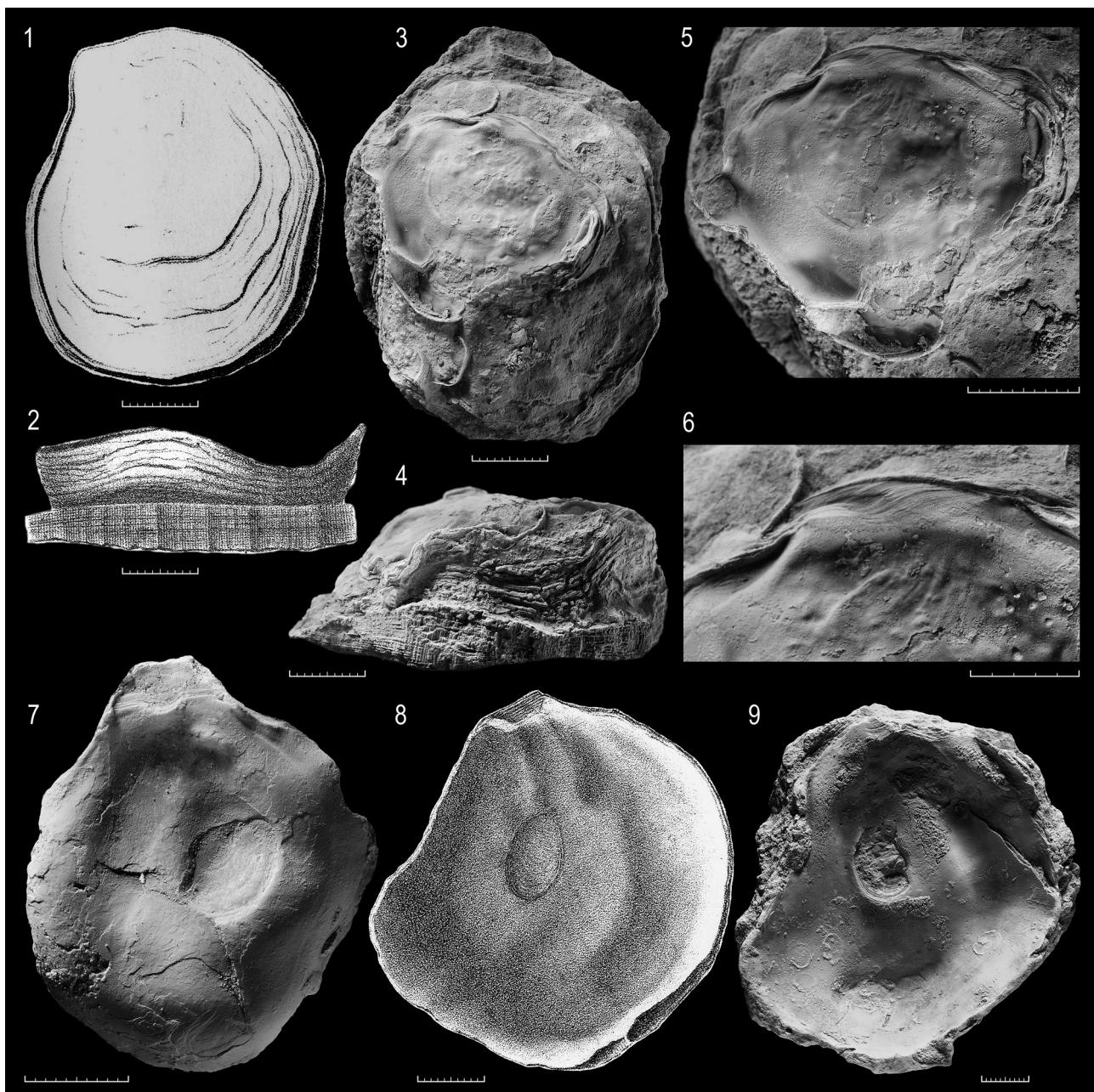


FIGURE 5. *Circunula n. gen. cotyledon* (Contejean, 1859). 1–4. Lectotype: 1, idealized drawing of a bivalved specimen, refigured from Contejean (1859, pl. 24, fig. 15), MC 27E-105, Rôce in Montbéliard, Lower Kimmeridgian; 2, anteroventral view of LV attached on a *Trichites* fragment (refigured from Contejean 1859, pl. 24, fig. 16); 3, external view of RV (with attached paralectotype, revealed during preparation); 4, anteroventral view. 5–6. Paralectotype, small LV (MC 27E-105a), attached on lectotype: 5, interior view; 6, prosodetic ligament area. 7. Paralectotype, RV interior, with opisthodetic ligament area, MC 27E-104, same locality and age as the lectotype. 8–9. Paralectotype, MC 27E-108, Arbouans near Montbéliard, France, Upper Oxfordian; 8, thick-shelled LV, idealized drawing refigured from Contejean (1859, pl. 24, fig. 17); 9, same LV, interior view. Scale bars 5 mm and 10 mm.

Lectotype (designated herein). *Ostrea cotyledon* Contejean, 1859 (pl. 24, figs. 15–16), MC-27-E-105: Bivalved specimen growing on a fragment of *Trichites* sp., with attached younger LV (paralectotype) MC-27-E-105a (internal features uncovered by present author) (Fig. 5.1–3). Rôce in Sainte-Suzanne, Montbéliard (Département Doubs, Franche-Comté), France. Coordinates ca. 47°30'20.33"N, 6°47'51.00"E. The exact position of the locality is unknown.

Lower Kimmeridgian, *cymodoce* Zone; “Niveau 6” of Contejean (1859), "Calcaires et Marnes à Ptérocerès" (= "Marnes du Rang" in eastern France), equivalent of the Banné Member of the Swiss Reuchenette Formation, Upper Jurassic.

Material. Lectotype (see above, MC 27E-105), paralectotypes MC 27E-105a and MC 27E-104 (from type locality) (Fig. 5.1–5). Paralectotype MJ 27E-108 from Arboans (between Montbéliard and Audincourt), Upper Oxfordian “*Natica* Limestone” (“Calcaires à Natices”, niveau 2 of Contejean (1859), equivalent of the Vorbourg Member, Lower Vellerat Formation of Switzerland); Musée Cuvier in Montbéliard (Fig. 5.7–9).

Others—Numerous specimens from the Banné Marls (*cymodoce* Zone) from Vâ Tche Tchâ (VTT), Alombre aux Vaches (ALO), Cras d’Hermont (CRA), Chevenez-La Scierie (CHS) in northwestern Switzerland and several specimens from a hardground at the base of the *lallierianum* Subzone (*mutabilis* Zone) of Sur Combe Ronde (SCR). One specimen from Blauen (Upper Oxfordian) of the Thurmann Collection (S 1469, = A.1.10.5.7; Pl. 3.19) in the MJSN Porrentruy (Appendix, Table 1).

Description. Shape, size—Left valve almost entirely cemented, larger than RV; ventral shell margin may become detached from surface, bending upwards at angles between 90° and 110°; posteroventral margin usually highest (see paleoecology); RV rather flat, ventrally partly concave, commissural shelf bending upwards, emulating free LV margin (Pl. 1.5d, Pl. 4.1, 4). Examined specimens between 1.1–7.5 cm high (Appendix, Table 1). Sculpture—Free part of LV with fine, even-spaced commarginal growth steps (Pl. 1.3b, 5c); very thin shells occasionally revealing external sculpture of attached surface consisting of minute, discontinuous, partly bifurcating, antimarginal and concentric furrows, few antimarginal riblets, and pustules (Pl. 2.5a,b,e, 7a,b) (Pl. 3.3b,c,e).

RV with weak commarginal growth lines and steps, and few antimarginal riblets (only on well preserved shells) (Pl. 2.2b, 4b, 5b, 6), becoming weakly squamous towards ventral margin (Pl. 1.5b); xenomorphic sculpture rare (smooth attachment surfaces preferred) (Pl. 1.5a,b).

Ligament area—Small, more or less triangular, alivicular-areate (Fig. 6.1–2); some shells with an initial prosogyrate twist (Fig. 6.1; Pl. 3.3b, 4–5), (Fig. 7.1–3; Pl. 3.4); resilifer weakly concave with slightly convex bourrelets in both valves, but less elevated in RV; early growth stages overgrown by projection of posterodorsal hinge margin (Fig. 7.2–3).

Internal shell characters—Umbonal cavity lacking. Posterior adductor scar (PAM) round, except dorsally, oblate (Pl. 1.1b) to concave (Pl. 2.1); position in adults posterodorsal, close to shell centre. Large specimens occasionally with deep sickle-shaped gill depression between posterior shell margin and adductor scar, reaching from hinge to branchitellum (LV: Fig. 5.9; Pl. 2.1; RV: Fig. 5.7; Pl. 1.1b; Pl. 3.1).

Microstructure—RV with thin (*ca.* 170 µm) continuous outer shell layer of reclined prisms; middle-inner shell layers low-angle foliate without chambering. Prisms and sculptures, commonly bioeroded through grazing by regular echinoids (star-shaped trace fossil *Gnathichnus pentax* Bromley, 1975; Pl. 2.4b). Left valve not examined but apparently lacking chambers or vesicular shell layers (no indications under light microscope).

Prodissococonch, juvenile—Prodissococonch and earliest postlarval shell not preserved. “Juveniles” or smallest adults typically with strongly gyrate ligament area, usually opisthogyrate, but prosogyrate in 7 out of 22 specimens. Posterior bourrelet may be very narrow (Fig. 6.3). Shape of juvenile PAM often more crescentic to subrectangular than round and slightly closer to hinge than in adult (Fig. 7; Pl. 3.3b,c, 5). Small linear chomata on both sides of dorsal margin (Figs. 6–7; Pl. 3.2–5) down to height of adductor scar; anterior catachomata (LV) as parallel grooves (length 0.17–0.3 mm, width 0.09–0.17 mm), normal to and along commissural shelf. Posterior catachomata present, larger specimens with relict catachomata especially close to hinge but not always well developed. Chomata overgrown and absent in larger shells (Fig. 7.3; Pl. 1.1b, 4b). Most juveniles and small adults smooth internally (Figs. 6, 8; Pl. 3.3a, 4–5).

Remarks. Coiling—Early postlarval prosogyry is relatively common in *Circunula cotyledon* (e.g. VTT001-3215, VTT001-3238, VTT001-1613); this tendency is perhaps only matched by Jurassic *Catinula knorri* (Voltz, 1828) (Pl. 4.2, 3b). Prosogyry appears to be somewhat more common among specimens settling on the dark (protected?) interior of a bivalved *Trichites* shell (ALO009-1) or on the underside of *Isognomon* specimens (VTT001-1615, VTT001-3215), but overall observations do not support an environmental influence.

Chomata—*Circunula cotyledon* is the first Jurassic species with chomata that does not belong to Exogyrinae, Arctostreidae, or to *Pseudeligmus* (Malchus 1990, 1998, p. 402, fig. 5). Their restriction to the early postlarval growth phase and later overgrowth and disappearance is not unusual, however.

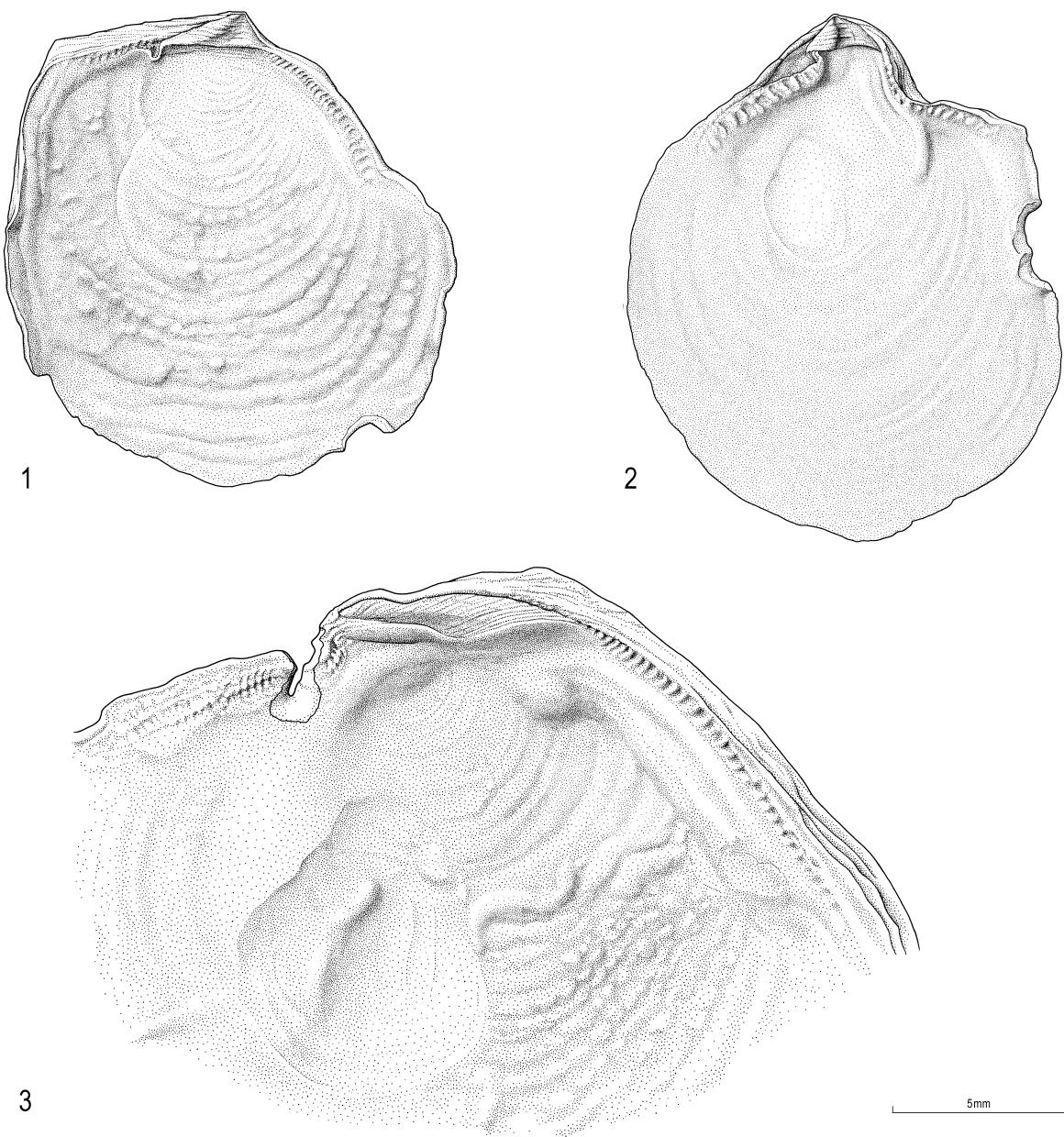


FIGURE 6. *Circunula n. gen. cotyledon* (Contejean, 1859). 1–3. Drawings of three juvenile specimens originally attached close together on a *Trichites*-shell (CGN-ALO009-1, see Fig. 8; Pl. 3.2–3), Alombre aux Vaches near Courgenay, Lower Kimmeridgian: 1, LV, umbo prosogyrate, ALO009-1-II; 2, LV, opisthogyrate, ALO009-1-I; 3, LV, opisthogyrate, ALO009-1-III. Scale x5.

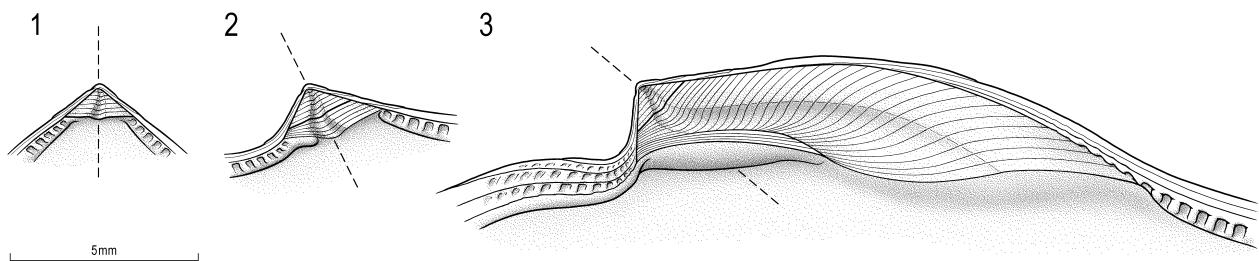


FIGURE 7. *Circunula n. gen. cotyledon* (Contejean, 1859). Ontogeny of ligament area (schematic). 1. LV, juvenile with a triangular, initially alivicular-areate ligament. 2. Recurving of the umbo (hypothetic). 3. Continuation of opisthogyrate twisting, ligament becomes prosodetic and opisthocline, posterior bourrelet overgrown by projection of the posterodorsal hinge margin; observations based on a group of juveniles (ALO009-1-I-IV, Figs. 6, 8). Scale x5.

Paleoecology. *Circunula n. gen. cotyledon* is a typical pioneer settler on limestone hardgrounds such as the basal hardground of the Banné Member, and layers 2000, 3000 of the Sur Combe Ronde section (Fig. 4B–C) where they become largest, develop the thickest shells and usually remain entirely attached (Pl. 1.2, Pl. 2.1, 7). They also occur commonly on *Isognomon* shells (Pl. 2.3) in oolitic and biomicritic sediments of the basal Banné Marls. Optimal conditions thus appear to have been medium to high energy environments in shallow marine carbonate settings, where most of the other oyster species could not survive.

Small articulated adults (2–3 cm) with a raised ventral margin are more typical of the highly fossiliferous marls of the middle Banné Member (Pl. 1.3, Pl. 2.4, Pl. 4.1), settling on large, smooth shell surfaces of *Isognomon*, *Ceratomya* (Pl. 1.5), and *Trichites* (Pl. 3.5). These deposits likely indicate calmer conditions.

Figure 8 and Plate 3.2–3 show a larger slab of a *Trichites* shell (ALO009-1, bivalved specimen) with *post mortem* settlement by more than 20 juvenile specimens. Overall, shells are attached with their ventral side directed towards the ventral margin of the *Trichites* shell. Specimens are much larger close to the margin than those attached more dorsally (Fig. 8). This orientation may indicate preferential growth close to nutrient-rich incoming current. The idea is supported by similarly oriented specimens of *Nanogyra* (*N.*) *nana* attached on the outer surface of the same *Trichites* shell (Pl. 6.1a–c).

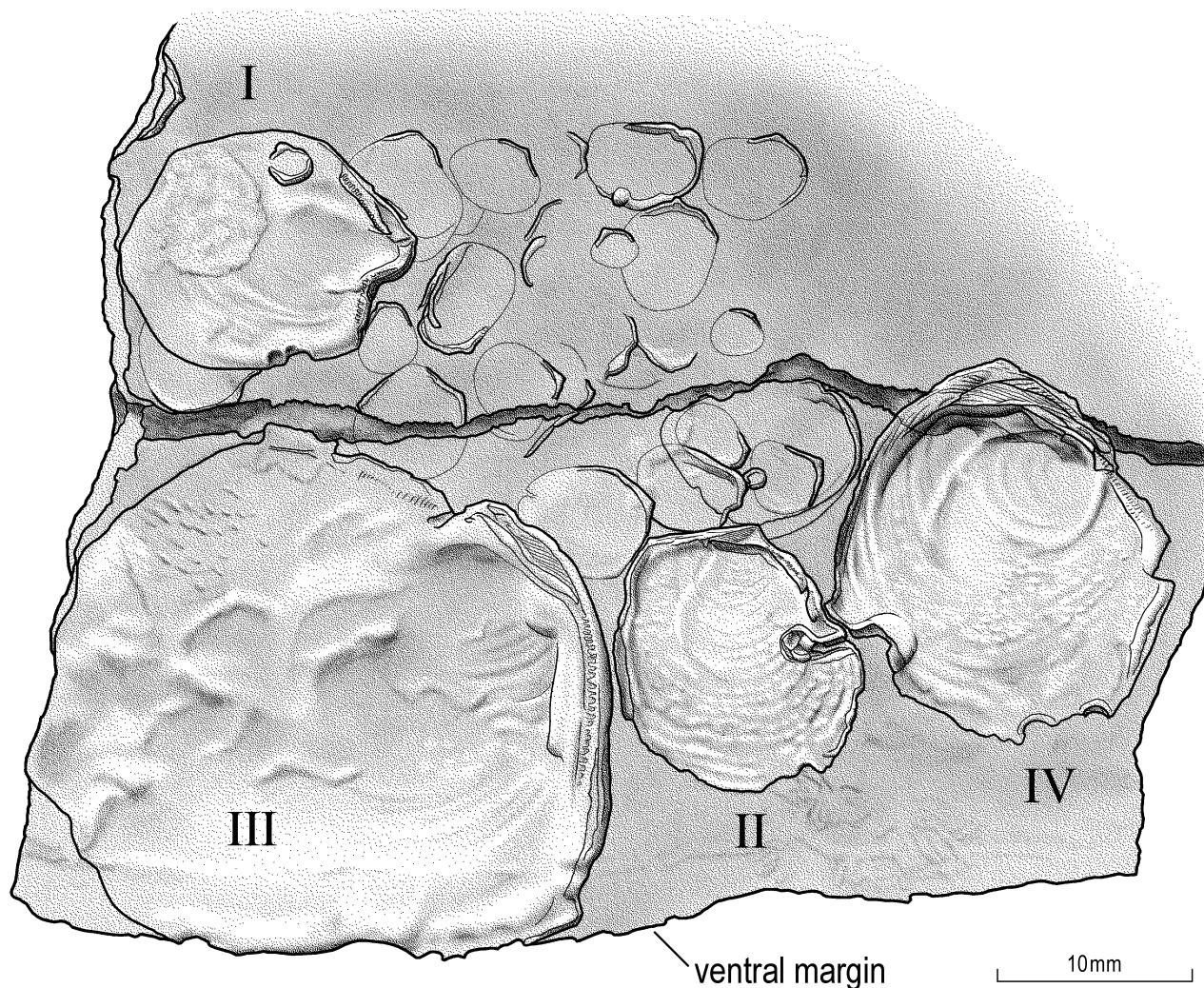


FIGURE 8. *Circunula n. gen. cotyledon* (Contejean, 1859). Group of juvenile LVs attached interior, of a bivalved *Trichites* (CGN-ALO009-1, largest oyster specimens labelled from I-IV, see also Fig. 6), close to its ventral margin; Alombre aux Vaches (Canton Jura), Lower Kimmeridgian, Banné Marls. Scale x1.5.

Occurrence. Upper Oxfordian to Upper Kimmeridgian of the Reuchenette Formation in Switzerland; Upper Oxfordian–Kimmeridgian in France; Kimmeridgian in Germany, Poland, Russia (Crimea); Tithonian in the Czech Republic.

Comparisons. The generic assignment of species discussed below remains tentative. The first three species could belong to *Circunula*, but there is no evidence of chomata, so far. Several more *Liostrea*-like species are discussed afterwards in alphabetical order.

Liostrea (Catinula) stoliczkai Cox, 1952 (p. 75, pl. 6, figs. 5–6)—This species was originally described by Cox (1952) from the Upper Bathonian of Soorkha (Kutch district, Gujarat, India). Morphological similarity with *C. cotyledon* may indicate that the two species are congeneric.

The species differs by having a tendency to develop a more quadrate outline, by being more strongly reflected upwards and growing higher ventrally (up to ca. 4 cm; fide Cox 1952, p. 75). The RV shows better developed antimarginal riblets, occasionally also radial furrows which reach near the ventral margin, and commarginally arranged tiny pustules (Cox 1952, pl. 6, fig. 6a). Remains of such pustules in *C. cotyledon* are only known from juvenile LVs (Fig. 6.1, 3; Pl. 3.3b,c,e). Judging from the figured LV in Cox (1952, pl. 6, fig. 6b), the PAM appears to be larger and more centrally situated than in *C. cotyledon*.

"*Liostrea*" *strigilecula* (White, 1877) (p. 163, pl. 8, fig. 3a–d)—This species was described from the Middle Jurassic Carmel Formation in SW Utah. It has a much larger adductor and a more inflated LV than *C. cotyledon*. It produces free-rolling oyster accumulations (ostreoliths) in shallow marine environments and also grows on hardgrounds (Wilson *et al.* 1998, p. 73, fig. 4A).

"*Ostrea*" *planaria* Rollier, 1917 (p. 550, pl. 39, figs. 1a–c)—The species comes from the "Terrain à Chailles" (Lower Oxfordian, *cordatus* Zone) of the ancient "Bistum Basel" (Switzerland) and the environment of Ferrette (Pfirt) in the Alsace, France.

The specimen figured in Rollier (1917) has a smaller attachment area and the ventral margin is less towering than in *C. cotyledon*. Both sides of the complete specimen are encrusted by serpulids and several specimens of *Nanogyra* (probably *N. nana*) suggesting a life mode under low energy conditions. Small, poorly preserved *Circunula*-like shells found by the author attached to corals in the somewhat younger marls and limestones of the Liesberg Member (N Switzerland) probably belong to the same species. It may be congeneric with *C. cotyledon*.

"*Ostrea*" *matisconensis* Lissajous, 1923 (p. 123, pl. 28, figs. 9–12)—This is a Bathonian species from France. Similar to *C. cotyledon*, it has a circular outline but it remains much smaller and develops antimarginal riblets on the unattached part of the ventral LV margin. These riblets may indicate an assignment to *Catinula* rather than *Circunula*.

"*Ostrea*" *matronensis* de Loriol in de Loriol, Tombeck & Royer, 1872 (p. 396, pl. 23, figs. 5–7)—The species occurs in the Portlandian (*gigas* Zone, Tithonian) of the Department Haute-Marne, France. It is characterized by a less oblique opisthogyrate resilifer and a higher ligament area; the umbo is more prominent and the overall shape tends to be more subtriangular than round. De Loriol (1872, pl. 23, figs. 6, 6a) figured a specimen attached to an ammonite, but otherwise settling grounds are unknown.

?*Liostrea moreana* (Buvignier, 1852) (p. 26, pl. 16, figs. 41–43)—This large species (up to 13 cm) was described from the Oxfordian ("coral rag") of the Meuse Department (Lorraine) in northeastern France. Differences to *C. cotyledon* are the larger adult size, the more capacious and stronger upward reflected left valve (up to 8 cm), a broader ligament area with a ventrally straight RV hinge margin, and absence of antimarginal ornament on the RV.

"*Ostrea*" *sandalina* Goldfuss, 1833(b) (pl. 79, figs. 9a–m)—The material from Goldfuss appears to belong to various species. Specimens of figures 9c–d come from a "black Jura-limestone" (Lower? Jurassic) of Osterkappeln and Lübke, NW Germany; specimens 9a–b, f–l are from oolitic ferruginous clay stones (probably Bajocian) of Streitberg, Gräfenberg, and Thurnau, Bavaria. Goldfuss also mentioned this species from white Oolites (Upper Jurassic) of Hildesheim and Goslar, northern Germany.

His specimens of figures 9c–d, h, l–m may indeed belong to *Circunula* **n. gen.** whereas figures 9i–k more likely represent *Liostrea* or *Praeexogyra*. Compare also specimens tentatively determined as ?*Praeexogyra sandalinoides* (de Loriol, 1901) from the Callovian of Western Pomerania (Pl. 15.3–4).

Cox (1952, p. 73, pl. 6, figs. 1–4, with synonyms) described material from the Bathonian of India and determined the species as *Liostrea (Catinula) sandalina*. However, typical specimens with a large attachment area and oval outline differ from *C. cotyledon* by a smaller adult height (around 3 cm), a less orbicular shape and a somewhat stronger upward reflected ventral margin.

Liostrea brasili Chavan, 1952 (p. 43, pl. 2, fig. 22)—The species from the Oxfordian of Calvados (France) has a similar shape, but a triangular ostreoid hinge, with a broad resilifer and a ventrally convex hinge line. It also has a well-developed umbonal cavity (Chavan 1952, pl. 2, fig. 22), which is absent in *Circunula* **n. gen.**

Subfamily Exogyrinae Vialov, 1936

Tribe Nanogyrini Malchus, 1990

Genus *Nanogyra* Beurlen, 1958

Type species. *Gryphaea nana* J. Sowerby, 1822, p. 114, pl. 383 (left figure); BM 43340c, Kimmeridge Clay, England.

Diagnosis (modified from Stenzel 1971, p. N1121). Thin-shelled, inequivale. Outline suborbicular, subtrigonal, elliptical, or ovate to comma-shaped (virguliform of authors); always opisthoglyrate, degree of spirality variable. Left valve moderately convex to globular, smooth or with antimarginal riblets, rarely with small plicae; RV overall slightly concave or convex, with sharp, curved anterior carina. Posterior ligament bourrelet reduced in length, usually forming a ridge with the dorsal margin during early growth stages. Chomata known since Bathonian [see below, *N. (P.) reniformis* (Goldfuss, 1833)(b)].

Microstructure largely compact foliate some small chambers may be present close to the umbo and shell margin, complex cross-foliation common. Right valve with outer, coarsely prismatic layer (Siewert 1972, p. 19; Malchus 1990, p. 109; Malchus & Aberhan 1998, p. 629). Most species do not exceed 3 cm in largest diameter, but for some larger species exceptional specimens may reach a height of up to 7 cm.

Remarks. The present diagnosis deliberately excludes ?*N. (Nanogyra) auricularis* (Goldfuss, 1833)(b) as described in Malchus & Aberhan (1998). The species has an unusual large size (*ca.* 10 cm), numerous large chambers, and a tendency to become uncoiled reaching a ligament area height of up to 4 cm. It is equally unclear whether the specimens from Europe and those from Chile belong to the same species. Malchus & Aberhan (1998) hypothesized that it represents a different genus.

Subgenus *Nanogyra* (*Nanogyra*) Beurlen, 1958

Diagnosis (modified from Stenzel 1971, p. N1121). Shell shape oval to subrectangular, rarely elongate, with a strong opisthoglyrate umbo and exogyroid hinge. Antimarginal sculptures and chomata absent. Microstructure as for the genus.

Nanogyra (*Nanogyra*) *nana* (J. Sowerby, 1822)

Fig. 9.3; Fig. 10; Pl. 5.1–8; Pl. 6.1–4; Pl. 16.2a,b, 4, 6b

- | | | |
|---|-------|--|
| * | 1822 | <i>Gryphaea nana</i> . sp. nov.—J. Sowerby: p. 114, pl. 383, fig. 3. |
| | 1829 | <i>Gryphaea mima</i> sp. nov.—Phillips: pl. 4, fig. 6. |
| v | 1832 | <i>Exogyra Bruntrutana</i> , nob.—Thurmann: p. 13 (nomen nudum). |
| | 1833b | <i>Exogyra auriformis</i> nobis—Goldfuss: p. 33, pl. 86, figs. 5a,b. |
| | 1833b | <i>Exogyra spiralis</i> nobis—Goldfuss: p. 33, pl. 86, figs. 4a,b. |
| | 1835 | <i>Exogyra spiralis</i> Goldf.—Roemer: p. 65. |
| n | 1839 | <i>Exogyra spiralis</i> . β —Roemer: p. 59, pl. 18, fig. 18 [= <i>N. (P.) welschi</i> (Jourdy, 1924)]. |
| | 1845 | <i>Exogyra reniformis</i> . (Goldfuss.)—d'Orbigny: p. 479, pl. 42, fig. 9, 10. |
| | 1846 | <i>Exogyra bruntrutana</i> Thurmann—Leymerie: pl. 9, fig. 7. |
| | 1850 | <i>Ostrea spiralis</i> d'Orb. 1847—d'Orbigny: vol. 2, p. 23, no. 380. |
| | 1851b | <i>Exogyra spiralis</i> Goldf.—Quenstedt: p. 503, pl. 40, fig. 35. |
| | 1853 | <i>Exogyra auriformis</i> Goldfuss—Morris & Lycett: p. 5, pl. 1, fig. 7. |
| | 1857b | <i>Exogyra spiralis</i> Goldfuss—Quenstedt: p. 752, pl. 91, figs. 31, 32. |
| v | 1859 | <i>Ostrea (Exogyra) Bruntrutana</i> Th. sp.—Contejean: p. 322. |
| | 1859 | <i>Exogyra spiralis</i> Glfd.—Trautschold: p. 115, pl. 2, figs. 12–13. |

- 1861 *Ostrea spiralis* d'Orb.—Thurmann & Etallon: p. 53.
- v 1862 *Ostrea auriformis* Cjt.—Thurmann & Etallon: p. 273, pl. 38, fig. 9.
- 1862 *Ostrea spiralis* d'Orb.—Thurmann & Etallon: p. 274, pl. 39, fig. 3.
- n 1862 *Ostrea nana* Et.—Thurmann & Etallon: p. 275, pl. 39, fig. 7 (= *Praeexogyra* sp.).
- ? 1862 *Ostrea quadrata* Et.—Thurmann & Etallon: p. 277, pl. 39, fig. 8.
- 1862 *Ostrea subnana* Et.—Thurmann & Etallon: p. 276, pl. 39, fig. 4.
- 1863 *Ostrea bruntrutana* (Thurmann).—Dollfus: p. 87, pl. 27, figs. 7–9.
- 1864 *Exogyra spiralis* Goldf.—Credner: p. 229.
- 1866 *Ostrea bruntrutana*, Thurmann.—de Loriol in de Loriol & Pellat: p. 113 (Portlandian records).
- 1871 *Exogyra bruntrutana* Voltz—Struckmann: p. 217.
- 1872 *Ostrea Bruntrutana* Thurm.—de Loriol, Royer & Tombeck: p. 399, pl. 24, figs. 7–18.
- 1872 *Ostrea dubiensis* Contejean—de Loriol, Royer & Tombeck: p. 407, pl. 24, figs. 19–25.
- 1877 *Exogyra nana* Sow.—Blake & Hudleston: p. 265.
- 1877 *Exogyra spiralis* Gldf.—Blake & Hudleston: p. 263.
- 1878 *Exogyra spiralis* Gldf.—Trautschold: p. 254, 259, 262, pl. 3, figs. 4a–f.
- 1892 *Ostrea (Exogyra) quadrata*, Etallon.—de Loriol: p. 347, pl. 36, figs. 9–11.
- ? 1892 *Ostrea (Exogyra) subreniformis* n. sp.—de Loriol: p. 347, pl. 36, figs. 12–14.
- 1893 *Exogyra Bruntrutana* Thurm.—Fiebelkorn: p. 397, pl. 14, fig. 4.
- 1893 *Ostrea bruntrutana* Thurmann—É. Greppin: p. 90, pl. 6, figs. 12, 14, 20.
- 1893 *Ostrea (Exogyra) quadrata* Etallon—É. Greppin: p. 91, pl. 6, figs. 9, 11, 13.
- 1897 *Exogyra bruntrutana* Thurm.—Futterer: p. 582, pl. 19, fig. 1, 1a.
- 1900 *Ostrea (Exogyra) bruntrutana* Thurmann—de Loriol: p. 135, pl. 17, fig. 5–8.
- 1900 *Exogyra bruntrutana* Thurm.—Müller: p. 532, pl. 18, fig. 11, 12.
- ? 1907 *Ostrea (Exogyra) nana*, Sow.—Thiéry & Cossmann: p. 29, pl. 3, fig. 22–23.
- 1916 *Exogyra nana* Sow.—Douvillé: p. 57, 77.
- 1921 *Exogyra bruntrutana* Thurmann—Newton: p. 394, pl. 11, fig. 6.
- 1923 *Exogyra Bruntrutana* Thurmann—Lewinski: p. 65, pl. 3, fig. 4, 5.
- 1924 *Exogyra nana* (Sow.)—Jourdy: p. 58, pl. 2, fig. C, P, R, pl. 5, fig. 2–4, 7, 9–11, pl. 6, fig. 1–3, 5, pl. 7, fig. 6, pl. 8, fig. 7, 8, pl. 9, fig. 1.
- 1924 *Exogyra bathonica* d'Orb.—Jourdy: p. 54, pl. 2, fig. B, pl. 5, figs. 5a,b, 12 e, f, pl. 7, fig. 5 a–d.
- 1926 *Exogyra cf. spiralis* Goldfuss—Tutcher in Buckman: p. 32, fig. 3.
- 1927 *Exogyra bruntrutana* Thurmann—Reed: p. 267, pl. 19, fig. 24.
- 1927 *Exogyra eminensis* n. sp.—Reed: p. 267, pl. 19, fig. 26.
- 1928 *Exogyra nana* Sow.—Arkell: pl. 21, fig. b.11.
- 1929 *Exogyra nana*, Sow. 1822—Weir: p. 20, pl. 1, fig. 11–13.
- 1929 *Exogyra bruntrutana* Thurm.—Cox: p. 151.
- 1930 *Exogyra nana* (Sow.)—Weir: p. 85, pl. 10, figs. 27–29.
- 1930 *Exogyra bruntrutana* (Th.) de Loriol—Basse: p. 120, pl. 4, fig. 11a–c.
- 1931 *Exogyra Vinassai* n. sp.—Diaz-Romero: p. 35, pl. 2, figs. 17–20, pl. 3, figs. 1–2.
- 1931 *Exogyra bruntrutana* Thurmann.—Dreyfuss: p. 297, 306.
- 1932 *Exogyra nana* (Sow.)—Arkell: p. 175, pl. 17, figs. 2–21, pl. 18, figs. 3–11, pl. 19, figs. 4, 4a, Fig. 48.
- n 1932 *Exogyra nana* Sowerby sp.—Corroy: p. 194, pl. 27, figs. 12–13.
- 1933 *Exogyra nana* (Sow.)—Oria: p. 40, pl. 4, fig. 10, Text–Fig. 8–9.
- 1935 *Exogyra nana* (Sow.)—Cox: p. 175, pl. 17, fig. 16a,b.
- 1939 *Exogira Vinassai* Diaz-Rom.—Stefanini: p. 205, pl. 22, fig. 18, pl. 23, figs. 1–11, text–figs. 16–18.

1946	<i>Exogyra bathonica</i> d'Orbigny—Gardet & Gerard: p. 43, pl. 7, fig. 24–25.
1947	<i>Exogyra nana</i> (Sowerby)—Arkell: p. 80, text–fig. 11, fig. 1.
1948	<i>Exogyra nana</i> (J. Sowerby)—Cox & Arkell: p. 20.
1952	<i>Exogyra nana</i> (J. Sowerby)—Cox: p. 92, pl. 10, figs. 2–4.
1955	<i>Exogyra nana</i> (Sow.)—Basse <i>et al.</i> : p. 664, pl. 27, fig. 3a–c.
1955	<i>Exogyra nana</i> (Sow.)—Gerasimov: p. 131, pl. 30, fig. 1–14.
1955	<i>Exogyra Bruntrutana</i> Thurmann—Schirardin: p. 46, pl. 2, fig. 13.
1958	<i>Nanogyra nana</i> (Sow.)—Beurlen: p. 205, 206, 207, 209, fig. 2.
1959	<i>Nanogyra nana</i> (Sow.)—Van de Poel: p. 222.
1959	<i>Exogyra nana</i> (Sow.)—Jaboli: p. 38, pl. 5, fig. 5.
1960	<i>Exogyra nana</i> (Sow.)—Rossi Ronchetti in Desio <i>et al.</i> : p. 95, pl. 11, fig. 6–8.
1964	<i>Exogyra nana</i> (Sowerby) 1822—Wellnhofer: p. 52, pl. 3, figs. 8–11, fig. 33.
1965	<i>Exogyra nana</i> (J. Sowerby)—Cox: p. 73, pl. 11, figs. 5, 6a,b.
1965	<i>Nanogyra nana</i> (Sowerby)—Freneix: p. 41 (89), pl. 5, fig. 2–6.
1969	<i>Nanogyra nana</i> (J. Sowerby)—Fischer, J.–C.: p. 96, pl. 10, fig. 17–20.
1969	<i>Exogyra nana</i> —Ziegler: pl. 6, figs. 1, 2, 4, 9–10.
1971	<i>Exogyra cf. nana</i> (J. Sowerby)—Jordan: p. 155, pl. 18, fig. 3.
1971	<i>Nanogyra nana</i> (J. Sowerby)—Pugaczewska: p. 281, pl. 1, figs. 3–5, 7, pl. 2, figs. 1–4, pl. 24, figs. 1–6, pl. 25, figs. 1–7, pl. 26, figs. 1–6, pl. 27, figs. 1–6.
1971	<i>Exogyra cf. nana</i> (Sowerby, 1822)—Wisniewska–Zelichowska: p. 48, pl. 29, figs. 8–10.
1976	<i>Nanogyra nana</i> (Sowerby, 1822)—Romanov: p. 110, pl. 5, figs. 1–15.
1977	<i>Nanogyra nana</i> —Fürsich: p. 342, 344, 345, 348, 349, 354, 356, figs. 5, 9, 10, 12–18, 20, 22–24, 26–28.
1978	<i>Nanogyra nana</i> (J. Sowerby, 1822)—Duff: p. 84, pl. 9, figs. 2–5.
1981	<i>Nanogyra nana</i> (Sowerby 1822)—Parnes: p. 33, pl. 4, figs. 26–27.
1984	<i>Nanogyra nana</i> (J. Sowerby)—Gu Zhi-wei, Chen Jin-hua & Sha Jin-geng : p. 137, pl. 28, figs. 7–22.
1984	<i>Nanogyra nana</i> (J. Sowerby, 1822)—Kelly: p. 49, pl. 7, fig. 1–7, 9–3, Text–fig. 33.
1986	<i>Exogyra nana</i> (Sowerby)—Li Xiao-chi: p. 482, pl. 3, fig. 11.
n	1990 <i>Nanogyra nana</i> (J. Sowerby 1822)—Clausen & Wignall: p. 123, pl. 6, fig. 3 (= <i>N. virgula</i> , RV).
	1990 <i>Exogyra nana</i> (Sowerby)—Turbina & Zakharov: p. 74, pl. 39, figs. 7–11.
	1994 <i>Nanogyra nana</i> (J. Sowerby)—Duff in Martill & Hudson: p. 103, pl. 6, figs. 4–5.
	1995 <i>Nanogyra nana</i> (Sowerby)—Jaityl, Fürsich & Heinze: p. 189, pl. 16, figs. 13–15, pl. 7, figs. 1–2.
	1996 <i>Nanogyra nana</i> (Sowerby, 1822)—Gerasimov <i>et al.</i> : pl. 19, figs. 1–4.
	1998 <i>Nanogyra nana</i> (J. Sowerby 1822)—Holzapfel: p. 108, pl. 6, figs. 6–7.
	1998 <i>Nanogyra nana</i> (J. de C. Sowerby)—Radley <i>et al.</i> : p. 84, fig. 3h–3k.
	1999 <i>Nanogyra nana</i> (J. Sowerby 1822)—Ahmad: p. 18, pl. 3, fig. 3.
	2002 <i>Nanogyra nana</i> (J. Sowerby, 1822)—Sha, Smith & Fürsich: p. 440, figs. 11, 12.1–12.29.
v	2006 <i>Nanogyra nana</i> —Hicks: p. 36.
v	2006 <i>Nanogyra nana</i> (J. Sowerby 1822)—Richardt: p. 9, 18.
n	2011 <i>Nanogyra nana</i> (J. Sowerby)—Kiessling <i>et al.</i> : p. 210, text–fig. 13, figs. I–J.

Type series (not seen). Lectotype—*Gryphaea nana* J. Sowerby, 1822, pl. 383, fig. 3 (left figure), BM 43340c, J. Sowerby Collection, Natural History Museum London (NHMUK), designated by Arkell 1932, p. 180; refigured in Duff (1978, pl. 9, fig. 4a,b), Kimmeridge Clay of Shotover Hill, near Oxford, England; coordinates: 51°45'11.46"N, 1°11'41.58"W (centre of Shotover Hill, Headington).

Paralectotype(s)—The bivalved specimen figured in J. Sowerby (1822, pl. 383, fig. 3, right figure). The

enumeration of the lectotype as BM 43340c suggests the presence of more material (at least three specimens), but no further data are obtainable from the literature.

Material. Several 100 specimens from the Banné Marls (*cymodoce* Zone, Lower Kimmeridgian) of Vâ Tche Tchâ (VTT), “Tunnel le Banné” (TLB) at Porrentruy, Alombre aux Vaches near Courgenay (ALO). Additional younger material comes from a hardground at the top of the *mutabilis* Zone (layer 4000, *lallierianum* Subzone, Upper Kimmeridgian) and the “Lower *Virgula* Marls” (layer 4500, *eodoxus* Zone) of Sur Combe Ronde (SCR) and Bois de Sylleux (BSY) near Courtedoux. For measurements see Appendix, Table 2.

Several large RVs on the original label identified as “*Ostrea bruntrutana* var. *portlandica* Thurmann” (= *Ostrea auriformis*, Ctr., in Thurmann & Etallon 1862, p. 273) from the Banné hill (Collection number MJSN S1067, A.2.16.4.06).

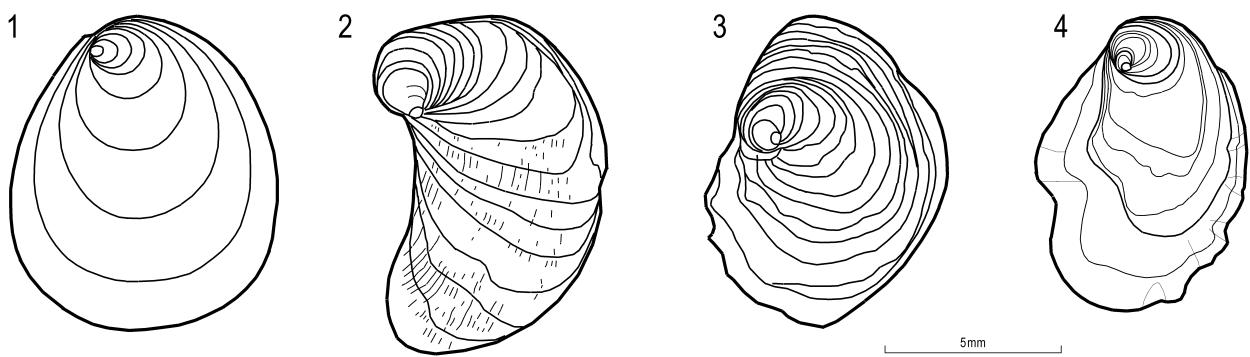


FIGURE 9. Comparison of juvenile RVs of *Gryphaea*, *Nanogyra*, and *Actinostreon*. 1. *Gryphaea ferruginea* Terquem, 1855, Aalenian, Poland (redrawn after Pugaczewska 1971b, fig. 1). 2. *Nanogyra (Palaeogyra) virgula* (Deshayes, 1831), Upper Kimmeridgian, Switzerland. 3. *Nanogyra (N.) nana* (J. Sowerby, 1822), Lower Kimmeridgian, Switzerland. 4. *Actinostreon marshii* (J. Sowerby, 1814), Callovian, Lithuania.

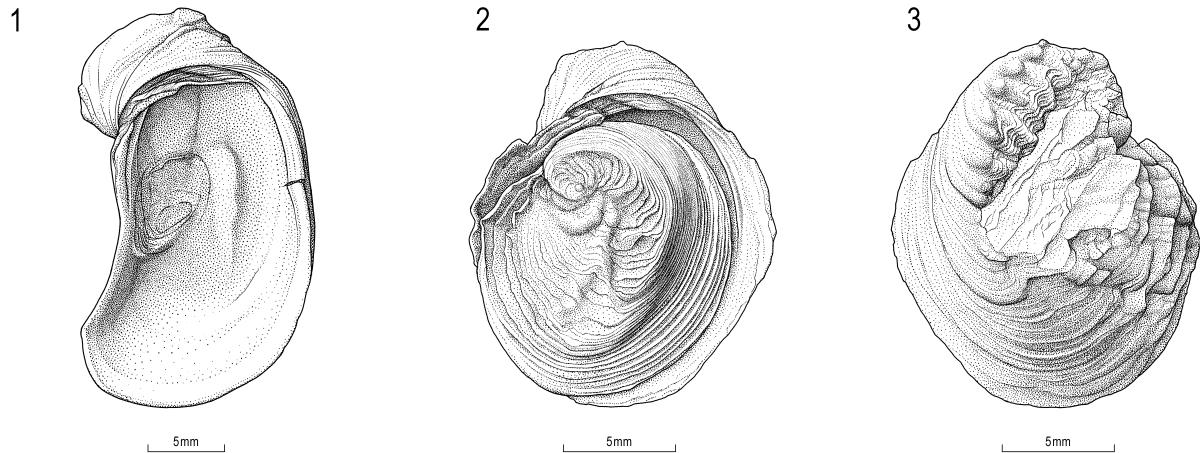


FIGURE 10. *Nanogyra (Nanogyra) nana* (J. Sowerby, 1822). 1. LV, interior, VTT001-3214; scale x2. 2–3. Articulated valves, VTT001-3210; scale x3: 2, LV, RV lateral; 3, LV lateral, posterior xenomorphic; Vâ Tche Tchâ, Banné Marls, Lower Kimmeridgian.

Description. Shape, Size—LV capacious, globular or cup-shaped, outline usually auriform but varies between ovate, suborbicular and subtrigonal; umbo rounded; maximal convexity along the anteroventral margin; RV flat to weakly concave (convex-concave type), in adults usually with an anterior, spirally coiled carina, separating an oblique downwards directed and partly concave anterior margin. Examined specimens less than 0.1 to 2.4 cm high (Pl. 6.4; Appendix, Table 2).

Sculpture—LV attachment scar often large, dependant on available substrate; free surface with concentric growth lines, antimarginal furrows rare, close to attachment scar (perhaps related to xenomorphic growth) (Pl. 5.1c, 4c). RV with faint concentric growth lines and mostly regularly spaced comm marginal, weakly squamous growth lamellae; antimarginal riblets always absent.

Ligament area—Narrow, exogyroid, prosodetic, deeply sunken; juvenile ligament area becoming overgrown by posterodorsal shell margin during spiral growth (Fig. 10.1–2; Pl. 5.1–7, Pl. 6.2–4). LV resilifer slightly concave, equal to or slightly broader than anterior bourrelet; posterior bourrelet narrow and mostly hidden under posterodorsal margin or “ligament ledge” (Pugaczewska 1971, p. 222).

Internal shell characters—Umbonal cavity small to moderate (Pl. 5.2a–b); adductor scar posterocentral, oval, dorsolateral borders often slightly biconcave, weakly impressed in depositional surface, ventrally elevated (buttressed) (LV: Fig. 10.1, RV: Pl. 5.3c) (Pl. 5.2a–b, 3c; small and weakly inserted Quenstedt scar present in RV (observed only in two specimens: VTT001-7427, VTT001-144), situated at the posterior lower end of the hinge margin (Pl. 5.3c). Commissural shelf weak and restricted to dorsal half. Chomata absent.

Microstructure—Regular foliated without chambers (Siewert 1972). RV with relatively thick outer prismatic layer, observable along the upturned growth crests of the anterior margin (Pl. 6.2a–b).

Prodissococonch, juvenile—Incomplete prodissococonch moulds visible on two RVs (Pl. 6.3a–b, and 4b–c); upper part and umbo with P1 lost (top of shell appearing flat, therefore); length of 2 measured moulds 325–344 µm, height 394 µm suggesting a prodissococonch size in the order of 350–400 µm.

Postlarval RV smooth, suboval, with straight truncated dorsal margin beyond prodissococonch (P) and a somewhat protruding posteroventral margin. First opisthogyrate torsion between ventral margin of the P and postlarval shell around 45°; strong torsion of 90° and first commarginal growth crests at ca. 0.7–1.2 mm height; shell prolongation shifted towards the former posterior margin (Pl. 6.3a and 4b,c); 2nd 90° turn between 1.7–2.5 mm, 3rd 90° turn between 2.5–10 mm and a final turn of 45° between 10 mm and adult height; altogether an opisthogyrate coiling of around 360° for adult specimens.

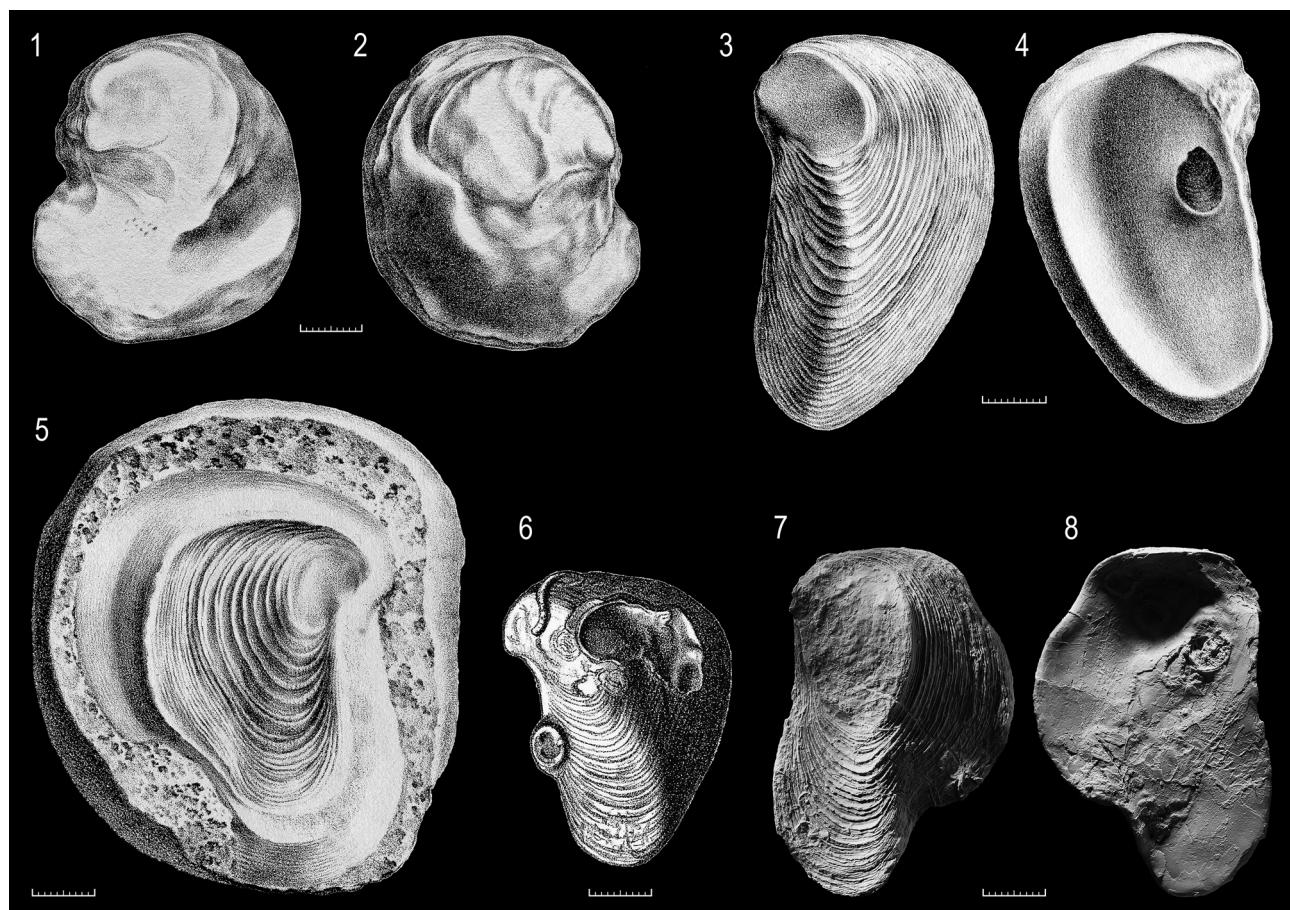


FIGURE 11. *Nanogyra* (*Nanogyra*) *auricularis* (Münster in Goldfuss, 1833)(b) and *N.* (*N.*) *rivelensis* (de Loriol, 1904). 1–2. *N.* (*N.*) *auricularis*, Amberg, Hettangian, Lower Lias. 1. LV lateral, reversely? (mirrored) drawn original in Goldfuss (1833(b), pl. 79, fig. 7a). 2. RV lateral (original, pl. 79, fig. 7b). 3–8. *Nanogyra* (*N.*) *rivelensis*. 3–5. *Ostrea* *striata* Münster in Goldfuss, 1833(b) (pl. 80, figs. 7a–c), senior synonym. 3. RV lateral (pl. 80, fig. 7b), Streitberg, Germany, Oxfordian. 4. RV interior (pl. 80, fig. 7c). 5. LV lateral (pl. 80, fig. 7a). 6. “*Ostrea*” *rivelensis*; RV lateral, original figure in de Loriol (1904, pl. 25, fig. 11), Mont Rivel, Oxfordian. 7. *N.* (*N.*) *rivelensis*. RV lateral, FPJ 750, Vue des Alps, Canton Neuchâtel, Switzerland, *antecedens* Subzone, Middle Oxfordian. 8. RV interior, same as 7. All scale bars 10 mm.

Paleoecology. In the low-energy marl facies of the middle Banné Member (Pl. 6.1a–c, Pl. 19.2a–d), *N. (Nanogyra) nana* settled preferentially on biogenic hard substrates, e.g. *Trichites mattheyi* (Roller, 1915), and occasionally also on the interior of dead shells of exposed infaunal bivalves such as *Ceratomya* (Pl. 19.1a,b) and *Integricardium*. In higher energy environments, it settled on stems of *Goniolina geometrica* (F.A. Roemer) and other dasycladacean algae (beds 70 and 300 of section VTT, Banné Marls). These *Nanogyra* specimens are all smaller than 1 cm, perhaps indicating a correlation with the bending strength of the dasycladacean stems.

The species also occurs as patch reef builder together with the crinoid *Apiocrinites roissyanus* d'Orbigny as found along the Transjurane Highway close to Boncourt (locality Queue au Loup, BON-QLP, Upper Oxfordian). The reef of up to one meter height and several meters length contains millions of *N. nana* specimens forming up to 10 cm thick layers. The preservation of complete, articulated crinoid crowns indicates a rather low-energy environment. Some round, bolder-shaped oyster accumulations, built by some thousand specimens of *Nanogyra nana*, were found nearby in the soft marls.

Fürsich & Hautmann (2005, p. 15) reported similar lenticular patch reefs (0.2–0.3 m high) at several levels within the Kamar-e-Mehdi Formation (Middle Callovian–Lower Kimmeridgian) in east-central Iran. These reefs were found in a low energy shelf lagoon associated with sponges and bivalves (*Trichites*, *Radulopecten*).

Occurrence. In Switzerland and France the species is restricted to the Upper Jurassic (Jourdy 1924, Ziegler 1969). Elsewhere, it occurs from Bajocian rocks in England (Arkell 1932) and Israel (Parnes 1981) up to the Lower Cretaceous of the Spilsby Sandstone of England. This latter occurrence includes *Nanogyra tombeckiana* (d'Orbigny, 1847) (in d'Orbigny 1843–1847), which Kelly (1984, p. 46) synonymized with *N. nana*.

Comparisons. Larval shells of the present material of *N. nana* (Pl. 6.3a,b, and 4b,c) are comparable with Jurassic liostreine, Cretaceous flemingostreine and Tertiary to Recent crassostreine larval shells. The phylogenetic significance of this observation is currently unclear. See Malchus (1995), Palmer (1989) and Plates 6.5 and 10.2–3a for comparisons of various fossil oyster prodissococonchs.

The following exogyrine species described by Thurmann & Etallon (1862) (bivalve volume of Thurmann & Etallon, 1861–1864) are considered synonymous with *N. (N.) nana*: *Ostrea bruntrutana* Thurmann & Etallon, *Ostrea bruntrutana* var. *portlandica* Thurmann (= “*Ostrea auriformis*, Ctj.”, in Thurmann & Etallon 1862, p. 273), “*Ostrea*” *spiralis* Goldfuss, 1833(b) and *O. subnana* Etallon in Thurmann & Etallon 1862. Of these, only *Ostrea bruntrutana* var. *portlandica* is preserved in the collection of the MJSN (S1067). For a comparable specimen from the “Lower Virgula Marl” of Courtedoux see Pl. 5.6.

In addition, *N. praevirgula* (Douvillé & Jourdy, 1874) appears to be a xenomorphic *N. nana* [see also comparisons under *N. (P.) virgula*]. For detailed discussions of the synonymy and variability of adult *N. nana* see Arkell (1932), Cox (1952), Duff (1978), Gautret (1982), Jourdy (1924), Kelly (1984), Kiessling *et al.* (2011), Pugaczewska (1971) and Sha *et al.* (2002). The following taxa, listed alphabetically, are considered different from *N. nana*.

N. (N.) auricularis (Münster in Goldfuss, 1833)(b) (p. 20, pl. 79, fig. 7a–b)—Münster and Goldfuss based their description of the new species on a single articulated shell (possibly holotype by monotypy, see ICBN 73.1.2) from the Liassic of Amberg (Franconia, Germany). According to Kuhn (1934, p. 6) the species appears to be restricted to the Lower Jurassic (Hettangian) in its type region. For comparison see also Jourdy's (1924, p. 53, pl. 1, figs. 1.1–1.5, pl. 7, fig. 3) specimen(s) from the Toarcian of France, and a single RV of *Nanogyra* (*N.*) cf. *auricularis*, with the mould of the rarely preserved prodissococonch, from the Upper Hettangian of Stuttgart-Vaihingen from the collection of the SMNS (Pl. 10.2).

The original figure in Goldfuss (here reproduced in Fig. 11.1–2) has an oval shape and a weakly twisted, apparently prosogyrate rather than opisthogyrate umbo, which is here interpreted as a technical error during the preparation of the lithographic plate. The figured specimen can be distinguished from *Nanogyra nana*, by a less coiled umbo, the weakly upraised ventral margin and a much smoother RV with only few growth interruptions. The height of 4.8 cm is relatively large for a *Nanogyra*.

Nanogyra (*N.*) *crassa* (W. Smith, 1819) (p. 30, fig. 6)—This species was first described from the Bradford Clay (Bathonian) of Bradford-on-Avon in Wiltshire, England (Cox & Arkell 1948, p. 20; Cox 1952, p. 90, pl. 10, fig. 1). “*Ostrea bathonica*” Thevenin, 1913 (p. 166, pl. 29, figs. 4–6) (ex. d'Orbigny, 1850) is a junior synonym (Fischer 1969, p. 95, pl. 10, fig. 21, 22). The same may hold true for *Exogyra carinata* Roemer, 1835 (p. 66, pl. 3, fig. 15) from the Portland limestone of the hill Langenberg near Goslar (Germany).

Differences to *N. nana* are a much larger adult size (occasionally more than 6 cm, the elongate, nearly linguiform outline, and a less curved umbo, with a well-developed resilifer and a large PAM).

Nanogyra (N.) monoptera (J.-A. & J.F.E. Eudes-Deslongchamps, 1858) (p. 159, pl. 5, figs. 1–4)—This is another early representative of the genus, known from the Toarcian of France. The species differs from *N. nana* by its sickle-shaped prolongation of the posteroventral margin, the presence of a posterodorsal auricle, and a minor inflation.

Nanogyra (N.) rivelensis (de Loriol, 1904) (p. 256, pl. 25, figs. 11–13)—The species is from the Argovian marly sponge facies (“Couche à Birmenstorf”, *transversarium* Zone, Middle Oxfordian) of the Mont Rivel near Champagnole (Franche-Comté, Department Jura, France), which also exists in the Swiss Jura chains (Fig. 11.7–8). *Ostrea striata* Münster in Goldfuss (1833)(b) (p. 22, pl. 80, figs. 3a–d) from the Oxfordian of Southern Germany is a senior synonym (see Gümbel 1862, p. 194–208, for type section). The name has rarely been used, however, and should be considered a nomen oblitum. This decision would also avoid confusion with *Chama striata* W. Smith, which is itself a suppressed senior synonym of *Nanogyra (P.) virgula* (Deshayes) (ICZN opinion 310). Original figures 3a–c in Goldfuss (1833)(b) are here reproduced as Figure 11.3–5.

Differences to *N. nana* are the much larger height (H 5.6 cm) and a more subrectangular shape, with a less twisted umbo (thus also a broader and less curved ligament area). The RV is dorsally nearly smooth, plain, occasionally covered by concentrically arranged small pustules, followed ventrally by growth lamellae (Fig. 11.3, 6–7). A well-developed anterior to nearly central carina separates a much broader area of towering commarginal growth laminae (Fig. 11.7). The LV is less inflated than in *N. nana* and covered by strong concentric growth squamae (Fig. 11.5).

Nanogyra ?(Nanogyra) roederi (de Loriol, 1904) (p. 254, pl. 25, figs. 14–21)—Roeder (1882, p. 36, pl. 1, figs. 3a–d, pl. 2, fig. 1) discovered the species in the “Terrain à Chailles” (Lower Oxfordian) near Ferrette (= Pfirt, Alsace, France) but identified it as “*Exogyra reniformis* Goldfuss”. The species is also present in the Lower and Middle Oxfordian of Switzerland.

De Loriol's species is almost homeomorphous to *N. nana*. However, it differs by a slightly protruding anterodorsal auricle, the lack of commarginal growth crests on the RV where the anterior area with steep towering growth laminae/crests is narrower in *N. roederi* than in *N. nana*. The laminae themselves are also thinner and less numerous (*ca.* 8 for *N. roederi* versus 10–20 for *N. nana*). Further differences are a smaller and more anteriorly located attachment area for *N. roederi* and a larger, more dorsally situated PAM of the RV. Presence or absence of chomata is unknown for *N. roederi*.

Nanogyra (N.) tramaicensis (Cox, 1952) (p. 94, pl. 10, figs. 5a–c, 6a–c)—This is a large, auriform species of *Nanogyra* from the Lower Oxfordian of western India (Tramau, Kutch district).

Differences to *N. nana* are the more subrectangular shape, a larger adult size (H 5.5 cm, L 4.3 cm, I 2.4 cm, dimensions of holotype), a less curved umbo and a convex RV without any concentric growth lamellae.

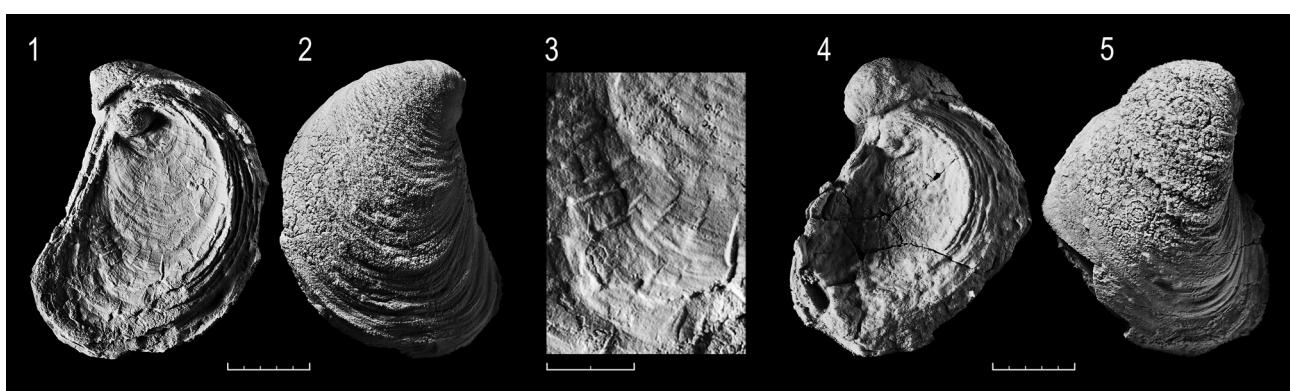


FIGURE 12. *Nanogyra ?(Palaeogyra) fourtaui* (Stefanini, 1925), Antalo Limestone, Mekele Outlier of northern Ethiopia, Oxfordian. 1–5. Refigured after original photographs of Kiessling *et al.* 2011, determined as *Nanogyra nana*: 1, bivalved specimen, RV lateral (= Kiessling *et al.* 2011, text-fig. 13-I-left), PaleoDB 93860 (MB.M.8125.1); 2, same, LV (= text-fig. 13-I-right); 3, same, magnified portion of RV; 4, bivalved specimen, RV (= Kiessling *et al.* 2011, text-fig. 13-J-left), PaleoDB 93860 (MB.M.8125.2.); 5, same, LV (= text-fig. 13-J-right). Scale bars 2 mm and 5 mm.

Nanogyra (Palaeogyra?) fourtaui (Stefanini, 1925) (p. 168, pl. 39, fig. 3)—This small species was originally described from the Callovian and Oxfordian of Somalia. The species was recently synonymized with *Nanogyra (N.) nana* (see Kiessling *et al.* 2011, p. 210; text-fig. 13, figs. I–J). However, this view is difficult to hold up after comparing the European *N. nana* with Stefanini's original figures and with Kiessling *et al.*'s figured images, which were kindly re-photographed at higher magnifications by M. Aberhan (NM Berlin) (Fig. 12.1–5).

The left valve of *N. fourtaui* tends to have a very small attachment scar, a remarkably pointed umbo which is much less opisthogryrate, and a much stronger posterior curvature than *N. nana*. Also, the posterior flank of the RV is pronouncedly concave and its surface lacks the shallow terrace-like growth steps of the European species. In addition, the surface shows some widely spaced minute antimarginal riblets on the posteroventral portion which have never been found on any European *N. nana* (Fig. 12.3). In fact, both characters would be more typical of the subgenus *N. (Palaeogyra)*. However, this cannot be ascertained without demonstrating the presence of chomata in the Somalian species. Unfortunately, all published images show tightly articulated shells so that internal characters of this species remain unknown.

Nanogyra (Palaeogyra) welschi (Jourdy, 1924) (p. 70; pl. 2, fig. V.s.; pl. 6, fig. 7; pl. 8, fig. 11o)—The species was originally described from the Lower Kimmeridgian of Tout-y-Faut (north of Saint-Jean-d'Angély, Charente-Maritime) in France. Eight syntypes are preserved in the Muséum national d'Histoire naturelle in Paris (No. MNHN.F.R52857). *Exogyra gumprechti* Schmidt, 1905 (p. 161, pl. 6, figs. 2–5) from the Lower and Middle Kimmeridgian of Pomerania (NW Poland) seems to be a widely overlooked senior synonym (Deecke 1907; Krause 1908).

The species is of similar shape and size as *N. nana* but possesses chomata (Pugaczewska 1971, p. 294; pl. 1, figs. 2, 6; pl. 33, figs. 1–5; pl. 34, figs. 1–3). It also differs by having a less curved and more pointed umbo, antimarginal riblets and furrows on the LV, and usually a nearly smooth RV with a weakly developed anterior carina and without upturning comm marginal growth crests of the anterior area.

Subgenus *Nanogyra (Palaeogyra)* Mirkamalov, 1963

Type species. *Ostrea virgula* Goldfuss, 1833(b) [= *Nanogyra virgula* (Deshayes, 1831)], original designation by Mirkamalov (1963, p. 152); Upper Jurassic, Germany.

Remarks. Mirkamalov (1963) introduced *Palaeogyra* as a genus, unaware of *Nanogyra* (Beurlen, 1958). Subsequently, Stenzel (1971: N1121) regarded *Palaeogyra* as a junior synonym of *Nanogyra*. That view does not reflect the morphologic differences (ornamentation, chomata) within Jurassic Exogyrinae which diverged into two distinct lineages during the Middle and Upper Jurassic. *Nanogyra (Palaeogyra)* is here considered as a subgenus of *Nanogyra* for species with developed chomata.

Original diagnosis. "Elongated bivalves, frequently curved, thin-shelled, lower shell with radial striations, upper shell smooth, plain. Upper Jurassic of Western Europe and the European part of Russia." (Mirkamalov 1963, p. 152) (translated herein from Russian).

Emended diagnosis. Inequivalve, outline virguliform or sickle-shaped (occasionally posteroventrally bilobate), oval or triangular; always opisthogryrate; degree of spirality variable but usually moderate; ligament area exogyroid, small and narrow, as for the genus; shell thin; microstructure as for the genus (Siewert 1972). Left valve flat to moderately convex; smooth or covered with fine antimarginal riblets or anteriorly with few antimarginal plicae; RV flat, nearly smooth, but antimarginals present; anterior carina absent, weak or distinctly developed; chomata always present in both valves. Species usually smaller than 3 cm (diagnosis based on *N. virgula*, *N. catalaunica*, *N. reniformis*, and *N. welschi*).

Nanogyra (Palaeogyra) reniformis (Goldfuss, 1833)

Fig. 13.1–2; Pl. 7.2–4; Pl. 8.1–2

* 1833b *Exogyra reniformis* nobis.—Goldfuss: p. 34, pl. 86, figs. 6a–c (not fig. 7 = *N. nana*).

1835 *Exogyra reniformis* Goldf.—Roemer: p. 65.

- 1845 *Exogyra reniformis*.—(Goldfuss.)—d'Orbigny: p. 479, pl. 42, fig. 9, 10.
- v 1859 *Ostrea (Exogyra) auriformis* Goldf. sp.—Contejean: p. 322.
- 1866 *Exogyra reniformis* Gf.—Giebel: p. 44.
- 1874 *Exogyra reniformis* Goldfuss—Brauns: p. 355.
- n 1882 *Exogyra reniformis* Goldfuss 1836—Roeder: p. 36, pl. 1, figs. 3a–e, pl. 2, figs. 1a,b.
- ? 1888 *Exogyra reniformis* Goldfuss. 1838—Schlippe: p. 115, pl. 1, fig. 13a,b.
- 1905 *Exogyra reniformis* Goldf.—Schmidt: p. 14.
- 1913 *Exogyra reniformis* Goldfuss—Wójcik: p. 31.
- 1924 *Exogyra reniformis* Goldfuss—Jourdy: p. 71.
- p 1924 *Exogyra nana* Sow.—Jourdy: pl. 2, fig. P.s., left fig. (right = *N. nana*), pl. 2, fig. R.s., left fig. (right fig. = *N. nana*).
- 1971 *Exogyra reniformis* Goldfuss, 1834-40—Pugaczewska: p. 291, pl. 31, figs. 1–5, pl. 32, figs. 1–7.

Type series (not seen). Two syntypes—*Exogyra reniformis* Goldfuss, 1833(b) (p. 34, pl. 86, fig. 6a–c). Buxweiler (= Bouxwiller, Department Bas-Rhin, Alsace), France; from "Fuller's Earth" equivalent, Middle Jurassic, Bathonian.

The types were not studied, and the original composition of the syntype series is presently unknown. However, Goldfuss (1833b, p. 34) gave a good description and figures (pl. 86, fig. 6a–c) allowing a taxonomic identification. The capacious variety, *Exogyra reniformis* var. *gibbosa* figured by Goldfuss (1833b, pl. 86, fig. 7) from the Corallian facies of the Kimmeridgian of Nattheim, Bavaria, Germany, is more likely *Nanogyra nana*.

Goldfuss' reference to Neuenburg (Tithonian?) could not be confirmed, but Roemer's detailed description and comparison with "*Exogyra*" *auriformis* Goldfuss suggests that *N. (P.) reniformis* also occurs in Osterkappeln in the Weser Mountains of Northwest Germany (Roemer 1835, p. 65).

Material. More than 20 LVs from the Banné Marls of Vâ Tche Tchâ (VTT) near Courtedoux (Canton Jura), Lower Kimmeridgian. Two additional specimens from the Contejean collection (MC-27E-38, MC-27E-40) labelled as *Ostrea auriformis* Goldf. by Contejean (1859) from the Lower Kimmeridgian (*cymodoce* Zone, Rang Marls or "Marnes à Ptérocerès") of Beauregard near Montbéliard (France) (for measurements see Appendix, Table 3).

Description. Shape, size—LV nearly entirely attached except for anterior shell margin which bends steeply upwards, posterior margin flat (Pl. 7.2–4), slightly larger than RV (Fig. 13.2); outline round to oval (ear-shaped), usually higher than long; umbo small, moderately opisthogryrate. RV weakly convex, almost flat; not of the typical convex RV type of Malchus (1990, p. 94). Examined specimens 0.6–1.75 cm in height (Appendix, Table 3). Sculpture—LV free margin with fine concentric growth lines and no or few weak, irregular growth crests (Pl. 7.3c); RV nearly smooth, with fine concentric growth lines and few inconspicuous growth ridges at its ventral third. Few thin antimarginal riblets (Fig. 13.2; Pl. 7.2b) restricted to ventral half of the shell; xenomorphic structures absent in present material because of smooth settling grounds.

Ligament area—Short and moderately prosodetic; resilifer only weakly sunken, anterior bourrelet relatively broad, posterior bourrelet reduced to a thin lamella, becoming partially overgrown by a lobe-like projection of the posterodorsal hinge margin.

Internal shell characters—Umbonal cavity missing (Pl. 7.2a) or weak (Pl. 7.3a–b); posterior adductor scar (PAM) of LV small, only shallowly inserted, slightly posterocentral (Pl. 7.3b), outline round to crescentic (Pl. 7.2a, 3b), dorsally truncated, and dorsocentrally slightly concave (Fig. 13.1), scar inconspicuous in some specimens (Pl. 7.4b).

Commissural shelf thin, well developed anterodorsally and fading towards the ventral margin; posterodorsally weak and posteroventrally absent (Pl. 7.3b, 4b). Numerous, well developed straight chomata (Pl. 7.2a, 3b, 4b) along anterodorsal part of the commissural shelf, vanishing ventrally; posterodorsal shelf of LV with few but well developed vermiculate chomata (Pl. 7.2–4; Fig. 13.1); posteroventral margin without chomata; LV posterior chomata (length 0.2–0.6 mm, width 0.09–0.18 mm) larger than anterodorsal chomata (length 0.07–0.16 mm, width 0.07–0.12 mm). Rare observations of thin antimarginal furrows at the inner side of the anteroventral margin (Pl. 8.2) could represent relict chomata.

Microstructure—Not examined, but see *Nanogyra (P.) virgula* for probably comparable features.

Prodissocoach, juvenile—One specimen (VTT009-33b) shows a relatively small internal calcitic mould underlying the prodissocoach and nepioconch (Pl. 7.2b,c) but was not examined under SEM. The length of the dorsally broken prodissocoach mould is ca. 250 µm.

The LV of the juvenile specimen VTT009-33a (Fig. 13.1) shows a narrow, weakly recurved ligament area, with a short (only 500 µm long) and thin, weakly elevated posterior bourrelet (dorsal of the projection of the posterodorsal hinge-margin), which disappears in later growth stages; the juvenile resilifer is initially very narrow, but becomes broader during growth and as wide as the anterior bourrelet.

Paleoecology. *Nanogyra (P.) reniformis* preferentially settled on the interior of dead, moderately large bivalve shells (Banné Marls, Appendix, Table 3). It was also found in the Lower Callovian of Liesberg (Herznach Member, Ifenthal Formation; Switzerland) in a shallow depression on a plain hardground surface, together with several attached specimens of *Pernostrea luciensis* (d'Orbigny, 1850). However, it was absent on the more exposed and eroded cavernous lateral continuation of this hardground. In contrast to its congeners, the present species seemed to have preferred protected habitats with low water energy.

Occurrence. The species is known from the Bathonian of France, Bathonian and Kimmeridgian of Germany, Callovian and Kimmeridgian of Switzerland, and the Oxfordian of Poland (Pugaczewska 1971, p. 294). In NW Germany, the species likely occurs in Osterkappeln (Weser Mountains), Galgenberg, Hoheneggelsen, Goslar and Hannover, all from the "Coral rag" (Oxfordian) (Roemer 1835, p. 65).

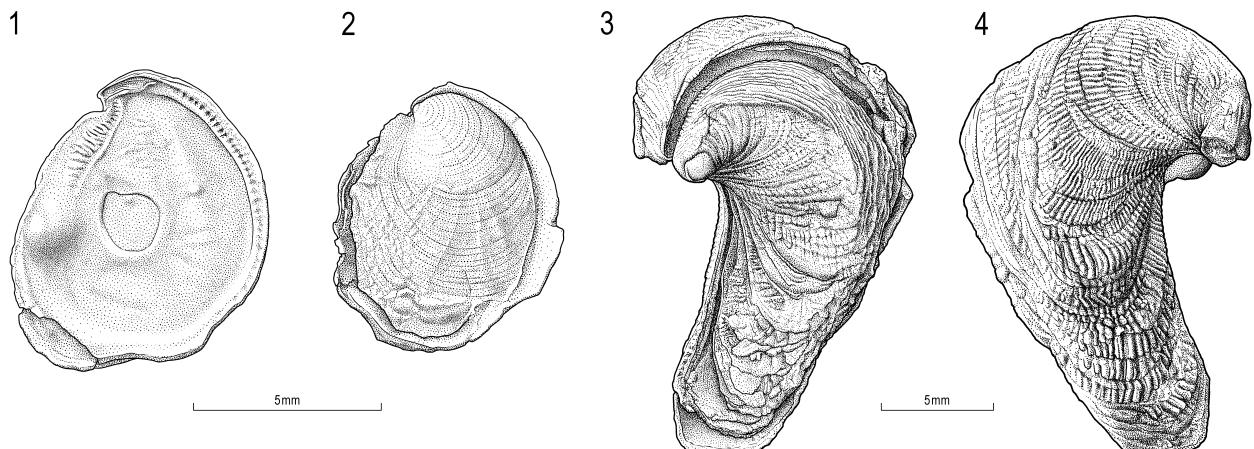


FIGURE 13. *Nanogyra (Palaeogyra) reniformis* (Goldfuss, 1833)(b) and *N. (P.) virgula* (Deshayes, 1831). 1–2. *N. (P.) reniformis*: 1, juvenile LV, interior, VTT009-33a; 2, juvenile bivalved specimen, VTT009-33b (Pl. 7.2a–b); Banné Marls of Vâ Tche Tchâ near Courtedoux, Switzerland, Lower Kimmeridgian; scale x5. 3–4. *N. (P.) virgula*, bivalved specimen; 3, RV, BSY009-915; 4, same, LV; "Lower Virgula Marls", Bois de Sylleux near Courtedoux, Switzerland, Upper Kimmeridgian.

Comparisons. The species was rarely mentioned in the past, probably because it was frequently confounded with the similar *Nanogyra (N.) nana* such as Goldfuss' *Exogyra reniformis* var. *gibbosa* (mentioned above) and "*Exogyra nana*" of Jourdy (1924, pl. 2, fig. R.s., fig. P.s). All *N. (Palaeogyra)* spp. possess chomata [see also *N. (N.) nana* and *Nanogyra (P.) virgula*].

Nanogyra (P.) catalaunica (de Loriol in de Loriol, Royer & Tombeck, 1872) (p. 401, pl. 23, fig. 15, 15a)—This species was described from the Upper Kimmeridgian of the Department Haute-Marne, France; the figured syntype is from the "Virgulien" *eudoxus* Zone of Blaise. Further specimens are from the Portlandian of Bure and Vaux in the same area.

The species differs from *N. (P.) reniformis* by its stronger inflation, the virguliform, strongly curved outline, a larger adult size (1.2–4.2 cm) and the presence of some well-developed antimarginal ribs on the anterior side of the LV. The chomata are more pronounced in *N. catalaunica* and cover nearly the whole anterior side and two-thirds of the posterior margin.

Nanogyra (P.) welschi (Jourdy, 1924) (p. 70, pl. 2, fig. V.s., pl. 6, fig. 7)—This species was described from the Virgulian (Upper Kimmeridgian) of Tout-y-Faut, close to Niort and Saint-Jean-d'Angely, region Poitou-Charentes (W France).

The species has a more triangular shape, a larger size and inflation and shows numerous fine ribs on the outer surface of the LV. Furthermore, it has a more pointed umbo, the posterior lobate protrusion is more pronounced, and chomata are better developed and are also present on the ventral margin (Pugaczewska 1971, pl. 33, 34).

Nanogyra ?(*P.*) *fourtaui* (Stefanini, 1925)—Taxonomic details are discussed under *N. nana*. This species has a more pointed umbo, a much smaller attachment area and finer antimarginal riblets close to the ventral margin of the RV.

Nanogyra (Palaeogyra) virgula (Deshayes, 1831)

Fig. 13.3–4; Pl. 8.3–8; Pl. 9; Pl. 10.1

- 1801 *Gryphaea angustata* Lamarck—Lamarck: p. 399 (nomen nudum, no description).
- 1817 *Chama striata* n. sp.—Smith: p. 45 (nomen nudum, adequate description).
- 1819 *Gryphaea angustata* Lamarck—Lamarck: p. 200 (nomen nudum, short description).
- 1821 *Ostrea virgula*—Defrance: p. 26 (nomen nudum, no description).
- 1830 *Exogyra virgula*, Voltz.—Thurmann: p. 13.
- * 1831 *Gryphæa virgula*, Def.—Deshayes: p. 90, pl. 5, figs. 12–13 (type, ICZN opinion 310).
- 1833b *Exogyra Virgula nobis*—Goldfuss: p. 33, pl. 86, fig. 3a,b.
- 1836 *Exogyra angustata* Lamarck—Bronn: p. 325, pl. 18, fig. 15a,b.
- 1836 *Exogyra angustata* Lamarck—Bronn: p. 325, pl. 18, fig. 15a,b.
- 1837 *Exogyra virgula*, Sow.—Koch & Dunker: p. 12.
- 1846 *Exogyra virgula* Goldfuss—Leymerie: pl. 9, fig. 6.
- 1851b *Exogyra virgula* Defr.—Quenstedt: p. 503, pl. 40, fig. 33.
- 1851 *Exogyra angustata*—Bronn & Roemer: p. 203, pl. 18, fig. 15a,b.
- v 1862 *Ostrea virgula* Defr.—Thurmann & Etallon: p. 275, pl. 39, fig. 10.
- 1872 *Ostrea virgula* d'Orbigny—de Loriol, Royer & Tombeck: p. 397, pl. 23, fig. 8–14.
- 1882 *Exogyra virgula* Defr.—Alth: p. 297, pl. 27, fig. 21.
- 1884 *Exogyra virgula* Defr.—Quenstedt: p. 766, pl. 59, fig. 14, Text-Fig. 270.
- 1893 *Exogyra virgula* Defr.—Fiebelkorn: p. 397, pl. 18, fig. 1–3.
- n 1893 *Ostrea (Exogyra) virgula* d'Orbigny (Defrance)—Greppin: p. 89, pl. 6, fig. 7, 8.
- 1910 *Gryphaea angustata* Lamarck—Douville: pl. 200.
- 1924 *Exogyra virgula* Defr.—Jourdy: p. 68, pl. 2, fig. V.i., pl. 3, fig. V 1–4, pl. 5, figs. 1, 8, pl. 6, fig. 4, pl. 8, figs. 9–10, pl. 9, figs. 2, 17–18, pl. 11, fig. 1.
- 1924 *Exogyra alata* n. sp.—Jourdy: p. 71, pl. 10, figs. 4–6 (for bilobate adult specimens).
- 1925 *Exogyra virgula* Defr. sp.—Dohm: p. 15.
- 1930 *Exogyra striata* Smith, W. 1817—Cox: p. 298, pl. 12, fig. 8, 9.
- 1933 *Exogyra virgula* (Deshayes)—Arkell: p. 440.
- 1964 *Exogyra virgula* (Defrance) 1820—Wellnhofer: p. 50, pl. 3, figs. 2–7, Text-Fig. 31 a–n.
- 1969 *Exogyra virgula*—Ziegler: pl. 2, figs. 1–3, 5, 6, pl. 5, figs. 1–21, pl. 6, figs. 12–15.
- 1970 *Exogyra virgula* (Defrance 1825)—Dmoch: p. 81, pl. 7, figs. 5–6.
- 1971 *Exogyra virgula* (Defrance, 1820)—Pugaczewska: p. 287, pl. 1, fig. 8, pls. 28–30.
- 1971 *Nanogyra striata* (William Smith, 1817)—Stenzel in Moore: p. N1122, figs. 1a–m.
- 1982 *Nanogyra virgula* (Defrance), 1820—Gautret: p. 35, pl. 5, figs. 1–6, 8–29, 32–38, 40–43, 46–47.
- 1983 *Exogyra striata* (W. Smith, 1817)—Birkelund et al.: p. 302.
- 1983 *Nanogyra virgula*—Birkelund et al.: p. 302 (with remark to the ICZN opinion 310).
- 1984 *Nanogyra striata* (Smith)—Buitrón: p. 95, pl. 2, figs. 7–10.
- 1984 *Nanogyra cf. striata* (W. Smith)—Gu Zhi-wei, Chen Jin-hua & Sha Jin-geng: p. 139, pl. 28, figs. 5, 6.

- 1984 *Nanogyra striata* (Smith 1817)—Pockrandt: p. 80, fig. 12a,b.
- 1986a *Nanogyra virgula* (Defrance)—Fürsich & Oschmann: p. 143, text-fig. 2a—c.
- 1986b *Nanogyra virgula*—Fürsich & Oschmann: p. 67, fig. 1, figs. 2a—f, figs. 6a—j.
- 1990 *Nanogyra virgula* Deshayes 1831—Clausen & Wignall: p. 123, pl. 6, fig. A.
- 1996 *Nanogyra striata* (Smith)—Colleté, in Colleté, Fricot, Matrion, Tomasson & Treffot: p. 19, fig. 18.
- 1998 *Nanogyra striata*—Breton: pl. 1, fig. 14.
- 1998 *Nanogyra virgula* (Defrance, 1820)—Machalski: p. 622, fig. 9 A—H.
- 1998 *Nanogyra virgula* (Deshayes)—Radley et al.: p. 84, figs. 3d—e.
- 2001 *Exogyra [Nanogyra] virgula* (Defrance)—B.M. Cox: p. 2731.
- 2006 *Nanogyra striata*—Hicks: p. 36.
- 2006 *Nanogyra striata* (Smith 1817)—Richardt: p. 9, 18.
- 2007 *Nanogyra virgula* (Defrance, 1821)—Delvene: p. 20, pl. 3, fig. 6.
- 2008 *Nanogyra virgula* (Defrance, 1821)—Scholz, Schweigert & Dietl: p. 125, fig. 16.

Holotype (not seen). *Gryphaea virgula* Deshayes, 1831: p. 90, pl. 5, figs. 12—13, by monotypy; non Defrance 1821, p. 26; validation as type by the ICBN, opinion 310 (Hemming 1954, p. 355). France, exact type locality and position unknown, probably from a virgula marl unit of the Paris Basin, probably Upper Kimmeridgian, Upper Jurassic.

Material. Few specimens from the Banné Marls (*cymodoce* Zone, Lower Kimmeridgian) of Vâ Tche Tchâ (VTT) near Courtedoux, Tunnel le Banné (TLB) at Porrentruy.

Numerous, mostly poorly preserved specimens from the *mutabilis* Zone (*lallieranum* Subzone, Upper Kimmeridgian) of Sur Combe Ronde (SCR), mostly from the “Lower Virgula Marl” (bed 4500, *eudoxus* Zone) at Sur Combe Ronde (SCR) and Bois de Sylleux (BSY) near Courtedoux (Switzerland) (for measurements see Appendix, Table 4).

Material from the “Lower Virgula Marl” of the Banné hill in Porrentruy (Thurmann-Collection, MJSN, S294/1—9, S294/11—12) (see Pl. 8.7—8 and Pl. 9.1—9).

Description. Shape, size—LV larger and much more inflated than flat RV; with a curved carina parallel to anterior margin; maximum convexity anterodorsal; outline variable but commonly comma-shaped (virguliform); larger (adult) specimens rarely with bialate (bilobate) ventral margin or, when attached to long objects, with an elongate xenomorphic outline (Pl. 8.5—6); umbo pointed, exogyroid (always opisthogyrate). RV of the convex-concave type (*sensu* Malchus 1990, p. 94). Coiling reaches *ca.* 225° (Pl. 9.10c—e: early shell is P1 and nepioconch; abrupt opisthogyrate twists of 90° between 1.5 and 4.3 mm shell height, 90° between 4.3 mm and 9 mm and *ca.* 45° between 9 mm and final height). Examined specimens 0.3—3 cm high (Pl. 9; Appendix, Table 4).

Sculpture—Attachment area usually few millimetres in diameter at tip of umbo (Pl. 9.1—5), but larger attachments with nearly the whole LV on hardgrounds or on other specimens and large objects also common. LV with fine antimarginal, dichotomous striae or thin riblets, crossed by inconspicuous commarginal growth lines and few irregularly spaced, growth ridges (Pl. 9.10a; Fig. 13.4); striation very narrowly spaced (Pl. 8.5) to rather coarse (Pl. 9.4b); striae restricted to outermost shell layers, eroded or chipped specimens from rock surfaces appearing smooth. RV nearly smooth, with commarginal growth lines, few growth crests (Pl. 9.10c—e; Fig. 13.3) and faint antimarginal striae (mainly on ventral half); anterodorsally bordered by a carina consisting of upturned crowded growth lamellae (Pl. 9.10e; Fig. 13.3); xenomorphic features rare and mostly weak (Pl. 8.6c; Pl. 9.9a).

Ligament area—Strongly twisted and prosodetic; juvenile ligament of LV narrow and deeply sunken, covered by the projected posterodorsal margin (overhang or ledge of Malchus 1990, p. 79). Visible part of the resilifer as a thin furrow, posterior bourrelet narrow, weakly elevated, anterior bourrelet twice as broad (Pl. 8.4a, 7a).

Internal shell characters—Umbonal cavity weak or absent; posterior adductor scar (PAM) in LV small, oval to kidney-shaped with truncated, convex dorsal end, situated posterocentral or slightly ventral of the midline (LV: Pl. 8.4a, 7a). PAM of RV high-oval, close to posterior margin (in the zenith of the curve) (Pl. 9.9b).

Commissural shelf well developed, in LV with small straight chomata (Pl. 8.4a, 7a, 7d), well developed dorsally, but may reach anteroventral margin (Pl. 8.4a). Posteroventral margin always without chomata (both valves); in LV posterior chomata (length 0.18—0.6 mm, width 0.08—0.1 mm) of the subligamental area larger than at

anterodorsal margin (length 0.16–0.26 mm, width 0.05–0.1 mm); posterodorsal chomata more narrowly spaced and slightly curved, grooves of anterior catachomata short but with 0.1 mm relatively wide. Relict chomata present in both valves at dorsal margin (LV: Pl. 8.4a, RV: Pl. 9.10b).

Microstructure—Not investigated, but according to Siewert (1972, p. 18–19) regularly foliated, with few lamellar lenses close to umbo and towards shell margin. Dense radial striation of LV restricted to thin layer of the outer shell (as proven by strongly abraded shells from bed 2100). Prismatic outer shell layer of RV almost entirely destroyed.

Prodissococonch, juvenile—Two RVs (BSY009-917; SCR002-1367) showing calcitic internal moulds of prodissococonch and nepicoconch (Pl. 9.10c–e) and, prodissococonch mould with missing umbo respectively (Pl. 9.11, Pl. 10.1a–b). Prodissococonch/nepicoconch boundary of first shell hardly visible at present magnification; sharp margin (< 2 mm) marking boundary between nepicoconch and later juvenile shell stage; nepicoconch with similar convexity and main growth direction as prodissococonch proper (species specificity of this observation not proven). Length of second, broken prodissococonch mould *ca.* 350 µm (Pl. 9.11 and 10.1a–b) (fide Malchus 2014, pers. comm.).

Paleoecology. In the Reuchenette Formation, the species occurs in abundance in marl beds 300 (*cymodoce* Zone), 2100 (*mutabilis* Zone), and in several lumachelles (4500, 6000, “Oyster Limestone”) above hardground bed 4000 (lower *eudoxus* Zone, *caletanum* Subzone) (see Fig. 4C).

In Bed 300, the species co-occurs with *N. (N.) nana*, *N. (P.) reniformis*, *Actinostreton gregareum*, large *Stegoconcha granulata* (J. Sowerby, 1822) in life position (upper part of this horizon), and a rich echinid fauna including *Hemicidaris mitra* Agassiz, *Pseudocidaris thurmanni* (Agassiz), *Polydiadema* sp., and *Pygurus* sp. Overall, individuals are small (< 1 cm). Many specimens were attached to cylindrical objects (Pl. 8.6); similar attachment scars on co-occurring *A. gregareum* are identifiable as *Goniolina geometrica* imprints (Pl. 18.1–3). The paleoenvironment was probably a shallow, low energy, marine setting with dasycladacean meadows.

Bed 2100 also contains *N. nana* and *Circumula cotyledon*. The abundance of *N. virgula* defines the beginning of the Virgulian facies of the old literature. Shells are remarkably larger than material from the Lower Kimmeridgian (Appendix, Table 4). The outer shell layers of most of the left valves are eroded, which is probably due to *in situ* (or parautochthonous) reworking under a higher energy environment.

The first marly layers above hardground bed 4000 represent a nearly monospecific *N. virgula* lumachelle of 1 m thickness called “Lower Virgula Marl” (“Marnes à *Virgula inférieur*”) referring to the lower lumachelles within the *eudoxus* Zone. The specimens are relatively small (mostly < 1.5 cm). Specimens are usually attached to small shells (including other specimens of *N. virgula*), tiny cerithiid gastropods or unidentified round, smooth objects. Bivalved specimens of *N. virgula* and of articulated infaunal *Trigonia*, *Myophorella*, *Thracia*, and of semi-infaunal *Gervillella* are common and suggest a calm, soft bottom paleoenvironment. The low diversity and small size of shells probably indicate unfavourable conditions for benthic life. *N. virgula* appears to be autochthonous and because of its abundance (high reproduction rate) to have been a r-strategist. The lumachelles of the “Upper Virgula Marl” (“Marnes à *Virgula supérieur*” sensu Contejean 1866; = “Oyster Limestone” of Jank 2006a–c), *ca.* 20 m higher in the section, were not investigated in detail for this study.

According to Ziegler (1969, text-figs. 9–10, pls. 3–4), *N. (P.) virgula* predominantly attached itself to unstructured, probably organic material such as algal leafs and thin oblong stems. Fürsich & Oschmann (1986a, p. 71, text-fig. 7) interpreted Kimmeridgian *N. virgula* lumachelles from the Aquitaine Basin (France) as nearshore situated storm shell beds. They suggested a life style as secondary soft substrate dweller similar to *Gryphaea*. The present findings from bed 300 suggest a similar life style as inferred by Ziegler (1969), but present evidence from layer 4500 does not support a preference for soft substrate.

Occurrence. Oxfordian–Tithonian in Europe, Oxfordian in France, Kimmeridgian in France, England, Germany, Poland, Lower–Upper Kimmeridgian in Switzerland (Banné Marls, Virgula Marls); Upper Jurassic (Kimmeridgian?) of Ukraine; Tithonian of Germany (Wellnhofer 1964, Ziegler 1969).

Remarks. Nomenclature—*Gryphaea angustata* Lamarck, 1801 and *Chama striata* Smith, 1817 are both senior synonyms of *Nanogyra virgula* (Defrance, 1821: *Gryphaea*). Of these, only *Chama striata* was accompanied by an adequate description, leading Cox (1930, p. 298, pl. 12, fig. 9) to re-establish the species as *Exogyra striata* (Smith, 1817) and to determine a lectotype.

Arkell (1951, p. 234), however, argued that the species name *virgula* had been commonly used during the past 150 years and was name-giving for the French “Marnes à *Exogyra virgula*”, the German “Virgula-Mergel”, and the

informal stratigraphic stage "Virgulien" of Thurmann (1852) (not 1833 as written in Arkell 1951). He therefore recommended declaring *virgula* a protected name which was supported by Cox (1951) and finally validated by ICBN opinion 310 (Francis Hemming, 1954, p. 355). Stenzel (1971, p. N1121) was apparently unaware of this formal act.

Evolution of *N. virgula* from *N. nana*—Jourdy (1924, p. 67) suggested that *N. virgula* evolved from *N. nana* via the transitional *N. praevirgula* (Douville & Jourdy, 1874), an idea that was followed by Thalmann (1966) and Ziegler (1969). However, the alleged transitional *N. praevirgula* (Douville & Jourdy, 1874), originally a *nomen nudum*, is doubtfully a valid species. According to the description and figures subsequently published by Jourdy (1924, p. 65, pl. 9, fig. 2, specimens 4–8 and 10–16), it appears more likely that the author was misled by phenotypic, slightly furrowed variants of *N. nana* caused by different attachment objects (e.g. *Goniolina*, Jourdy 1924, pl. 9, fig. 2.12) and sizes. In addition, there are older, chomata-bearing species such as *N. (P.) reniformis* (Goldfuss) or the Callovian *Nanogyra bigoti* (Jourdy, 1924) which are much more likely to have given rise to *N. (P.) virgula*.

Comparisons. *Exogyra alata* Jourdy, 1924 (p. 71, pl. 10, fig. 4–6)—This “species”, originally described from the Kimmeridgian of Saumont-la-Poterie (region Pays de Bray, Normandy, France), appears to be just an unusually shaped, large variant (up to a height of 4.7 cm and 7.2 cm length, Jourdy 1924, pl. 10, fig. 6) of *N. (P.) virgula*. [Jourdy (1924) wrote Gaumont rather than Saumont which is here deemed to be a wrong interpretation of G for S on the handwritten (by Peron) label; an internet search provided no results for a locality named Gaumont-la-Poterie but for Saumont-la-Poterie, which is mentioned in context with the Kimméridgien]. Only few adult and megalomorphic specimens in large collections of *N. virgula* have a bialate ventral margin with a sulcus between an additional anteroventral projection and the normally developed posteroventral margin [*N. virgula*, in de Loriol, Royer & Tombeck (1872, pl. 23, figs. 13–14)], but such phenotypic variations do not justify an independent species.

Nanogyra (Palaeogyra) catalaunica (Loriol in Loriol, Royer & Tombeck, 1872)—Taxonomic issues are discussed under *N. (P.) reniformis*. *Nanogyra (P.) catalaunica* shares well-developed chomata with *N. (P.) virgula* but differs by the presence of up to five prominent radial costae on the anterior side, a less curved shape, and a larger adult size up to 5 cm (see Jourdy 1924, p. 71, pl. 8, figs. XI-p, 4 specimens). The costae (ribs) and general morphology are very similar to the Cretaceous genus *Ceratostreon* Bayle, 1878.

Nanogyra (P.) reniformis (Goldfuss, 1833)(b)—This long-ranging species occurs from the Bathonian to the Kimmeridgian in Europe. It is smaller than *N. virgula*, less inflated and auriform (ear-like) rather than comma-shaped. The LV also has a much larger attachment area and lacks antimarginal ornamentation on the LV. Chomata are better developed posterodorsally and disappear towards the ventral margin (in contrast to *N. virgula*).

Nanogyra (P.) welschi (Jourdy, 1924)—Taxonomic details are provided under *N. (P.) reniformis*. *Nanogyra (P.) welschi* is distinguishable by its oval shape, less inflation, a larger PAM, stronger developed chomata, and lack of antimarginal riblets (Pugaczewska 1971, p. 294, fig. 5c,d, pl. 1, fig. 2, 6, pl. 33–34).

Nanogyra ?(N.) bigoti (Jourdy, 1924) (p. 57, pl. 6, fig. 6)—This species was first described from the Callovian of Chemilli (Department Orne, France). It differs from *N. virgula* by having a smooth LV. The presence or absence of chomata is unknown, but the general appearance is closer to *Nanogyra (Nanogyra) nana*.

Nanogyra (N.) monoptera (J.A. Eudes-Deslongchamps & J.F.E. Eudes-Deslongchamps, 1859) (p. 32, pl. 5, figs. 1–4)—It was first described from the "couches à *Leptaena*" of the Lower Jurassic (Toarcian) from May-Sur-Orne, Calvados (France). It differs from *N. virgula* by a strongly developed posterodorsal auricle in both valves, the more dorsally situated and larger PAM, and lack of chomata and of antimarginal ornamentation (see also Jourdy 1924, p. 52, pl. 2, fig. T, pl. 7, fig. 4; Malchus & Aberhan 1998, p. 630).

Nanogyra (Nanogyra) michalskii (Lewinski, 1923) (p. 66, pl. 4, figs. 1–3)—This species from the Volgian (Tithonian) in Poland has a comparable shape to *N. virgula* but with strongly developed costae; it lacks chomata, which places it in *N. (Nanogyra)*.

Praeexogyra acuminata (J. Sowerby, 1816) (p. 82, pl. 135, fig. 2)—A more detailed discussion is given under the comparisons of *Praeexogyra dubiensis*. This species resembles *Nanogyra (P.) virgula* in shape, size, and by the presence of fine antimarginal riblets on the RV. Main differences are the lack of a twisted umbo, and therefore not exogyroid ligamental area, and lack of both chomata and antimarginal riblets on the LV.

Family Flemingostreidae Stenzel, 1971

Subfamily Crassostreinae Scarlato & Starobogatov, 1979

Helvetostrea new genus

Type species. *Ostrea sequana* Thurmann & Etallon, 1862; lectotype designation herein (see under species); Upper Oxfordian, Switzerland (Canton Jura).

Diagnosis. Inequivalve, left valve moderately inflated, outline irregularly ovate, rectangular to slender-spatulate; umbo truncated owing to large attachment area. Outer surface with thick (squamous) irregular growth lamellae. Ligament area becoming very high (similar to *Saccostrea*), growing essentially ventrally in adult; resilifer deep and flanked by equally broad bourrelets. Umbonal cavity (LV) deep; adductor scar round to high-oval, posterocentral to posterodorsal. Left valve with many large structural chambers, hollow or filled with sparry cement or sediment; internal structures of RV unknown.

Etymology. Word combination derived from *Helvetia* (= neo-Latin for Switzerland) and the Recent oyster genus *Ostrea*. The gender is female.

Remarks. Species of *Helvetostrea* differ from *Liostrea*, *Pernostrea*, *Africogryphaea*, and *Deltoideum* by developing a large *Saccostrea*-like ligament area, a deep umbonal cavity and many large shell chambers, the latter eventually leading to considerable growth in thickness. They differ from most *Praeexogyra* species by being highly chambered, except for “*P.* hebridica” (see discussion under *Praeexogyra*). *Helvetostrea* is distinguished from *P. hebridica* and from *Crassostrea* species by having an essentially round and posterodorsal adductor scar and from *Saccostrea* by lacking chomata.

The genus differs from *Ostrea* (and actually the entire subfamily Ostreinae) in its well-developed umbonal cavity and its adductor outline and position. In addition there is no evidence to assume brooding for any Jurassic, and in fact any Mesozoic oyster species, as is characteristic of Recent Ostreinae (Malchus 1995; Malchus & Sartori, 2013; own data herein). The Middle Jurassic (Bajocian, Bathonian) *Helvetostrea* n. gen. *explanata* (Goldfuss, 1833)(b) may be the oldest representative of the genus currently known.

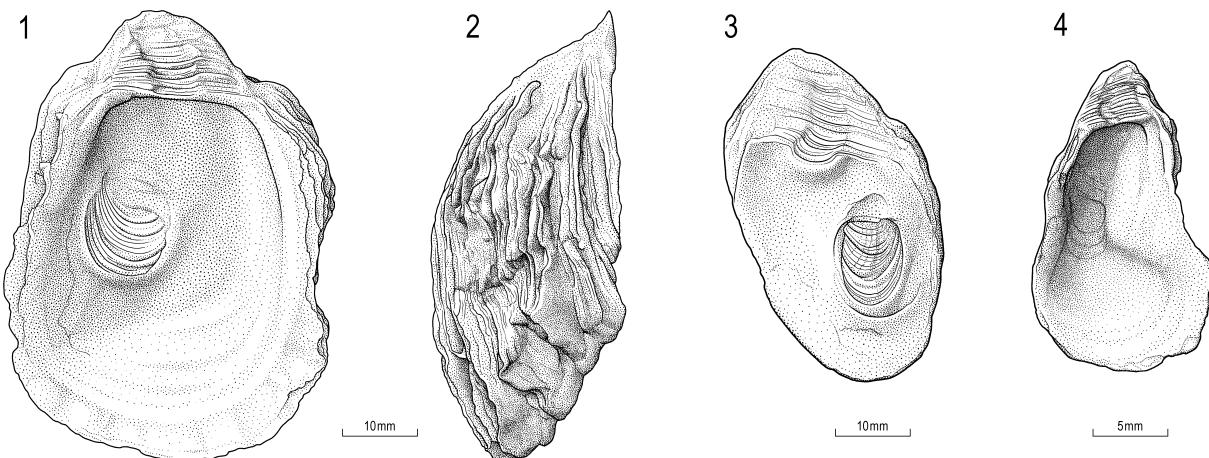


FIGURE 14. *Helvetostrea* n. gen. *sequana* (Thurmann & Etallon, 1862). Specimens attached to each other (Pl. 11.1a–d), CTD-TCH002-306, Tchâfouè near Courtedoux, Upper Kimmeridgian, *mutabilis* Zone: 1, LV, interior (306a); 2, same LV, anterior view; 3, RV (306b), served as settling object for LV of Fig. 14.1; scale x1; 4, juvenile LV (306c), posteriorly attached to LV (306a).

Helvetostrea n. gen. *sequana* (Thurmann & Etallon, 1862)

Figs. 14–16; Pl. 4.7–9; Pl. 11.1–5; Pl. 12.1–2; Pl. 20.2

- ? 1848 *Ostrea sequana*—Dufrénoy & de Beaumont: p. 594.
1852a *Ostrea Sequana* nob.—Thurmann: p. 213 (nom. nud.).

- 1854 *Ostrea Sequana* Th.—Thurmann: p. 354 (nom. nud.).
- 1858 *Ostrea sequana* Thurm.—Oppel: p. 150, 164, 165.
- 1861 *Ostrea Sequana*, Th. —Thurmann & Etallon: p. 37, 64.
- 1862 *Ostrea Sequana*, Th.—Etallon: p. 407.
- * 1862 *Ostrea sequana*, Th.—Thurmann & Etallon: p. 270, pl. 38, fig. 6.
- 1870 *Ostrea Sequana*, Th.—Greppin, J.-B.: p. 104.
- 1887 *Ostrea sequana* Th.—Roberts: p. 238.
- 1917 *Ostrea Sequana* (Thurm.) Etallon—Rollier: p. 589.
- 1971 *Liostrya sequana* (Thurmann, 1862)—Pugaczewska: p. 257, pl. 16, figs. 1–4.

Lectotype (designated herein). *Ostrea sequana* Thurmann & Etallon, 1862, p. 270–271, pl. 39, fig. 1, left valve. The type specimen (refigured on Fig. 15.1) was not traceable in the MJSN Porrentruy and is apparently lost. However, ICZN Article 74.4 permits the designation of an illustration as lectotype when the type specimen is lost or not traceable.

Combe d'Essert-Tainie, a gorge (not traceable on the available maps of the region) but situated most likely northwest of Bressaucourt (near Chevenez, Ajoie, Canton Jura), "Marnes à Astartes" (now Bure Member, Vellerat Formation, *Epipeltoceras bimammatum* Zone), Upper Oxfordian; coordinates: 47°23'17.36"N, 7°02'15.98"E; the coordinates refer to Bressaucourt.

Material. Lectotype (see above) and paralectotype (AC1766, B.4.15.4.1)—Only one small rock-sample from the type series was traceable in the MJSN Porrentruy. The small piece of grey, dense limestone contains several cross-sections of weathered and only partially preserved specimens exhibiting the typical hollow chambers of *H. sequana* but no other shell details. Due to the poor preservation none of the specimens is suitable to be chosen as lectotype.

The original label of the paralectotype refers to *Ostrea sequana* nob, Th. 1846, from Bressaucourt. However, according to Etallon's introduction to the "Lethea bruntrutana" (Thurmann and Etallon, 1861, p. 3), the species name was initially a *nomen nudum* based on an unpublished note by Thurmann (1848) titled "Sur l'*Ostrea sequana*". Therefore, Dufrénoy & de Beaumont (1848) and Thurmann (1852, 1854) can only have referred to this unpublished name, whereas the valid introduction is given in Thurmann & Etallon (1862).

Others—One small ("juvenile") LV from the basal Banné Member (horizon 300, *cymodoce* Zone, Lower Kimmeridgian) of Vâ Tche Tchâ near Courtedoux (VTT001-1169b, Pl. 11.3) and more than 20 larger ("adult") specimens (mostly LV, Pl. 4.7–8; Pl. 11; Pl. 12.1–2) from the "Virgulien" facies of the uppermost Courtedoux Member, Upper Kimmeridgian (horizons 2400–3500, *mutabilis* Zone, *lallierianum* Subzone) of Sur Combe Ronde (SCR) and Tchâfouè (TCH) near Courtedoux. The best preserved specimens are listed in the Appendix, Table 5.

Two small and thin-shelled specimens labelled as *Ostrea sequana* Thurmann (MJSN S.1337, A.2.18.2.4) from the Koby collection in the MJSN belong to an undetermined liostreine species.

Description. Shape, size—Highly variable including subrectangular, trapeziform, subtrigonal shapes. LV sometimes much elongated in height, always higher than RV, usually moderately inflated, greatest convexity close to umbo. Attachment area commonly restricted to umbonal region, medium-sized in separately growing individuals (Pl. 4.7, 9a; Pl. 11.2, 4a) or large when growing in clusters (Pl. 4.8, Pl. 12.2a). RV (only two specimens known; Pl. 11.1b; Appendix, Table 5) relatively small and flat, with subrectangular shape and slightly convex, shell thickness at the ventral margin 3–4 mm. Observed maximum size 8 cm (height) (Appendix, Table 5).

Sculpture—LV with thick growth lamellae, irregular, imbricating (spaces between squamae filled with sediment, later overgrown by new shell foils); occasionally with few undulating radial ribs; shell surface of folds and depressions, in some cases pustular. Single RV relatively smooth, with few weak comm marginal furrows and fine growth lines.

Ligament area—Overall growing ventrally, ostreoid, with a straight or slightly undulating resilifer, rarely anteriorly directed (Fig. 14.3–4; Pl. 11.2). LV resilifer deep, flanked by equally broad, elevated bourrelets (Fig. 15.2); outer bourrelet flanks dipping steeply towards commissure (*ca.* 30–60°) (Pl. 11.4a; Fig. 15.5), confined anteriorly and posteriorly by deep narrow troughs (Fig. 15.2, 4; Pl. 11.2). RV resilifer supported by a callous-like shell buttress (sensu Stenzel 1971, p. N1029, N973, fig. J14a,b) (Fig. 14.3; Pl. 11.1b)

Internal shell characters—LV commissural shelf, dorsally narrow and bounded by inner lateral ridge; shelf broadening ventrally. Posterior adductor scar subcircular to high-oval, dorsally truncated or weakly concave, scar slightly sunken below general depositional surface; position essentially posterodorsal (*ca.* 1/3 sub-posterocentral). (Fig. 14.3–4; Fig. 15.2; Pl. 11.1a,b). PAM insertion in RV with projected ventral border (Pl. 11.1b) (buttressed sensu Stenzel 1971, p. N1029). Quenstedt muscle scar not seen. Chomata and relict chomata questionable (Pl. 11.3a,b, 5c,d).

Microstructure—LV with thick regularly to partly complex cross-foliated outer-middle layer; middle-inner layers largely chambered, some (probably originally) hollow (Pl. 12.1a,b), some filled with chalky deposits (mocret); some filled with sediment or diagenetic cement (Pl. 12.2b,c; Pl. 20.2a–d).

Prodissocoach, juvenile—Prodissocoach and early juveniles unknown.

Paleoecology. At its type locality, the species formed aggregates or small buildups (“framestones”) of up to several decimetres thickness intercalated between coral-bearing, calcareous marls and unfossiliferous marls („Zone Astartienne“); the lateral extensions are unknown. Thurmann & Etallon (1861, p. 37; 1862, p. 271, pl. 39, fig. 1) found the species together with *Nanogyra nana* (= *Exogyra bruntrutana* Thurmann), for example, in the “Lumachelle à *Exogyra bruntrutana* et *Ostrea sequana*”. The species is associated with a diverse coral fauna of the „Zone à polypiers“ (Thurmann & Etallon 1861, p. 37, 62), crinoids (genus *Apiocrinites*) and terebratulid brachiopods.

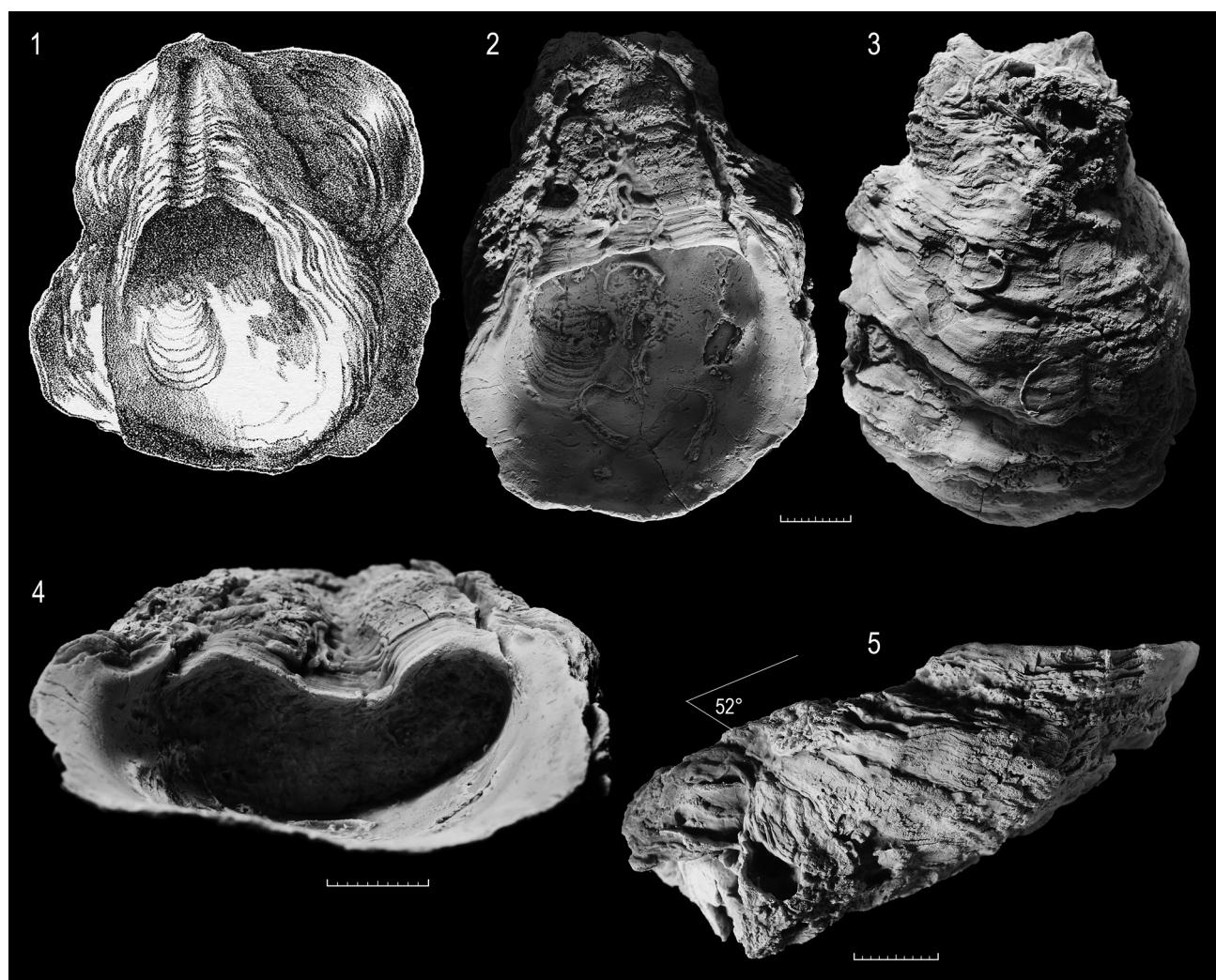


FIGURE 15. *Helvetostrea* n. gen. *sequana* (Thurmann & Etallon, 1862). 1. Lectotype, refigured from Thurmann & Etallon (1862, pl. 39, fig. 1); LV attached on other specimens of the same species, Bressaucourt near Chevenez (Canton Jura), Upper Oxfordian. 2–5. LV, CTD-SCR003-1237, Sur Combe Ronde (bed 2400), Upper Kimmeridgian, *mutabilis* Zone: 2, interior; 3, lateral; 4, ventral view into the umbonal cavity with cross-sectional shape of ligament area; 5, posterior side view, with distinct angle (52°) between commissure and ligament area. Scale bars 10 mm.

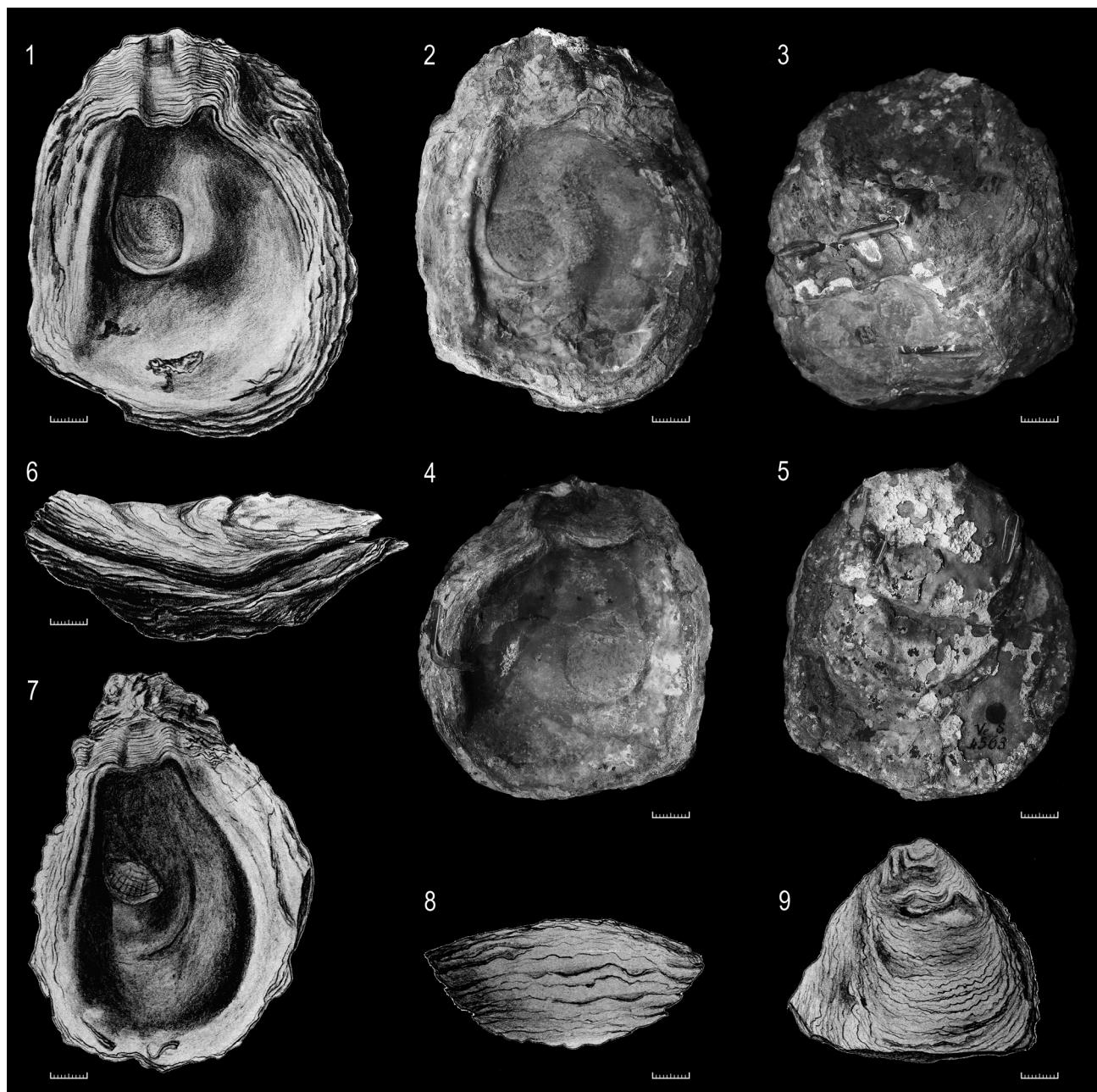


FIGURE 16. *Helvetostrea?* *caprina* (Rollier, 1917) and *H. oxfordiana* (Rollier, 1917). 1. “*Ostrea*” *caprina*, refigured from Rollier (1917, pl. 39, fig. 2), LV, from Gösgen (Aargau), NE Switzerland (Geissberg Member, Late Oxfordian). 2–6. ?*Helvetostrea* n. gen. *caprina*, same specimen as Fig. 16.1, here designated as lectotype, coll. ETHZ, Ve.S. 4563; 2, LV interior, hinge area poorly drawn in the original figure (compare Fig. 16.1); 3, LV, lateral; 4, RV, interior; 5, RV, lateral; ETH Zürich, photos by Dr. Pika-Biolzi (Zürich), specimen not whitened; 6. Lectotype, anterolateral (both valves re-articulated), refigured from Rollier (1917, pl. 40, fig. 2b). 7–9. *Helvetostrea oxfordiana*. Figured bivalved type specimen of *Ostrea oxfordiana*, cf. Rollier 1917, pl. 40, fig. 1a–c, ETHZ Ve.S. 5146, Klein-Kembs (Kleinkems) near Lörrach (Baden-Württemberg), Germany (“Terrain à Chailles”), Lower Oxfordian, *Cardioceras cordatum* Zone: 7, LV, interior; 8, LV ventral view; 9, RV lateral. Scale bars 10 mm.

In the study area, the species occurs as autochthonous element in horizons 2600 and 2900–3000, and allochthonous in horizons 300 (Banné Marls) (one small juvenile LV, VTT001-1169b, Pl. 11.3; Pl. 14.6), 2400, 2700 (Pl. 11.1d), and 3500 (Fig. 4C).

Horizon 2600 is a mostly fine-grained, partially iron-oolitic limestone yielding numerous aggregates of *H. sequana* LVs. Aggregates are reminiscent of ostreoliths described by Wilson *et al.* (1998), with irregularly arranged specimens of different growth stages, growing in all directions which suggests several overturns (Pl. 4.8; Pl. 12.2).

Shell surfaces are covered by serpulids and small LVs of *Nanogyra nana* and *Gastrochaenolites* borings. In one case, *Lithophaga* sp. is preserved in its borehole. The species co-occurs with stenohaline bivalves (*Gervillella*, *Cercomya*, *Myopholas*, *Anisocardia*) and the echinoid *Pygurus* sp.

Horizon 2900 is a fossiliferous lithoclastic limestone with numerous LVs of *Helvetostrea*; co-occurring fauna includes species of *Trichites*, *Gervillella*, *Cucullaea*, *Myopholas*, *Placunopsis*, rare *Myophorella* (shells replaced by calcite), and recrystallized coral heads up to 20 cm in size. This accumulation may represent a condensation horizon. It is truncated by a hardground (horizon 3000) penetrated by *Gastrochaenolites* sp. and overgrown by large, strongly abraded specimens of *Circunula cotyledon*.

The autochthonous or paraautochthonous occurrences and associated faunas suggest that *Helvetostrea sequana* lived preferentially in shallow, fully marine environments where it formed buildups (type locality), small clusters, or ostreoliths.

A similar setting was described by Wilson *et al.* (1998) for the American ostreoliths which were formed by *Circunula? strigilecula* reaching sizes of up to 50 cm. They occurred on hardgrounds and oolitic shoals but also in lagoonal facies (Middle Jurassic Carmel Formation, Utah, USA). Fürsich *et al.* (1994) reported reefoidal frameworks several meters wide and up to 3.5 m high constructed by *H. expansa*, red algae (*Solenopora "portlandica"*), the cyclostome bryozoan *Hyporosopora portlandica* (Gregory), and some cemented *Plicatula damoni* (Cox, 1925). Hoffmann & Krobicki (1989) described a buildup of 2 m lateral and 0.8 m vertical extension from the Middle Jurassic of Poland constructed by *H. explanata* (Goldfuss) surrounded by a dysaerobic mudstone facies. The buildup occurs in high energy sediments, deposited as an intercalation during a "regressive" phase, well documented by a shell bed with many clasts (including hiatus-concretions) with borings of *Gastrochaenolites lapidicus* Kelly & Bromley, 1984 and encrusting serpulids at the base of the buildup (Hoffmann & Krobicki 1989, p. 308–309, fig. 3).

Comparisons. Species of *Helvetostrea* n. gen. and morphologically similar forms are discussed below in alphabetical order.

"*Ostrea*" *caprina* Rollier, 1917 (pl. 39, fig. 2, and pl. 40, fig. 2a,b; pl. 39, fig. 2 is refigured on Fig. 16.1)—The species was first mentioned by Moesch (1867: p. 148) from Gösgen near Olten (Aargau) and found in the "*Perna*" beds of the Geissberg Member (sensu Gygi 1969), Upper Oxfordian (*bimammatum* Zone) of northeastern Switzerland. However, Rollier (1917, p. 562) was the first to provide a valid description. The type series consisted of one bivalved specimen with both shells isolated and an unknown number of other specimens mentioned in the text from different locations, but only the figured bivalved specimen (ETHZ Ve.S. 4563) of Rollier (1917: pl. 39, fig. 2, pl. 40, fig 2a,b) is still preserved in the collections of the ETH Zürich. It is here chosen as lectotype of *Helvetostrea caprina* (Rollier, 1917) and figured on Fig. 16.1, 2–6.

This species is less inflated than *H. sequana*, more subrectangular and lacks an umbonal cavity. Shell habitus and ligament area of the lectotype LV (Fig. 16.1–2) mimic a RV, but the adductor position and presence of an attachment area confirm that it is a LV. The comparison of the original figures of Rollier (1917) with photographs of the lectotype reveals a mismatch of the real proportions and hinge morphology (Fig. 16.1–6).

"*Ostrea*" *expansa* J. Sowerby, 1819 (p. 65, pl. 238, fig. 1)—This species was first described from the Tithonian Tisbury Limestone Member of the Portland Stone Formation (*Titanites anguiformis* Zone) in Wiltshire, England. Sowerby's figured specimen, a silicified RV, was assumed to be lost (Cox 1929, p. 147). However, Spamer & Bogan (1989) may have found the original or a syntype and potential lectotype in the Bennett-collection at the Academy of Natural Sciences of Philadelphia (USA) which is listed as "*Ostrea expansa* J. Sowerby 1819, pl. 238, top figure [1]; syntype(?), ANSP 56158 (B.C. 287; Bennett's[?] no. 196); Fonthill, Wiltshire". The Fonthill Abbey Wood is situated 3 km northwest of Tisbury.

Sowerby's figure is somewhat reminiscent of the flat, broadly crescentic shape of *Deltoidium* (Rollier 1917, p. 566: *Deltoidium expansa*). However, the overall shape is spatulate without a concave posterodorsal margin typical of *Deltoidium*. Furthermore, the shell is thicker and larger, and the PAM more centrally situated. Despite these differences, Cox (1925, p. 130) assumed a transition between *Deltoidium delta* (Smith, 1817) [= *O. deltoidea* J. Sowerby, 1816, non Lamarck 1806, = *Ostrea sowerbyana* Brönn, 1836, replacement name for the former] and *O. expansa*. Pugaczewska (1971, p. 269), Fürsich *et al.* (1994) and Fürsich & Hautmann (2005) assigned the species to *Liostrea*. However, the spatulate shell shape and presence of large shell chambers below the ligament area suggest that *O. expansa* belongs to *Helvetostrea*. The species differs from *H. sequana* by a broader resilifer, slender bourrelets, a larger PAM, a convex RV and a small umbonal cavity (Fürsich *et al.* 1994, p. 138, 141, fig. 5).

Remarkable is the distribution of both species in rocks representing shallow marine environments that are overlain by paleosoils with dinosaur track sites of the Lower Purbeck Formation in England (Ensom & Delair 2007) and, respectively, the Kimmeridgian track-bearing horizons (tidal-flat laminites) of the Reuchenette Formation in Switzerland (Marty 2008).

"*Ostrea*" *explanata* Goldfuss, 1833(b) (p. 22, pl. 80, fig. 5)—This is the oldest species that could be attributed to *Helvetostrea*. Goldfuss described it from a Middle Jurassic Oolite (Bajocian?) of Southern Germany (region of Bayreuth and Würtemberg, type locality not specified). In Europe, it ranges from the Bajocian to the Early Callovian in England, France and Poland (Hoffmann & Krobicki, 1989, p. 308; Pugaczewska, 1971, p. 245).

The species is usually determined as *Liostrea* (e.g. Pugaczewska 1971) coinciding with its ancient synonymization with *Liostrea eduliformis* (Schlotheim, 1820) by Roemer (1835) and Schlippe (1888) (here considered as a *Pernostrea*). Specimens figured by Goldfuss (1833)(b) show a broad but short ligament area which is also more reminiscent of *Pernostrea*, whereas a right valve figured by Pugaczewska (1971, pl. 9, figs. 5a,b) has a remarkably undulated hinge line and ligament similar to *Helvetostrea*. Hence, "*O.*" *explanata* sensu Pugaczewska (1971) may belong to *Helvetostrea*. However, it differs from *H. sequana* by its larger size (in height), more rectangular and less inflated shape, and lack of an umbonal cavity (Hoffmann & Krobicki, 1989, p. 308).

"*Ostrea*" *oxfordiana* Rollier, 1917—This rare species was originally described from the "Terrain à Chailles" facies (*Pholadomya* marls, Early Oxfordian, *cordatus* Zone) of Klein-Kembs (Kleinkems) from the "Isteiner Klotz", a prominent ridge some kilometres north of Lörrach (Baden-Württemberg, Germany). The figured holotype (fixed by monotypy, ICZN 73.1.2.; see also ICZN 73.1.5. which implies that a holotype can consist of a set of disarticulated components) consisted of a rather well preserved LV and a corresponding but damaged RV (Rollier 1917, pl. 40, figs. 1a–c, here refigured in Fig. 16.7–9). It belonged to the Casimir Moesch collection held at the ETH in Zürich (Ve. S. 5146, according to Rollier 1917); unfortunately, its current whereabouts is unknown (Pika-Biolzi, pers. comm. 2011).

The species could be a *Helvetostrea* that differs from *H. sequana* by having a more pronounced umbo, possibly due to a smaller attachment area, shorter ligament area, lesser convexity of the LV, more prolonged commissural shelf, and a shallower umbonal cavity.

In contrast, *Liostrea oxfordiana* sensu Pugaczewska (1971, p. 249, pl. 13, figs. 5–9) from the Lower Kimmeridgian of West Pomerania (Poland) as well as *Liostrea quadrangularis* Arkell, 1927, sensu Pugaczewska (1971, p. 250, pl. 8, figs. 1–4) are more likely phenotypes of *Liostrea polymorpha* (Münster in Goldfuss, 1833)(b) (Pugaczewska 1971, pl. 19, figs. 5–8). All these species differ from *H. sequana* by a markedly opisthogyrate ligament area, and a weakly sickle-shaped outline.

"*Ostrea*" *ermontiana* Etallon, 1862 (in Thurmann & Etallon, 1861–1864, p. 270, pl. 38, fig. 6)—The species was erected as a substitute for *Ostrea gryphoides* Contejean, 1859, which is a junior homonym of *Ostrea gryphoides* von Zieten, 1830, and *Ostrea gryphoides* Schlotheim, 1813. Contejean's (1859, p. 320, pl. 25, figs. 1–5) material came from the Upper Oxfordian "Calcaires à *Cardium*" and Lower Kimmeridgian "Marnes et Calcaires à ptérocorées" of Montbéliard (France) (housed at the Musée Cuvier in Montbéliard, MC 27E125 = LV in Contejean 1859, pl. 25, figs. 1, 3; MC 27E126 = LV, pl. 25, figs. 2, 4; MC27E127 = LV, pl. 25, fig. 5). However, all specimens are exfoliated internal moulds with few shell remains. Because the specimens are, at face value, indeterminable, and because there is no other material mentioned, the figured LV of *O. ermontiana* is here considered as lectotype. The specimen was found in the "Hypostrombien inférieur" (= Nautilid Beds, Reuchenette Formation, Lower Kimmeridgian) of Fahy near Porrentruy, but neither the holotype nor any other material potentially representing this species was found in the Jurassica-Museum (MJSN) Porrentruy. One additional complete and well-preserved specimen, determined as *Ostrea ermontiana* Etallon, was found in the collection Scheurer (MC-27E122) from the "Calcaire à *Corbis*" (cymodoce Zone) at Baume in Audincourt (France). It also contains a note by Scheurer that *O. gryphoides* is *O. ermontiana*.

The figured lectotype in Thurmann & Etallon (1862) is a small LV gryphaeoid shell (L 5.5 cm, H 3.5 cm) with an orthogyrate ligament area, which appears as drawing similar to *H. sequana*. After comparison of the available material an assignment of *O. ermontiana* to *Helvetostrea* can be excluded and the species can certainly be assigned to *Gryphaea* (*Bilobissa*).

Differences to *H. sequana* are the presence of a deep radial posterior sulcus (Thurmann & Etallon 1862, pl. 38, fig. 6, posterior view), which is characteristic of *Bilobissa*, the thin and not chambered shell, the nearly smooth LV and a RV with antimarginal threads (preserved on specimen MC-27E122). The relationship of *Gryphaea*

(*Bilobissa*) *ermontiana* (Etallon in Thurmann & Etallon, 1862) to *Gryphaea* (*B.*) *dilatata* (J. Sowerby, 1816) has not been investigated, but the occurrence of this species in the Early Kimmeridgian (*cymodoce* Zones) of the Reuchenette Formation in Switzerland and nearby France represents one of the last records of *Gryphaea* in Europe, beside its record from Poland (Pugaczewska 1971, p. 277).

“*Crassostrea*” *tetoriensis* Komatsu *et al.*, 2002—This oyster is only known from the Middle Jurassic of Japan (Bathonian, Ushimaru Formation, Tetori Group) (see Fujita 2003, fig. 2, for stratigraphy). Like *Helvetostrea* species, “*C.*” *tetoriensis* Komatsu *et al.* 2002, p. 1043, figs. 3, 5–7 developed numerous chambers in the LV, a deep umbonal cavity, an elongated ligament area, lack of chomata, and inequivalve shells without radial ornament. It also occurs below non-marine deposits with dinosaur bones and tracks (compare paleoecology of *H. sequana*). The species differs from *Helvetostrea sequana* by its very high, elongate-spatulate outline (*C. tetoriensis*: H/L ratio 2.9–3.7; *H. sequana* H/L 1.23–1.86), thin, mainly simple compact foliated shells with small chambers, usually filled with chalky deposits, a small reniform PAM not supported by a ventral shell swelling (buttress), narrow bourrelets and tiny attachment area (Komatsu *et al.* 2002, p. 1043). In addition, the species was most probably adapted to euryhaline, muddy, intertidal, soft bottom environments.

“*Ostrea*” *hebridica* (Forbes, 1851)—The species was originally described from the upper part of the Middle Jurassic (Bathonian) “Great Estuarine Series” of Loch Staffin, Isle of Skye, Inner Hebrides of Scotland (Arkell 1934, p. 11–12).

Most of the previous authors, including Hudson & Palmer (1976, p. 87), accepted a close relationship between “*O.*” *hebridica* and *Praeexogyra acuminata*. However, “*O.*” *hebridica* is extensively chambered and euryhaline (Hudson & Palmer 1976) whereas *P. acuminata* is an essentially compact foliated (Siewert, 1972) euhaline species, co-occurring with ammonites in England as well as in Switzerland (Arkell 1934; own data from the “*Acuminata* Beds” of the Hauptrogenstein Formation, Germany and Switzerland).

Shell chambering and euryhaline preference may indicate a closer, perhaps congeneric relationship with “*C.*” *tetoriensis*. Shell chambering could also indicate a link to *Helvetostrea*. However, the species differs from all *Helvetostrea* species by its more ventrally positioned, crescentic to reniform PAM without ventral shell buttress, with a pointed umbo, usually tiny attachment area, short ligament area, generally slender outline, curved posterodorsal margin, and antimarginal riblets and furrows, especially the early ontogenetic ribbed “*Catinula*” stage (Arkell 1934; Hudson & Palmer 1976). In addition, all *Helvetostrea* species are euhaline.

Subfamily Liostreinae Vialov, 1983

Genus *Praeexogyra* Charles & Maubeuge, 1953

Type species. *Ostrea acuminata* J. Sowerby, 1816 (p. 82, pl. 135, fig. 2) (left and right figure); non *Ostrea acuminata* J. Sowerby, 1816, pl. 135, fig. 3, = *Praeexogyra hebridica* (Forbes, 1851). “Lower Fuller’s Earth”, Bathonian, Middle Jurassic, Bath in Somerset, England; coordinates: 51°22'26.40"N, 2°22'35.70"W (centre of Bath).

Lectotype (designated herein). BM L.78248, J. Sowerby Collection of the Natural History Museum UK (London), refigured in Arkell (1934, pl. 2, fig. 29, 29a) and Stenzel (1971, Fig. J79.2a–b); see also Cox & Arkell (1948, p. 18).

Paralectotype—BM L.77830, figured in J. Sowerby (1816, pl. 135, fig. 2, middle figure), also in Arkell (1934, pl. 2, fig. 28, 28a) and Stenzel (1971, fig. J79.1a–b).

Diagnosis. Shell tiny to small (up to 3 cm), inequivalve, outline crescentic, reniform or ovate, little higher than long (H/L ratio 1.2–1.6); umbo usually pointed, opisthogyrate; attachment area small- to medium-sized; LV capacious, slightly to moderate convex in anteroposterior direction, less curved dorsoventrally, posterior margin concave to a variable degree. RV flat with a concave centre, anteroventral margin occasionally upturned. Surface of LV with regularly spaced comm marginal swellings or weakly squamous growth welts, with depressed and relative smooth interspaces of variable distance, antimarginal riblets and furrows rare and when developed than only weak and with restriction to the attachment area or the umbo. RV relatively smooth, with weak comm marginal depressions and ventrally always with fine, antimarginal riblets. Ligament area short and opisthogyrate (rarely prosogyrate); resilifer broad and slightly recurved, with posterior bourrelet narrower than anterior. PAM of lunate shape, dorsally

convex or slightly biconcave (dorsocentrally convex and both sides slightly concave); position posterocentral, muscle scar not ventrally elevated (buttressed). Umbonal cavity (LV) usually absent or very weak (*ca.* 1 mm depth), both valves thin-shelled (1–2 mm thick).

According to Carter (1990, p. 358), *P. acuminata* has an outer layer of nearly vertical simple prisms of 80–90 µm (RV) and 20 µm (LV) thickness, a middle shell layer ranging from homogeneous „mosaic“ (LV) or regular foliated (RV) to irregular CCF, and an inner layer with regular foliated structure. Siewert (1972, p. 22) described a compact (regular) foliated structure, occasionally with few small lenses, filled with sparitic cement.

Remarks. The present diagnosis is based on *P. acuminata*, *P. dubiensis* and *P. monsbeliardensis*. The phylogenetic position and composition of the genus is as yet unresolved. Douvillé (1904) considered *P. acuminata* to be a typical example of his newly established *Liostrea*, whereas Rollier (1911) and Dutertre (1931) assigned the type species to *Exogyra*. Arkell (1934) noted that the hinge has nothing “exogyrine” about it and described it as *Ostrea* (“*Liostrea*”). Charles and Maubeuge (1953) created *Praeexogyra* as a new subgenus of *Catinula* assuming that it is transitional between *Catinula* and “true” Jurassic Exogyrinae (Gryphaeidae). Stenzel (1971, p. N1100, N1104) considered all three taxa, *Catinula*, *Praeexogyra*, and *Liostrea* as genera within Gryphaeinae rather than Exogyrinae.

Charles & Maubeuge (1953) also included *Ostrea sowerbyi* Morris & Lycett, 1853, and *O. subrugulosa* Morris & Lycett, 1853, in their new genus *Praeexogyra*, ignoring the fact that both are junior synonyms of “*Ostrea*” *hebridica* Forbes, 1851 (Arkell 1934). However, whereas *P. acuminata* is *Liostrea*-like in many shell characters, “*Ostrea*” *hebridica* is crassostreine in these aspects (ostreine according to Hudson & Palmer 1976) thus sharing more characters with the Japanese Jurassic “*Crassostrea*” *tetoriensis* Komatsu & Chinzei in Komatsu *et al.*, 2002, than with *Praeexogyra* or *Liostrea*. In addition, both species seem to prefer euryhaline environments. These latter two species are therefore thought to belong to the same, but as yet unnamed, independent lineage within the Crassostreinae.

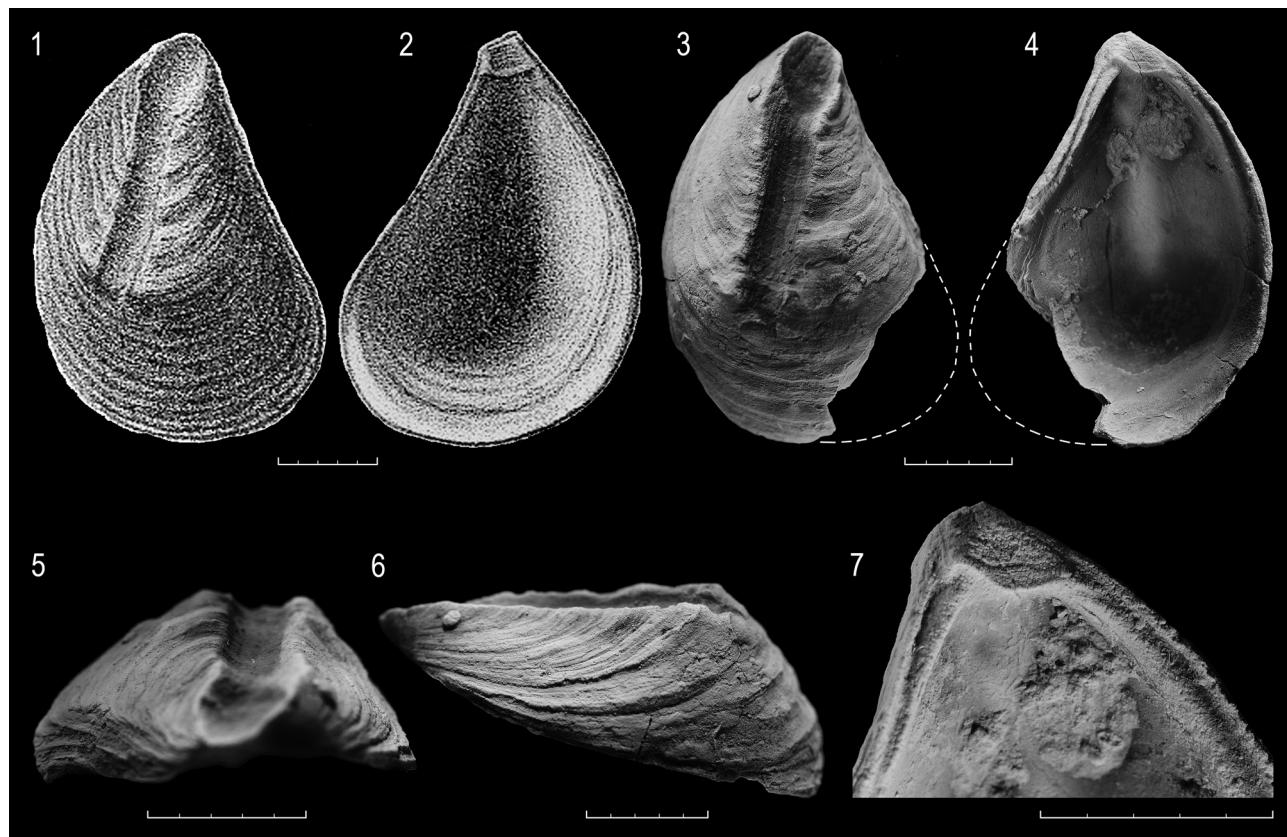


FIGURE 17. *Praeexogyra dubiensis* (Contejean, 1859). 1–7. MC-27-E-112, lectotype, designated herein, Oxfordian, Bussurel near Montbéliard, France. 1, LV lateral, scanned from Contejean (1859, pl. 21, fig. 4); 2, LV interior, scanned from Contejean (1859, pl. 21, fig. 5); 3, LV lateral, with cylindrical attachment scar, probably from an algal stem; 4, interior; 5, dorsal view; 6, anterior view; 7, magnified portion of dorsal region. Scale bars 5 mm.

***Praeexogyra dubiensis* (Contejean, 1859)**

Fig. 17; Pl. 13.5a–d; Pl. 14.6a–c

- | | |
|--------|--|
| 1859 | <i>Ostrea exogyroides</i> Roem.—Contejean: p. 46, 47, 49, 210. |
| * 1859 | <i>Ostrea dubiensis</i> Contj.—Contejean: p. 320, pl. 21, figs. 4–11. |
| 1862 | <i>Ostrea dubiensis</i> Contj.—Thurmann & Etallon: p. 272, pl. 39, fig. 6. |
| 1866 | <i>Ostrea Dubiensis</i> Contejean—de Loriol & Pellat: p. 115, pl. 11, figs. 2–3. |
| n 1872 | <i>Ostrea dubiensis</i> Contejean—de Loriol, Royer & Tombeck: p. 407, pl. 24, figs. 19–25. |
| 1878 | <i>Ostrea Dubiensis</i> Cjt.—Choffat: p. 70. |
| 1882 | <i>Ostrea Dubiensis</i> Contejean, 1859—Roeder: p. 31, pl. 3, fig. 10a,b. |
| 1917 | <i>Ostrea Dubiensis</i> Contejean—Rollier: p. 590. |
| 1923 | <i>Ostrea cf. Dubiensis</i> Contejean—Lewinski: p. 65, pl. 3, figs. 6–8. |
| 1927 | <i>Ostrea dubiensis</i> Contejean—Pčelinčev: p. 78. |
| 1935 | <i>Ostrea (Liostrea) dubiensis</i> Contejean—Cox: p. 171, pl. 17, figs. 4–5. |
| ? 1936 | <i>Ostrea dubiensis</i> Contejean—Arkell: p. 366, pl. 55, figs. 4a,b, 5. |
| ? 1936 | <i>Ostrea (Liostrea) cf. dubiensis</i> Contejean—Reed: p. 6. |
| 1939 | <i>Liostrea dubiensis</i> (Contej.)—Stefanini: p. 194, pl. 22, fig. 3. |
| 1952 | <i>Liostrea (Catinula) dubiensis</i> (Contejean)—Chavan: p. 40, pl. 2, figs. 20–24. |
| 1955 | <i>Ostrea dubiensis</i> Contejean, 1858—Gerasimov: p. 127, pl. 28, fig. 7. |
| 1958 | <i>Liostrea dubiensis</i> (Contejean)—Hudson: p. 419. |
| 1971 | <i>Liostrea dubiensis</i> (Contejean, 1859)—Pugaczewska: p. 252, pl. 14, figs. 1–7. |
| 1976 | <i>Liostrea cf. dubiensis</i> (Contejean)—Gu Zhi-wei et al: p. 244, pl. 48, fig. 1. |

Lectotype (designated herein). *Ostrea dubiensis* Contejean, 1859, pl. 21, figs. 4–5, MC-27-E-112; single LV, damaged anteroventrally); Bussurel near Montbéliard (Department Haute-Saône, Franche-Comté, France), "Calcaire à Natices" (Contejean 1859, p. 320), Upper Oxfordian (*bifurcatus* Zone), equivalent of the Vorbourg Member of the Vellerat Formation in Switzerland.

In the stratigraphic part of his monograph, Contejean (1859, p. 46, 47, 49, 210) mentioned the abundant occurrence of *Ostrea exogyroides* Roemer, 1835, indicating that it came from a 50 cm thick blue or greyish oolitic marl-unit, which grades laterally into solid limestone (Contejean 1859, p. 210, section Bussurel). However, the species name does not appear in the systematic part. Instead, Contejean (1859, p. 320) mentions a new species, *O. dubiensis*, the original label stating that it was collected from a railroad cutting at Bussurel close to Héricourt, northwest of Montbéliard (France) which coincides with the locality given on page 210 for *Ostrea exogyroides*. It is also consistent with remains of a blue grey marly matrix still adherent to the here designated lectotype of "*O.*" *dubiensis*. It appears very likely, therefore, that Contejean changed his mind concerning the determination of this species while earlier parts of his volume were already in print. Apart from the "Calcaire à Natices", Contejean (1859, p. 320) recorded *O. dubiensis* from the somewhat younger "Calcaire à Térébratules" (Upper Oxfordian) but there is no mentioning of a type locality.

The species name refers to the nearby located river Doubs (ancient name with Celtic roots was Dubis). The ending "s" in Doubs or Dubis is aphonic in spoken French. There is no reason to assume that the original spelling *dubiensis* was an inadvertent error by Contejean (in the sense of ICZN 32.5); the emendation by Rollier (1917, p. 590) and Pugaczewska (1971, p. 255) to "*dubisensis*" appears therefore unjustified.

Material. Lectotype (see above and Fig. 17), and paralectotypes—MC-27-E-113 (Contejean 1859, pl. 21, figs. 8–9), lacks the hinge; MC-27-E-114, RV (Contejean 1859, pl. 21, fig. 10); MC-27-E-116, LV attached on a RV (Pl. 15.1a–f, 2a–b).

All former syntypes, stored in the Museum Cuvier, were available for study. Contejean (1859) did not determine a holotype, and the type series was not revised before. The figured syntypes of Contejean (1859, pl. 21, figs. 4–11) could be easily identified by comparison with his published drawings. The lectotype was chosen for its identification as one of the figured types, and its preserved hinge and attachment area, which show a characteristic

attachment cast, probably of an alga (Fig. 17.1, 3, 5). However, it lacks part of the anteroventral shell margin (Fig. 17.1, 3–4).

Others—One additional single RV (VTT001-1171) from the Banné Marls of Vâ Tche Tchâ (*cymodoce* Zone, Lower Kimmeridgian) was traceable in the collections of the PAL A16. This specimen and a questionable juvenile LV (VTT001-3238) are figured on Pl. 14.5–6. For measurements see Appendix, Table 6.

Description. Shape, Size—Thin-shelled, convex, inequivale, outline elongate to ovate or drop-shaped, always higher than long; umbo pointed, posterodorsal margin weakly curved or straight. LV moderately inflated, with a small- or medium-sized attachment area and the highest inflation always posteroventrally. RV normally flat, some specimens posteroventrally concave, or xenomorphic. Small, largest dimension of examined specimens 1.3–2.6 cm.

Sculpture—LV nearly smooth, with weak, irregular spaced concentric swellings and faint growth welts, with narrow, depressed interspaces, without radial elements (Fig. 17.3, 6; Pl. 15.1d). RV nearly smooth, with fine commarginal swellings and few antimarginal threads close to the ventral margin (Pl. 15.2b).

Ligament area—Visible initial portion in small adults prosodetic, but overall uncoiled, trigonal, small, with weakly sunken, relatively broad resilifer (Fig. 17.7); bourrelets small, weakly elevated, ventral edge of ligament area slightly undulated, ligament area not supported by shell buttress (sensu Stenzel, 1971).

Internal shell characters—LV without or with a weakly developed umbonal cavity, commissural shelf narrow (LV), PAM slightly biconcave (Malchus 1990, tab. 9) with convex dorsocentral bump (LV: Fig. 17.4; Pl. 15.1c; RV: Pl. 15.1f), attachment scar weak, ventrally not elevated, position posterocentral close to posterior margin, ventral margin of PAM directed towards posteroventral angle. Chomata absent.

Microstructure—Broken edge of thin-shelled lectotype revealing regularly foliated shell under the microscope, without chambers; RV with thin prismatic outer layer visible under light microscope (magnification x40). Because of the rarity of the available material, no thin section was prepared.

Prodissococonch, juvenile—Earliest shell stages not preserved.

Paleoecology. Most specimens from the study area are left valves, attached solitarily, and with small, often indistinct attachment scars; only one specimen was found attached to a RV of the same species. Some xenomorphic imprints indicate that the species was able to attach to marine plants, (Fig. 17.3, 5). Left valves show little if any signs of transport, and the co-occurrence of large “*Natica*” sp. and an essentially marly background sedimentation with ooids and biotrititus suggest a marine, shallow subtidal environment, influenced only by weak currents. The coarser sediment fraction of this facies is probably allochthonous.

Occurrence. The species occurs from the Lower Oxfordian to Upper Kimmeridgian in France (Contejean 1859; de Loriol & Pellat 1866) and is abundant in the Upper Oxfordian near Montbéliard (Contejean 1859). It is relatively rare in the Kimmeridgian of NW Switzerland. However, Thurmann & Etallon (1862, p. 272) also mentioned it from the “Marnes à Astartes” (Bure Member, Vellerat Formation).

Outside France and Switzerland, the species occurs in the Oxfordian of England (Arkell 1936; Hudson 1958; Reed 1936), Upper Oxfordian–Lower Kimmeridgian of Russia (Crimea, Caucasus) (Gerasimov 1955; Pčelinčev 1927), and the Tithonian of Poland (Pomerania and Polish Lowlands) (Lewinski 1923; Pugaczewska 1971). It has also been reported from the Callovian and Oxfordian of Somalia (Cox 1935; Stefanini 1939) and the Upper Jurassic of China (Gu Zhi-wei *et al.* 1976).

Comparison. *Praeexogyra acuminata* (J. Sowerby, 1816)—The type species of *Praeexogyra* is widespread in Europe (Pugaczewska 1971, p. 243) and common in the “*Acuminata* Beds” of the Upper Bajocian and Lower Bathonian (Arkell 1934, p. 7, for detailed biogeographic and stratigraphic distribution). Other than *P. dubiensis*, the type species is usually slender comma shaped, tapering posteroventrally, the LV is covered by prominent, evenly spaced concentric, weakly angulate swellings separated by wide interspaces and in rare cases shows faint antimarginal riblets at the umbo (ribbed variety, see Arkell 1934, p. 9).

“*Ostrea*” *hebridica* Forbes, 1851 (p. 110, pl. 5, figs. 4a–c)—The species originates from the Middle Jurassic of Loch Staffin (Isle of Skye, Inner Hebrides), Scotland. It differs from *P. dubiensis* in having a much larger and elongated shell, rather prominent and wider spaced concentric swellings, antimarginal riblets and furrows close to the umbo of LV, RV with long antimarginal riblets, and large shell chambers which are absent in the thin-shelled *P. dubiensis*. The long ligament area and the thick shell with many large chambers exclude “*O.*” *hebridica* from *Praeexogyra* (see remarks under that genus).

Praeexogyra monsbeliardensis (Contejean, 1859)—The species co-occurs with *P. dubiensis* in the Kimmeridgian of the Reuchenette Formation. *P. monsbeliardensis* is usually larger, more capacious and of

reniform shape. The attachment area is much larger and covered with antimarginal furrows and riblets (when exposed, Fig. 19.4–5), and the surface of the LV is ornamented with many commarginal growth swellings, separated by concentric depressions.

"Ostrea" sandalinoides de Loriol, 1901 (p. 110, pl. 6, figs. 15–16)—The species was first described from the Lower Oxfordian “Terrain à Chailles” (= Sornetan Member, Bärschwil Formation, *cordatum* Zone) of the Jura Bernois (Montenay, Trembliaz) in NW Switzerland. De Loriol (1901) synonymized Oxfordian material from Ferrette (Haute-Rhin, France) that had been erroneously determined as *Ostrea sandalina* Goldfuss, 1833, by Roeder (1882, p. 32, pl. 1, fig. 2). De Loriol’s species is also typical of Middle Callovian (*jason* Zone) glacial erratic boulders in Northern Germany (Pl. 15.3–4) and equivalent erratic boulders in NW Poland (material housed at the University of Greifswald, Germany). Although very similar to *P. dubiensis*, the species possesses a more pointed and stronger opisthogyrate umbo (Pl. 15.3b) and a smaller and shorter ligament area. The presence of weak antimarginal riblets of the RV distinguishes the species from *Liostrea* spp. Juvenile RVs tentatively attributed to this species have a *Liostrea/Crassostrea*-like prodissoconch (Pl. 6.5 and Pl. 10.3a–b).

Praeexogyra monsbeliardensis (Contejean, 1859)

Figs. 18–19; Pl. 12.3–4; Pl. 13; Pl. 14.1–4; Pl. 21

- * 1859 *Ostrea Monsbeliardensis* Contej.—Contejean: p. 321, pl. 26, fig. 1–4.
- 1861 *Ostrea Monsbeliardensis* Cjt.—Thurmann & Etallon (in 1861–1864): p. 53.
- 1862 *Ostrea Monsbeliardensis* Contj.—Thurmann & Etallon (in 1861–1864): p. 272, pl. 38, fig. 8.
- 1867 *Ostrea Monsbeliardensis*, Contej.—Favre: p. 471.
- 1870 *Ostrea Monsbeliardensis*, Cjt.—Greppin, J.-B.: p. 104.
- 1875 *Ostrea Monsbeliardensis* Contj.—Blake: p. 207, 221.
- 1892 *Ostrea monsbeliardensis*, Contej.—Roberts: p. 76.
- 1897 *Ostrea monsbeliardensis* Contej.—Reed: p. 45.
- 1971 *Liostrea monsbeliardensis* (Contejean, 1859)—Pugaczewska: p. 260, pl. 17, figs. 5–9.

Lectotype (designated herein). *Ostrea monsbeliardensis* Contejean 1859 (pl. 26, figs. 1–3), MC-27-E-141: bivalved specimen (Fig. 19.1–2). Rôce in Sainte-Suzanne, Montbéliard (Department Haute-Saône), France. Coordinates: ca. 47°30'20.33"N, 6°47'51.00"E (exact position of locality unknown). Lower Kimmeridgian, *cymodoce* Zone, niveau 6 sensu Contejean (1859), "Marnes à Ptérocères" (facies and time-equivalent of the Banné Member, Reuchenette Formation in Switzerland) = "Marnes du Rang", Contini & Hantzpergue 1973.

The label associated with the four figured syntypes of Contejean (1859, pl. 26, figs. 1–4) mentions Beauregard and Rôce as “type” localities and Marnes of the niveau 6 of Contejean (= “Marnes et Calcaires à ptérocères” [marls and limestones with *Harpagodes*] as reference to the horizon. Obviously, the label mentioned two different localities and the material might have been assembled in one box after removing the specimens from the original tray. Both sites are close to each other, Beauregard being a locality *ca.* 3 km northeast of Montbéliard and Rôce referring to the ancient locality "Côte de Rôce" (Contejean 1859, p. 203) in the district Sainte-Suzanne in Montbéliard (Fig. 3). However, Contejean (1859, p. 72) mentioned the occurrence of *Ostrea monsbeliardensis* in Rôce, but not in Beauregard and the name of the species is apparently the latinized form of Montbéliard (“Monsbeliard”). It appears reasonable to assume Rôce in Montbéliard rather than Beauregard as type locality. Remains of a brown-grey marl on the lectotype specimen are typical of weathered samples of the “Marnes à Ptérocères” or “Marnes du Rang” of the *cymodoce* Zone.

Material. Lectotype (see above), and Paralectotypes—MC 27E-138–140, and 142; Musée Cuvier in Montbéliard. Paralectotype MC-27E-139, a LV not figured in Contejean (1859), was prepared by the author to reveal the shell interior (Fig. 18.1–3).

Others—More than 20 specimens from the Banné Marls (*cymodoce* Zone, Lower Kimmeridgian, Reuchenette Formation) of Vâ Tche Tchâ near Courtedoux. One juvenile LV from the Banné marls of Glovelier (Glov. 5.2.98 MB/3-60, FPJ-collection, Fig. 18.4, Pl. 13.3). For measurements see Appendix, Table 7.

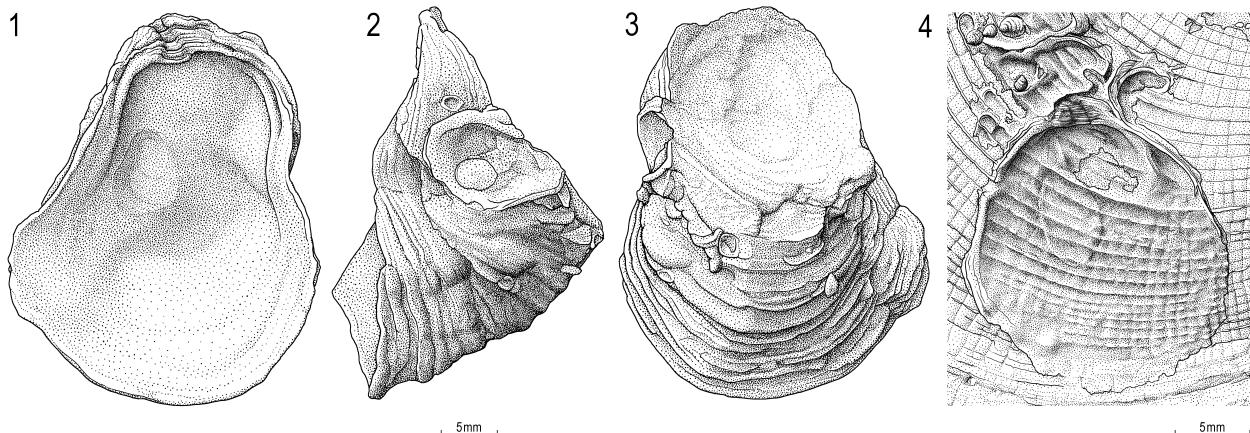


FIGURE 18. *Praeexogyra monsbeliardensis* (Contejean, 1859). 1–3. LV, MC-27E-139, paralectotype, Contejean Collection (Musée Cuvier in Montbéliard, France): 1, interior; 2, anterior; 3, lateral, with large attachment area; scale x1. 4. Juvenile LV, attached to *Camptonectes auritus*, FPJ Glov. 5.2.98 MB/3-60, Glovelier (Banné Marls, Lower Kimmeridgian).

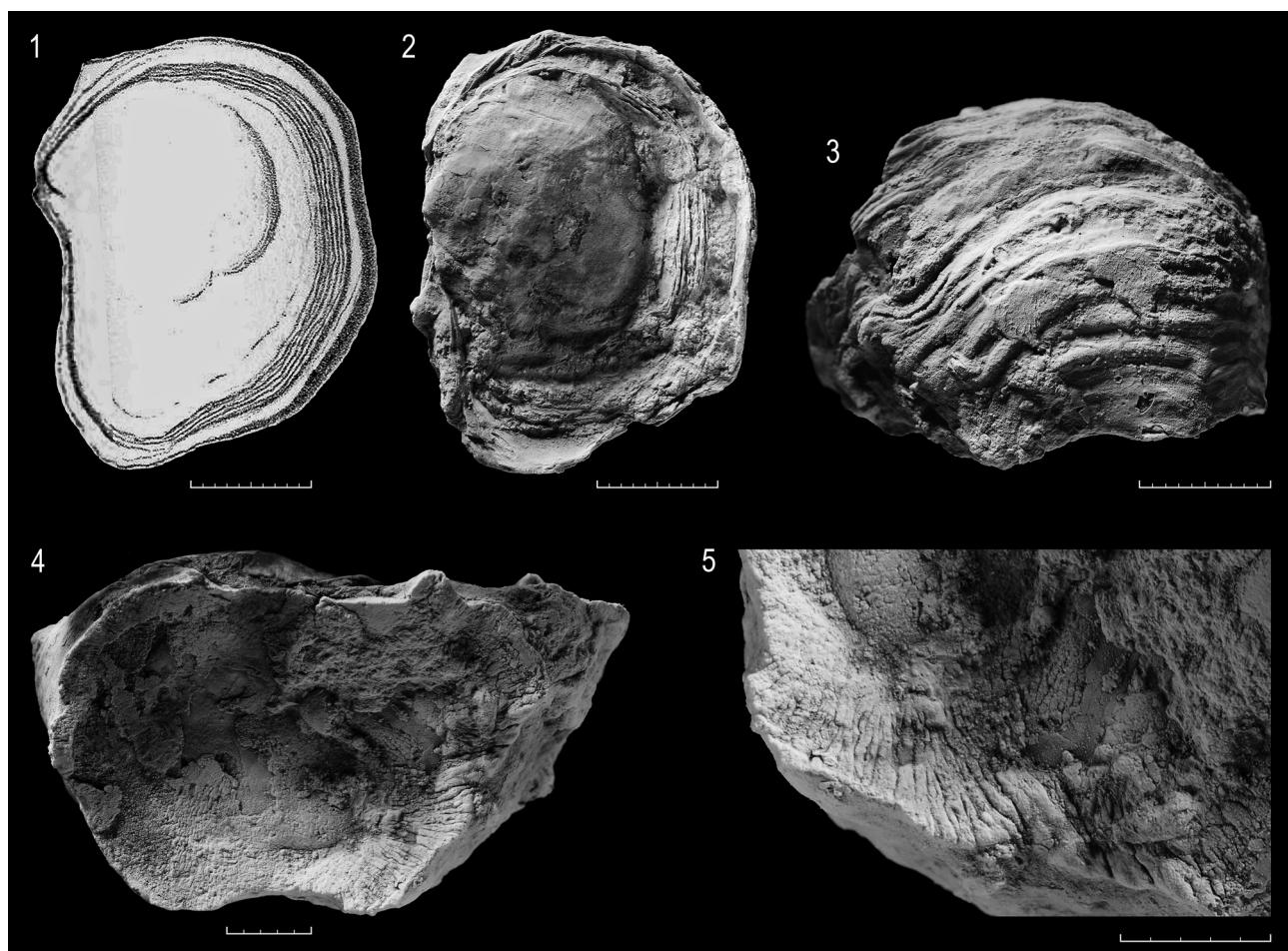


FIGURE 19. *Praeexogyra monsbeliardensis*. 1–5. Lectotype, MC-27-E-141 (designated herein): 1, refigured drawing of Contejean's (1859) fig. 1 of pl. 26; 2, RV lateral; 3, LV anterodorsal view; 4, LV, attachment area; 5, magnified portion of ventral margin, with antimarginal furrows; “Côte de Rôce” in Montbéliard, France, Lower Kimmeridgian, *cymodoce* Zone. Scale bars 10 mm (Figs. 1–3); 5 mm (Figs. 4–5).

Description. Shape, size—Thin-shelled, strongly inequivalve, outline oval, subrectangular to subtrigonal or slightly reniform, usually higher than long. LV capacious, scoop-shaped and slightly opisthocline towards the posteroventral margin, attachment area usually large; posterior margin weakly concave, in some specimens well

curved and with a weak to well-developed posterior sulcus (Pl. 12.4d; Pl. 14.3a). Most RVs evenly flat (Pl. 13.2a, 6a), occasionally with concave depression close to ventral margin (Pl. 14.3a) or dorsally slight convex. Examined specimens 2.2–4.0 cm high.

Sculpture—LV with squamous lamellae and swellings, interspaces with fine commarginal growth lines. Radial sculptures rare; fine divaricating furrows on ventral edge of attachment area (Fig. 19.4–5), in some specimens also a few antimarginal furrows close to the ventral margin (Pl. 13.4b,d). RV covered by narrowly spaced concentric growth lines with few growth squamae; occasionally thin plicae near ventral margin (Pl. 13.5b). RV shell surface usually heavily bioeroded by grazing regular echinoids (Pl. 12.3b, 4c); details of original shell structure thus rarely preserved.

Ligament area—Somewhat oblique, usually prosodetic, in some specimens opisthodetic (Pl. 13.5; Pl. 14.2).

Internal shell characters—LV dorsally with narrow commissural shelf; umbonal cavity small, better developed in small (“juvenile”) shells. PAM high-oval, large in relation to shell size, somewhat posterior to the centre; small Quenstedt muscle in some RVs, around 2–3 mm below the posterior bourrelet (Pl. 13.2c, 6b). No chomata.

Microstructure—Mostly regular foliated (RF) with some complex CF, without chambers (Pl. 21.1a–h).

Prodissococonch, juvenile—Earliest shell stages not preserved.

Paleoecology. The oyster is often found in small groups (Pl. 12.3a) settling on shells of *Isognomon*, *Eopecten*, or flat parts of *Trichites*. Complete articulated shells *in situ* associated with large and complete *Trichites* shells are common in the soft marl intercalations of the Banné Member. All *in situ* RVs and many *Trichites* shells show gnawing traces of *Gnathichnus pentax* Bromley, caused by regular echinoids such as *Pseudocardiaris thurmanni* (Agassiz, 1840), suggesting grazing on living animals (Pl. 12.3b, 4c).

Several regular echinoid species co-occur in this part of the section and prove fully marine conditions, whereas the highly diverse and abundant epibenthic bivalve fauna of more than 80 species indicates nutrient-rich seawater. It is therefore assumed that *P. monsbeliardensis* has been adapted to a fully marine, low energy, marly environment which is typical of the middle and upper section of the Banné Marls.

Occurrence. *P. monsbeliardensis* is known from the Oxfordian and Lower Kimmeridgian of France and Switzerland and from the Kimmeridgian of England and Poland (Pugaczewska 1971).

Comparisons. *Praeexogyra acuminata* (J. Sowerby, 1816) (p. 82, pl. 135, fig. 2)—The type species has already been discussed under *P. dubiensis*. The differences to *P. monsbeliardensis* are the same: pointed umbo, usually strongly curved posterior margin, the generally more slender, comma-shaped outline, more prominent growth squamae, and occasional fine antimarginal ribs close to the umbo. Similar riblets have only been found on the margin of the attachment area of the lectotype of *P. monsbeliardensis* but not on the free parts of the shell (Fig. 19.4–5).

Praeexogyra dubiensis (Contejean, 1859) (p. 320, pl. 21, figs. 4–11)—This species co-occurs in the Reuchenette Formation, but overall rare in the Kimmeridgian. Compared to *P. monsbeliardensis*, it is only attached by a tiny part of the umbo, and is also smaller, less opisthogyrate, and more triangular or drop-shaped. The concentric swellings on the LV are less developed. The species seems to have preferred somewhat higher energy water (e.g. oolitic/bioclastic shoals), whereas *P. monsbeliardensis* appears to have been restricted to the lower energy marls and marly limestones of the middle and upper parts of the Banné Member.

"Ostrea" hebridica Forbes, 1851 (p. 110, pl. 5, figs. 4a–c)—This species has been discussed and illustrated in detail by Arkell (1934, p. 9–15, pls. 3–4) from the Bathonian of England and Scotland (see also discussion under *P. dubiensis*). The species differs from *P. monsbeliardensis* by its larger size and more elongate and posteriorly stronger recurved shape (except for the elongated, straight morphotype). The attachment area is much smaller, and the umbo more pointed and stronger opisthogyrate. The distance between the marked growth squamae is at least twice as wide as in *P. monsbeliardensis*. The ostreoid hinge is similar to the one known from *P. monsbeliardensis* (compare Arkell 1934, pl. 4, figs. 6, 13–14, 16 with pl. 8, figs. 2–3), but the ligament area is larger (in comparison more than twice as high). Both species are known to have radial furrows and ribs in the dorsal third of the LV. But in *O. hebridica* the radial elements are also visible (if developed) on the LV behind the attachment area, whereas they are restricted to the attached part in *P. monsbeliardensis*. Long antimarginal riblets are well developed on the RV of some specimens (Arkell 1934, pl. 4, fig. 8) and much stronger than in *P. monsbeliardensis*. Furthermore, large chambers in the LV of *O. hebridica* are unknown from the thin-shelled *P. monsbeliardensis*.

"Ostrea" pustulosa Sharpe, 1850 (p. 188, pl. 24, 4a,b)—The species was originally described by Sharpe (1850) from the Kimmeridgian of Torres Vedras/Sobral in Portugal. Fürsich (1981), Fürsich *et al.* (2009), Schneider

(2009) and Schneider *et al.* (2010) included it in *Praeexogyra*. However, the two figured syntypes of Sharpe (1850) do not fit in the diagnosis by Stenzel (1971) or the modified diagnosis of *Praeexogyra* used in this study.

In contrast to *P. monsbeliardensis* the LV is much thicker, the shape oval to subrectangular, somewhat longer than high and not recurved. The LV surface (Sharpe 1850, pl. 24, fig. 4a) is dorsally covered with broad radial ribs and rough concentric growth squamae. The ligament area of the other LV (Sharpe 1850, pl. 24, fig. 4b) is relatively high and broad (around one half of the shell length), the hinge is massive with prominent bourselets and a deep resilifer. The juvenile part of the resilifer is curved anteriorly (prosodetic), but the resilifer is in general orthogyrate directed. This species is probably better assigned to *Helvetostrea* **n. gen.**

Liostrea? *moreana* (Buvignier, 1852) (p. 26, pl. 16, figs. 41–43)—This Oxfordian species was originally described from the Department de la Meuse and is widely distributed in France, England and Poland (Arkell 1932 in 1929–1937, p. 157–159). The generic position is uncertain (Arkell 1932 in 1929–1937, p. 158), but the majority of modern authors refer it to *Liostrea*.

This species is somewhat larger, around twice as long as the average adult shell of *P. monsbeliardensis*, but the shape, attachment size and shell inflation appear comparable. Differences are a weakly concave or straight posterior margin, the terminal and centrally situated umbo (which is not opisthogyrate), and a remarkably wide ligament area with a broad resilifer, which is at least three times as wide as in *P. monsbeliardensis*. The most upturned region of the shell is posteroventral in *Liostrea?* *moreana* but anteroventral in *P. monsbeliardensis*. The round and dorsally convex PAM is close to the centre in *L.?* *moreana* (cf. Buvignier 1852, pl. 16, figs. 41, 43; Arkell 1932, text-fig. 27) but high-oval and situated close to the posterior margin in *P. monsbeliardensis* (Pl. 14.2a). Further information especially concerning its shell microstructures and chambering would be needed to clarify the generic position of *L.?* *moreana* (see also under *Circunula cotyledon*).

Circunula cotyledon (Contejean, 1859) (p. 319, pl. 24, fig. 15–17)—This species co-occurs with *Praeexogyra monsbeliardensis* in the Banné Marls and is occasionally attached to the same object (e.g. *Trichites*) which may lead to confusion. *C. cotyledon*, however becomes twice as long and several millimetres thick, its attachment area is larger and the ventral margin less bent upwards. The shape is more circular and the ventral margin of the LV nearly smooth without traces of commarginal swellings which are typical of *P. monsbeliardensis*. The ligament area is broader; the PAM is rounder and more centrally situated, somewhat inserted and commonly ventrally buttressed in both valves, which is in strong contrast to the non-inserted and not elevated PAM of *P. monsbeliardensis*.

Family Arctostreidae Vialov, 1983

Subfamily Palaeolophinae Malchus, 1990

Genus *Actinostreon* Bayle, 1878

Type species. *Ostrea solitaria* J. de C. Sowerby, 1824 (p. 105, pl. 468, fig. 1); subsequent designation by Douvillé, 1879, p. 92. Weymouth (Dorset, England), „*Trigonia clavellata*” Beds (Arkell 1933 in Arkell 1929–1937, p. 186), Middle Oxfordian, Upper Jurassic. The whereabouts of the type is unknown.

Diagnosis (modified from Stenzel 1971, p. N1158). Subequivalve, outline elongate oval and curved (crescentic); strongly plicate; adductor scar roundish, dorsally flattened or with slight sinus, position dorsocentral to posterodorsal; small straight chomata at least in some species; shell chambers numerous, small to medium-sized (about 6–10 cm), lenticular, predominantly (empty) filled with sparry cement.

Remarks. Malchus (1990) assumed that *Actinostreon* lacks chomata but later corrected that view (Malchus, 1998) based on Polish material from M. Machalski. It is still unknown, however, when species of that genus began to develop chomata.

There exists some confusion concerning the taxonomic position of *Actinostreon* and concept of the genus that warrants clarification. Bayle (1878) introduced the genus name on his legends to plate 132 [“*Actinostreon solitarium* Sowerby, sp.”, figs. 2–6] and plate 143 [“*Actinostreon syphax* (Coquand, 1854)”, figs. 1–3] without any diagnosis or further explications.

When Malchus (1990, p. 102, table 17) placed *Actinostreon* in the newly established Oscillophini (Palaeolophinae, Palaeolophidae) [now Arctostreidae Vialov, 1983 (Carter *et al.* 2011, p. 8)] he was unaware of the

existence of *Actinostreon syphax*, as the corresponding plate 143 was missing in his xerox copy of Bayle (1878) (Malchus, pers. comm., 2014).

Malchus did, however, study a Moroccan specimen of “*O.*” *syphax* which showed compact foliated shell microstructure, in strong contrast to the multi-chambered *Actinostreon gregareum* and *A. solitarium* specimens studied by others and by him. He considered *syphax* as a member of highly plicate compact foliated oysters of the genus *Ambigostrea*, Liostreinae (Ostreidae), today Flemingostreidae (Carter *et al.*, 2011).

Unfortunately, Malchus (1990) inadvertently listed the palaeolophid (now arctostreid) genus *Actinostreon* also under the liostreine tribe Ambigostreini (Malchus, 1990, p. 68–70, p. 176). In addition, he erroneously used Bayle’s original combination “*Actinostreon syphax*” on page 86 and in the figure legend to plate 25, figure 6. These *lapsus calami* (Malchus, pers. comm., 2014) have lead at least once to an ambiguous taxonomic assignment (Dhondt *et al.* 1999, p. 69–70, 74) and has contributed to a contentious argument about the validity of the phylogenetic distinction between fossil and recent plicate oysters (Hautmann 2001, 2006; Malchus 2008). However, independent of these errors, it seems that current molecular phylogenetic results favor Malchus’ view of convergent development of *Lopha*-like oysters (see introduction to the systematics chapter).

In addition to this problem, there also exist doubts concerning the first valid introduction of the species *syphax* and of its valid spelling. Coquand (1854) spelled his species *scyphax* (p. 143, 144, 153, pl. 4) as well as *syphax* (p. 150) but later used *syphax* (Coquand 1862). It appears, therefore, that Coquand (1862) is the first revisor of his own species choosing *syphax* as the valid spelling (see IZCN 2000 online, Art. 24.2.3. and 24.2.4.).

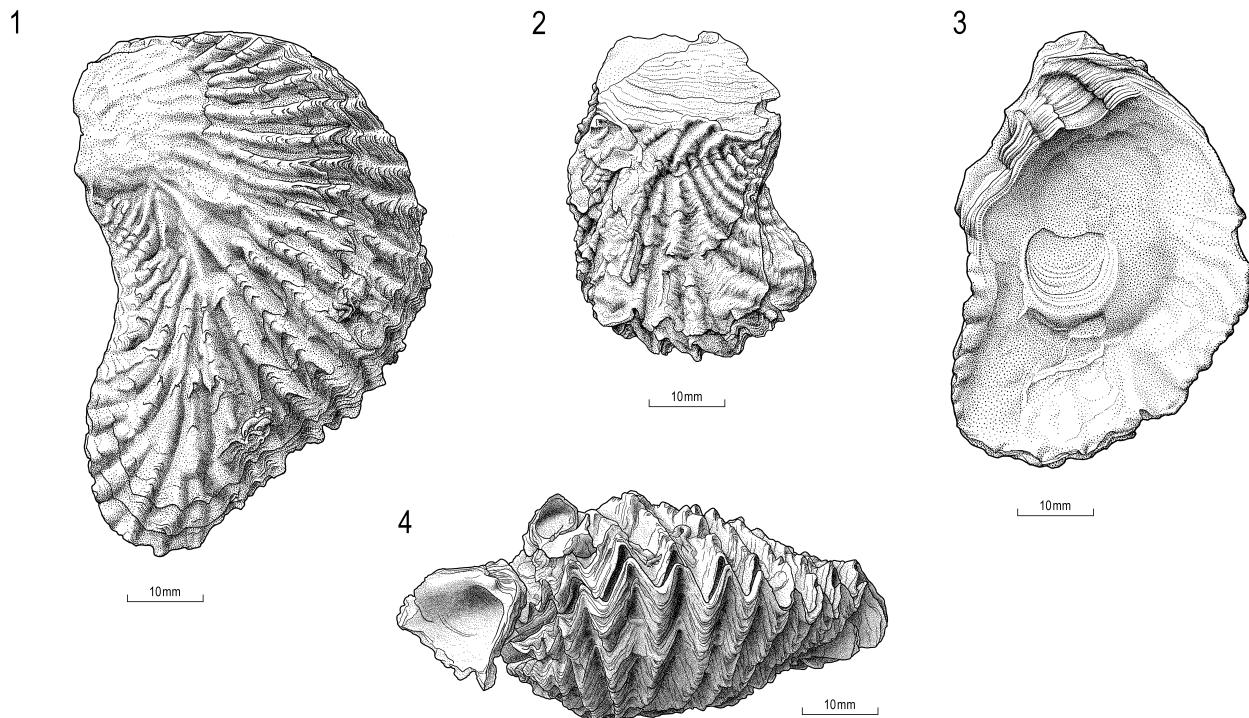


FIGURE 20. *Actinostreon gregareum* (J. Sowerby, 1815). 1. RV, VTT006-77, lateral. 2. LV, VTT001-1455, lateral. 3. LV, VTT009-41, interior. 4. Both valves, VTT001-1700, ventral; all specimens from Vâ Tche Tchâ near Courtedoux, Switzerland, Lower Kimmeridgian.

Actinostreon gregareum (J. Sowerby, 1815)

Fig. 20; Pls. 16–18; Pl. 19.1–2; Pl. 22

- * 1815 *Ostrea gregarea* n. sp.—J. Sowerby: p. 19, pl. 111, figs. 1, 3.
- 1815 *Ostrea palmetta* n. sp.—J. Sowerby: p. 20, pl. 111, fig. 2.
- 1817 *Ostrea crista-galli* n. sp.—W. Smith: p. 20, Coral Rag and Pisolite plate, fig. 4.
- 1822 *Ostrea gregaria* [sic] Sow.—Young & Bird: p. 238, pl. 9, fig. 16.

- 1824 *Ostrea solitaria* n. sp.—J. de C. Sowerby: p. 105, pl. 468, fig. 1.
- 1825 *Ostrea costatum* n. sp.—J. de C. Sowerby: p. 143, pl. 488, fig. 3.
- 1831 *Ostrea gregarea* Sow.—Deshayes: p. 106, pl. 13, fig. 2.
- p 1833b *Ostrea gregaria* Sow.—Goldfuss: p. 7, pl. 74, figs. 2a–f.
- ? 1833b *Ostrea pulligera* nob.—Goldfuss: p. 5, pl. 72, figs. 11a–c.
- 1835 *Ostrea solitaria* Sow.—Roemer: p. 58, pl. 3, figs. 2a–c, pl. 13, fig. 4.
- 1836 *Ostrea gregaria* [sic] Sow.—Bronn: p. 314, pl. 18, figs. 16a,b.
- n 1837 *Ostrea gregaria* [sic] Goldfuß—Koch & Dunker: p. 50, pl. 6, fig. 2.
- 1840c *Ostrea carinata* n. sp.—J. de C. Sowerby: pl. 22, fig. 8.
- n 1853 *Ostrea gregarea*, Sow., var.—Morris & Lycett: p. 4, pl. 1, fig. 2.
- ? 1853 *Ostrea gregarea*, Sow.—de Verneuil & Collomb: p. 164, pl. 3, fig. 6.
- ? 1857b *Ostrea gregaria* [sic] Sow.—Quenstedt: p. 751, pl. 41, fig. 28.
- 1857b *Ostrea pulligera ascendens* Quenstedt—Quenstedt: p. 751, pl. 91, fig. 29.
- ? 1859 *Ostrea gregaria* [sic] Sow.—Trautschold: p. 115, pl. 2, fig. 15.
- 1861 *Ostrea solitaria*, Sow.—Thurmann & Etallon: 53.
- ? 1862 *Ostrea semisolitaria*, Et.—Etallon in Thurmann & Etallon: p. 279, pl. 40, fig. 1.
- 1862 *Ostrea solitaria*, Sow.—Thurmann & Etallon: p. 281, pl. 40, fig. 4.
- ? 1862 *Ostrea vallata*, Etallon—Thurmann & Etallon: p. 278.
- 1871 *Ostrea gregarea* Sow.—Phillips: p. 323, pl. 13, fig. 19.
- ? 1871 *Ostrea gregarea* ? Sow.—Phillips: p. 181, pl. 10, fig. 4.
- 1871 *Ostrea gregarea*, Sow.—Terquem & Jourdy: p. 131.
- 1872 *Ostrea pulligera* Goldfuss—de Loriol *et al.*: p. 402, pl. 24, figs. 1–6.
- 1875 *Ostrea pulligera* Goldfuss—de Loriol & Pellat: p. 377, pl. 24, figs. 4–5.
- 1875 *Ostrea Pulligera* (Quenst.)—Pillet & Frommentel: p. 133, pl. 14, figs. 24–25.
- 1878 *Alectryonia Potieri*, Bayle—Bayle: pl. 131, figs. 2–5.
- 1878 *Actinostreon solitarium*, Sowerby, sp.—Bayle: p. 132, figs. 2–6.
- 1880 *Ostrea solitaria* Sow.—Damon: pl. 9, fig. 2.
- 1882 *Ostrea gregaria* [sic] Sow.—Roeder: pl. 3, figs. 12a,b.
- 1883 *Ostrea (Alectryonia) rastellaris*, Münster var. *moravica* Boehm—Boehm: p. 658, pl. 70, figs. 27–30.
- 1888 *Ostrea (Alectryonia) costata* Sow., 1825—Schlippe: p. 112, pl. 1, figs. 11–12.
- ? 1888 *Ostrea (Alectryonia) Marshi* Sow., 1814—Schlippe: p. 114, pl. 1, fig. 14–18.
- 1892 *Ostrea (Alectryonia) Pulligera* (Goldfuss)—de Loriol: p. 342, pl. 36, fig. 4.
- 1892 *Ostrea (Alectryonia) solitaria*, Sow.—de Loriol: p. 313, pl. 36, figs. 5, 6.
- 1893 *Ostrea solitaria* Sow.—Fiebelkorn: p. 396, pl. 13, fig. 14.
- 1893 *Ostrea (Alectryonia) pulligera* Goldfuss—Greppin: p. 87, pl. 6, fig. 17, 18.
- 1894 *Ostrea (Alectryonia) vallata* Etallon—de Loriol: p. 75, pl. 9, figs. 5, 6.
- 1897 *Ostrea gregaria* Sow.—Reed: p. 45.
- 1897 *Ostrea solitaria* Sow.—Reed: p. 45.
- 1900 *Ostrea pulligera* Goldf.—Müller: p. 532, pl. 18, figs. 13–14.
- 1900 *Ostrea gregarea* Sow. var. *pterophora*, nob.—Cossmann: p. 47, pl. 5, figs. 3, 6.
- 1900 *Alectryonia Asellus*, Merian sp.—Greppin: p. 147, pl. 17, fig. 1–2, 5.
- 1900 *Alectryonia* cfr. *rastellaris* (Münster)—Greppin: p. 149, pl. 16, fig. 8.
- n 1901 *Exogyra gregarea* Sow.—Raspail: pl. 12, fig. 11.
- 1901 *Alectryonia flabelloides* Schloth.—Raspail: pl. 12, fig. 3.
- 1903 *Ostrea (Alectryonia) gregarea* Sow.—Remeš: p. 218, pl. 21 (4), figs. 8a,b (Tithonian).

- 1903 *Ostrea (Alectryonia) pulligera ascendens*, Qu.—Remeš: p. 218, pl. 21 (4), figs. 6a,b, 7a,b.
- 1903 *Ostrea (Alectryonia) aff. solitaria* Sow.—Remeš: p. 217, pl. 21 (4), figs. 5a,b.
- 1910 *Alectryonia gregarea* Sowerby—Lissajous: p. 343, pl. 8, fig. 17.
- 1910 *Alectryonia pulligera* Goldfuss—Lissajous: p. 334, pl. 8, fig. 18.
- 1911 *Ostrea (Rastellum) gregarea* Sow.—Rollier: p. 277.
- 1911 *Ostrea (Exogyra) semisolitaria* Etallon—Flamand: p. 924, pl. 9, figs. 2, 2a, 3–4, 5, 5a, 6.
- 1922 *Alectryonia costata* (Sowerby)—Cossmann: p. 4, pl. 5, figs. 5–8.
- 1924 *Alectryonia pulligera*—Jourdy: pl. 1, fig. 3, no. 2.
- 1925 *Alectryonia pulligera* (Goldf.)—Weir: p. 86, pl. 12, fig. 5.
- 1925 *Alectryonia rastellaris* (Münster)—Weir: p. 86, pl. 12, figs. 15–17.
- 1925 *Alectryonia solitaria* (Sow.)—Weir: p. 85, pl. 12, fig. 9.
- 1925 *Alectryonia aff. solitaria* (Sow.)—Weir: p. 86, pl. 12, fig. 8.
- 1931 *Ostrea (Alectryonia) gregaria* [sic], Sow.—Yin Tsan-hsun: p. 123, pl. 11, fig. 17.
- 1931 *Ostrea (Alectryonia) solitaria*, Sow.—Yin Tsan-hsun: p. 124, pl. 11, fig. 18.
- 1931 *Lopha pulligera* (Goldf.)—Diaz-Romero: p. 40, pl. 3, fig. 12, 13.
- 1933 *Lopha gregarea* (Sow.) var. *solitaria*—Orta: p. 34, pl. 2, figs. 7, 1–3, pl. 4, figs. 4–6, 8.
- 1933 *Lopha gregarea* (J. Sowerby)—Arkell: p. 183, pl. 22, figs. 5, 6, pl. 23, figs. 1–4.
- 1933 *Lopha solitaria* (Sowerby)—Arkell: p. 185, pl. 22, fig. 4, pl. 23, figs. 5–7.
- 1935 *Lopha solitaria* (Sow.)—Cox: p. 171, pl. 17, figs. 9–12.
- 1936 *Alectryonia gregarea* Sow.—Besairie: pl. 7, fig. 17.
- 1938 *Alectryonia gregarea* Sowerby—Chavan & Montocchio: p. 72, fig. 122a.
- 1939 *Lopha Perdalianae* (MGH.)—Stefanini: p. 195, pl. 22, figs. 4, 5.
- 1939 *Lopha solitaria* (Sow.)—Stefanini: p. 197, pl. 22, figs. 6–7.
- 1952 *Lopha gregarea* (J. Sowerby)—Cox: p. 96, pl. 4, fig. 2, pl. 10, figs. 7–13.
- 1956 *Lopha gregarea* (J. Sow.)—Agrawal: p. 89, pl. 9, fig. 13.
- 1959 *Lopha solitaria* (Sowerby)—Jaboli: p. 36, pl. 5, fig. 1.
- 1960 *Lopha solitaria* (J. de C. Sowerby)—Joubert: pl. 9, figs. 1, 2a–c.
- 1960 *Lopha gregarea* (J. Sowerby)—Tamura: p. 239, pl. 2, fig. 24.
- 1961 *Lopha cf. gregarea* (Sowerby, 1815)—Sibiriakova: p. 102, pl. 13, figs. 11–13.
- 1964 *Lopha Solitaria* (J. Sowerby)—Maithani: p. 510, pl. 31, fig. 2.
- 1965 *Lopha gregarea* (J. Sowerby)—Cox: p. 68, pl. 9, fig. 5.
- 1965 *Lopha solitaria* (J. de C. Sowerby)—Cox: p. 69, pl. 9, fig. 4.
- 1965 *Lopha solitaria* (Sowerby) s.s.—Fréneix: p. 72 (24), pl. 3, figs. 1, 2.
- 1965 *Lopha solitaria* (Sowerby) *matmatensis* n. ssp.—Fréneix: p. 73 (25), pl. 3, figs. 4a,b, 5a,b, 6a,b, 7a,b, text-fig. 7a, c.
- 1965 *Lopha solitaria* (Sowerby) *subpulligera* n. ssp—Fréneix: p. 76 (28), pl. 3, figs. 3a,b, 5, 9a,b, 10, 11, 12a,b, 13, 14, text-fig. 7b, d1, d2.
- 1969 *Lopha gregarea* (J. Sowerby)—Fischer: p. 96, pl. 10, fig. 28.
- 1971 *Lopha solitaria* (J. de C. Sowerby)—Jordan: p. 152, pl. 20, figs. 4a,b, 5a,b.
- 1971 *Alectryonia pulligera* (Goldfuss, 1834)—Pugaczewska: p. 234, pl. 8, figs. 1–15.
- 1971 *Alectryonia flabelliformis* (Nilson in Goldfuss, 1840)—Pugaczewska: p. 238, pl. 4, figs. 1–10.
- 1971 *Alectryonia gregarea* (Sowerby, 1816)—Pugaczewska: p. 227, pl. 3, fig. 7, pl. 5, figs. 1–8, pl. 6, figs. 1–8, pl. 9, figs. 2–3, pl. 10, fig. 3.
- 1971 *Alectryonia rastellaris* (Münster, 1833)—Pugaczewska: p. 232, pl. 6, fig. 9, pl. 7, figs. 1–3, 5–7.
- 1971 *Alectryonia solitaria* (Sowerby, 1825)—Pugaczewska: p. 230, pl. 3, figs. 1–6, pl. 9, fig. 1.
- 1971 *Alectryonia vallata* (Etallon, 1862)—Pugaczewska: p. 236, pl. 19, fig. 3a–b, 4.

1973	<i>Ostrea solitaria</i> Sow.—Contini & Hantzpergue: p. 150, 152.
1973	<i>Ostrea pulligera</i> Gold.—Contini & Hantzpergue: p. 175.
1976	<i>Lopha solitaria</i> (Sowerby)—Ma Qi-hong in Gu Zhi-wei <i>et al.</i> : p. 323, pl. 35, figs. 34–35.
1977	<i>Lopha (Rastellum) gregarea</i> (Sow.)—Andreeva: pl. 5, figs. 1–5.
1979	<i>Lopha solitaria</i> (Sowerby)—Wen Shi-xuan: p. 303, pl. 92, fig. 8.
1984	<i>Lopha gregarea</i> (Sowerby)—Radulović & Mitrović-Petrović: p. 110, pl. 3, figs. 4–5.
1985	<i>Lopha asellus namtuensis</i> Reed—Zhang Zuo-ming <i>et al.</i> : p. 115, pl. 45, fig. 5.
1985	<i>Lopha cf. gregarea</i> (Sowerby)—Zhang Zuo-ming <i>et al.</i> : p. 115, pl. 45, fig. 3, 4.
1988	<i>Arctostrea gregaria</i> [sic] (Sowerby)—Reiff: pl. 29, fig. 3.
?	1989 <i>Lopha gregarea</i> (Sowerby)—Matyia, Gutowski & Wierzbowski: pl. 3, fig. 4.
1990	<i>Lopha (Actinostreon) gregarea</i> (J. Sow. 1816)—Clausen & Wignall: p. 124, pl. 6, fig. c.
1990	<i>Lopha (Rastellum) gregarea</i> (Sowerby, 1815)—Dykan & Makarenko: p. 83, pl. 16, figs. 13, 15–20.
1990	<i>Lopha (Lopha) pulligera</i> (Goldfuss, 1834)—Dykan & Makarenko: p. 82, pl. 16, figs. 11, 12.
?	1994 <i>Actinostreon solitarium</i> (J. de C. Sowerby 1824)—Aberhan: p. 30, pl. 12, figs. 8–10.
n	1995 <i>Lopha (Lopha) solitaria</i> (J. de C. Sowerby, 1824)—Monari: p. 166–167, pl. 2, fig. 7.
1995	<i>Actinostreon gregareum</i> (J. Sowerby 1815)—Jaityl <i>et al.</i> : p. 186, pl. 13, fig. 13, pl. 14, figs. 1–5.
1997	<i>Lopha gregarea</i> (Sowerby, 1815)—Bernad: p. 14, pl. 2, fig. 4–7.
1998	<i>Actinostreon gregareum</i> (J. Sowerby, 1816)—Machalski: p. 614, fig. 4a–d, g–m.
1998	<i>Actinostreon</i> sp.—Machalski: p. 627, fig. 11A–I.
1998	<i>Lopha solitaria</i> —Breton: pl. 1, fig. 11.
1998	<i>Actinostreon gregareum</i> (J. Sowerby 1815)—Holzapfel: p. 105, pl. 6, figs. 18–19, 21.
1998	<i>Actinostreon costatum</i> (J. de C. Sowerby 1825)—Holzapfel: p. 104, pl. 6, figs. 8–14.
1999	<i>Actinostreon gregareum</i> (J. Sowerby 1815)—Ahmad: p. 15, pl. 6, fig. 3.
2002	<i>Actinostreon gregareum</i> (J. Sowerby 1815)—Gahr: p. 123, pl. 3, fig. 12.
2002	<i>Actinostreon gregareum</i> (J. Sowerby, 1816)—Sha, Smith & Fürsich: p. 433, figs. 6, 7.1–7.14.
2005	<i>Actinostreon solitarium</i> (J. Sowerby, 1824)—Scholz: p. 26, pl. 4, figs. 4–7.
2006	<i>Actinostreon gregareum</i> —Hicks: 36.
2006	<i>Actinostreon gregareum</i> (J. Sowerby, 1816)—Richardt: 9, 18.
2011	<i>Actinostreon solitarium</i> (J. de C. Sowerby)—Kiessling <i>et al.</i> : p. 209, fig. 13G.

Lectotype (not seen). *Ostrea gregarea* J. de Sowerby, 1815: p. 19, pl. 111, fig. 3; subsequent designation by Arkell 1933: p. 185, pl. 22, fig. 5, BM. 44120a (NHMUK). Westbrook near Bromham, Wiltshire, England, Berkshire Oolite Series?, Coral rag, Oxfordian, Upper Jurassic.

Material. More than 1000, mostly articulated specimens, including numerous juvenile specimens, from the Banné Marls of the Reuchenette Formation of Vâ Tche Tchâ near Courtedoux (Ajoie, Switzerland), Lower Kimmeridgian (Appendix, Table 8).

Description. Shape, size—LV slightly larger and more inflated than RV; shape largely influenced by attachment size; rather undisturbed growth broadly curved with posteroventral branchitellum; otherwise round, oval, elongated, trigonal to sickle-shaped; umbones small, acute, slightly recurved; opisthogyrate, rarely prosogyrate (e.g., Pl. 16.5a–b, d). Examined specimens between 1.4–7 cm in height (Appendix, Table 8)

Sculpture—Attached portion of shell often with replicates of overgrown objects (Pls. 16.3a,b, 4; 17.1a, c, 4b; 18.1a, 2a,c, 4a,b). Detached shell margin plicate; plicae growth direction roughly antimarginal, initially often with wavy, later typically with chevron shaped cross section; number of plicae increasing by splitting and intercalation; number variable (ca. 5–35), usually more than 20; plicae become squamous ventrally.

Ligament area—Well developed, initially curved, prosodetic, later growing anteroventrally, bourrelets in LV thick, convex, in adults almost as wide as resilifer; bourrelets in RV less convex, resilifer less sunken, may become convex tending to alivicular-arcuate (see definition in Carter *et al.* (2012) (Pl. 17.3a–d, Pl. 18.6).

Internal shell characters—Umbonal cavity small to absent. Adductor scar large, weakly raised ventrally, position slightly posterodorsal. Quenstedt muscle scar present in both valves, but rarely observable (Pl. 17.3b–c). Chomata present in all (eco)phenotypes, straight type, rather small (length between 0.3–0.6 mm, width 0.09–0.3 mm) and faint, on anterior and posterior dorsal shell margin, occasionally reaching further ventral than adductor scar, especially in juveniles (Pl. 17.4a).

Microstructure—Both valves with light-weight shell architecture; outermost prismatic shell layer not seen in either valve (eroded?); visible (non-chambered) outer-middle layers homogeneous “mosaic” to complex cross foliated (*ca.* 500 µm thick); middle-inner layers with many small and medium large chambers, small chambers especially below rib crests, convex or biconvex in cross-section; chambers typically empty (or filled diagenetically with sparry cement), maret absent or very rare (Pl. 22), chamber walls predominantly regular foliated, walls of void chambers often collapsed.

Prodissococonch, juvenile—Prodissococonch and earliest postlarval shell unknown (but see Pl. 19.4a–d). Small juveniles tend to have a stronger coiled umbo than adults (Pl. 18.4a–b, 5). The PAM of juveniles is oval (Pl. 18.3b); however, it rotates during ontogeny so that the anterior margin of the juvenile PAM becomes the adult dorsal adductor margin.

Paleoecology. *Actinostreon gregareum* is typical of the marls and marly limestones of the Banné Marls (Ajoie, Switzerland) where specimens are often found articulated. As its name suggests, the species is gregarious, occasionally forming aggregates of dozens of specimens (Pls. 16.2a,b; 17.2a,b; 19.2a–d) (compare with the often solitary growth of the ecomorph “*A. solitarium*”). Individuals or small clusters often settle on large bivalve and gastropod shells. Elongate morphotypes are commonly attached to the spines of the gastropod *Harpagodes* or to the delicate stems (Pl. 16.3a,b; Pl. 17.4a,b) and thalli of *Goniolina* (calcareous algae) (Pls. 17.4; 18.1–3) (compare also Pugaczewska 1971, pl. 6, figs. 2a,b, 8a,b; for specimens settling on spines of sea urchins).

Present sedimentary and biogenic evidence suggests that *A. gregareum* thrived in relatively calm subtidal environments. Arkell (1933, p. 184) associated the species with coral reef settings (the *Trigonia hudsoni* Limestones, Corallian, Upper Oxfordian, England). Fürsich (1977) and Sha *et al.* (2002) reported high-energy conditions as the favoured environment. All settings from which the species has been described indicate fully marine conditions.

Occurrence. In Switzerland, in the Lower Kimmeridgian Vabenau and Banné Members of the Reuchenette Formation, Bathonian–Tithonian of Central and Eastern Europe, Toarcian–Kimmeridgian of Spain, Tithonian of Czech Republic, Bajocian–Kimmeridgian of Israel, Oxfordian–Kimmeridgian of Arabia, Toarcian–Kimmeridgian of East Africa, Bajocian–Bathonian of Iran, Bajocian of Australia, Sinemurian–Aalenian of Chile, Bathonian–Oxfordian of India and China, Oxfordian–Kimmeridgian of Burma, Upper Jurassic of Japan (see Sha *et al.* 2002, p. 435).

Comparisons. *Actinostreon gregareum* is remarkably polymorphic even within the rather calm paleoenvironments of the Banné Marls. Because of its many transitional forms with populations described from more turbulent regimes, it is virtually impossible to separate the numerous alleged morphospecies described by Pugaczewska (1971) and previous authors.

The present approach largely agrees with the assessments and extensive synonymies given by Aberhan (1994), Cox (1952), Gahr (2002), Jaityl *et al.* (1995), Sha *et al.* (2002), and Siewert (1972). However, this makes *A. gregareum* a stratigraphically suspiciously wide-ranging species which still requires corroboration. The following list briefly discusses presumably distinct species in alphabetic order and with more doubtful cases towards the end.

Actinostreon marshii (J. Sowerby, 1814) (p. 103, pl. 48)—The species was first described from the Upper Cornbrash (Bathonian) in the neighbourhood of Felmersham near Bedford (Bedfordshire, England), but is also known from the Bajocian to Oxfordian in Europe (Pl. 19.3–4 for specimens of the Callovian of Lithuania) and from the Upper Bathonian to the Kimmeridgian of India (see Cox 1952, for synonymy and occurrence).

The species is characterized by few (7 or 8) strongly developed plicae and reaches a larger adult size with thicker shells than *A. gregareum* (Pl. 19.3). Adult specimens seem to lack chomata. The figured small specimen from Lithuania also lacks them (Pl. 19.4a–d) but this should be tested for juvenile shells in general. Usually the species does not form clusters, but exceptions are known, e.g., in the Oxfordian of the Vaches Noires (Normandy, France) (Fürsich, pers. comm. 2014). It occurs in relatively calm and, judged by its common association with ammonites, also deeper paleoenvironments.

Actinostreon namtuensis (Reed, 1936) (p. 9, pl. 1, fig. 1, 1a–b)—The species was originally described as *Lopha asellus* Merian var. *namtuensis* from the Bathonian of Burma. Sha *et al.* (2002) considered it a synonym of *A. gregareum*. However, unlike *A. gregareum*, this species has a non-curved shell (despite a small attachment area) and develops more than 30 plications which are much finer than in *A. gregareum*.

?*Actinostreon arietis* (Schäfle, 1929) (p. 63, pl. 6, figs. 2–3)—The species was originally described from the Lower Sinemurian (*Arietites* Limestone) of Vaihingen (Stuttgart, Germany). The only figured specimen is the holotype which lacks the umbo and ventral shell portions. The remaining shell (ca. 6.6 cm high) is not curved and shows about 12 coarse plications (Schäfle 1929). Internal features and microstructures are unknown. In the light of the poor remains of the species, Schäfle's allusion to the essentially crescentic genus *Arctostrea* from the Lower Cretaceous is incomprehensible.

?*Actinostreon erucum* (Defrance, 1821) (p. 31)—Defrance (1821) introduced the name as *Ostrea eruca* without figure and information about the origin of the type material in his oyster chapter of the *Dictionnaire Scientifique Naturelle*. The species is known from the Upper Callovian to Lower Oxfordian of the “falaise du Calvados” (Normandie, France) (Bigot 1893, 1904; Raspail 1901, pl. 11, fig. 8). Bigot (1893, p. 136, pl. 2, figs. 4–6; 1904, *Palaeontologia universalis*, 73, 73a) figured the type material of Defrance (1821) and supposed Patrie (= Le Mesnil-Patry?) close to Villers-sur-Mer as the most likely type locality. The species was suggested by Cox (1952, p. 105) as a replacement name for *Ostrea hastellata* (Schlotheim, 1820) [itself an invalid short form for *Ostracites cristahastellatus* Schlotheim, 1820].

The species is narrowly sickle-shaped without being attached to a cylindrical object, thin-shelled, and the central area lacks plicae. This species was attributed to several other oyster genera such as *Arctostrea* or *Rastellum* (Cox, 1952, p. 103–106). In fact, the shape and plicae pattern are more reminiscent of the type species of Upper Cretaceous *Agerostrea* (Flemingostreinae) which is a compact foliated genus (Malchus, 1990, p. 160, pl. 15, fig. 8) (see also, Klinger & Malchus, 2008; Stenzel, 1971, fig. J133). However, there are no further characters available for a sound assessment.

?*Actinostreon pulligerum* (Goldfuss, 1833) (p. 5, pl. 72, fig. 11a–c)—The type material, from the Upper Kimmeridgian Corallian facies of Nattheim (Swabian Alb, Germany), compares well with a juvenile, round variation of *A. gregareum*, attached to a small object (Pl. 16, Figs. 5–6) (see also Arkell, 1933, p. 186). Unfortunately, little else is known about this species (Sha *et al.* 2002, p. 436).

?*Ambigostrea boucaudensis* (Choffat) (manuscript name of the unpublished 3rd volume of Choffat's monograph; according to Fürsich & Werner, 1988, p. 103)—According to Malchus (1990, p. 68–70), the Geological Museum in Lisbon (Portugal) holds some specimens (nrs. 2593–2598, 2600) from the Kimmeridgian of the Lusitanian Basin which were originally labelled as “*O.*” *pulligera* var. *boucaudensis* Choffat. Unlike typical *Actinostreon* species, this apparently undescribed variant or species is essentially compact foliated, develops nodular plicae, shows plenty of small but well developed relict chomata on its dorsal flanks, and has an ostreoid adductor scar. Malchus (1990) hypothesized that “*O.*” *pulligera* sensu Choffat could be the earliest representative of his newly established genus *Ambigostrea* (Malchus 1990, p. 85).

Small straight chomata and an ostreoid adductor scar are also present on the original figure of Goldfuss (pl. 72, fig. 11c) which may suggest that both Choffat's and Goldfuss' specimens belong to *Ambigostrea* rather than *Actinostreon*.

?*Rastellum rusticum* (Defrance, 1821) (p. 31)—The types of *Ostrea rustica* Defrance, 1821, are from the Middle Callovian of Gâprée (Basse-Normandie, Department Orne, France) (Bigot, 1904, *Palaeontologia universalis*, 72, 72a, figs. C.1–3, P.1–3) (Fig. 21.1–2). The species is identical with *Ostrea amata* d'Orbigny, 1850 (Bigot 1904, p. 72a) and is morphologically similar to *A. gregareum*.

Main differences are a narrower shape, a thinner shell and the larger number of plicae (30–50), covering the whole shell including the umbonal area, absence of chomata, and the more posterodorsally situated oval adductor scar (Fig. 21.3–7). The shell was chambered as indicated by a collapsed shell layer on the inner (depositional) surface of a specimen from Villers-sur-Mer, France (Calvados, Middle Oxfordian, *plicatilis* Zone) (FPJ-collection, nr. 5369; Fig. 21.5–6) and Liesberg, Switzerland (Middle Callovian, *coronatum* Zone) (FPJ, nr. 5367). This type of breakage is typical of specimens with larger (hollow) shell chambers.

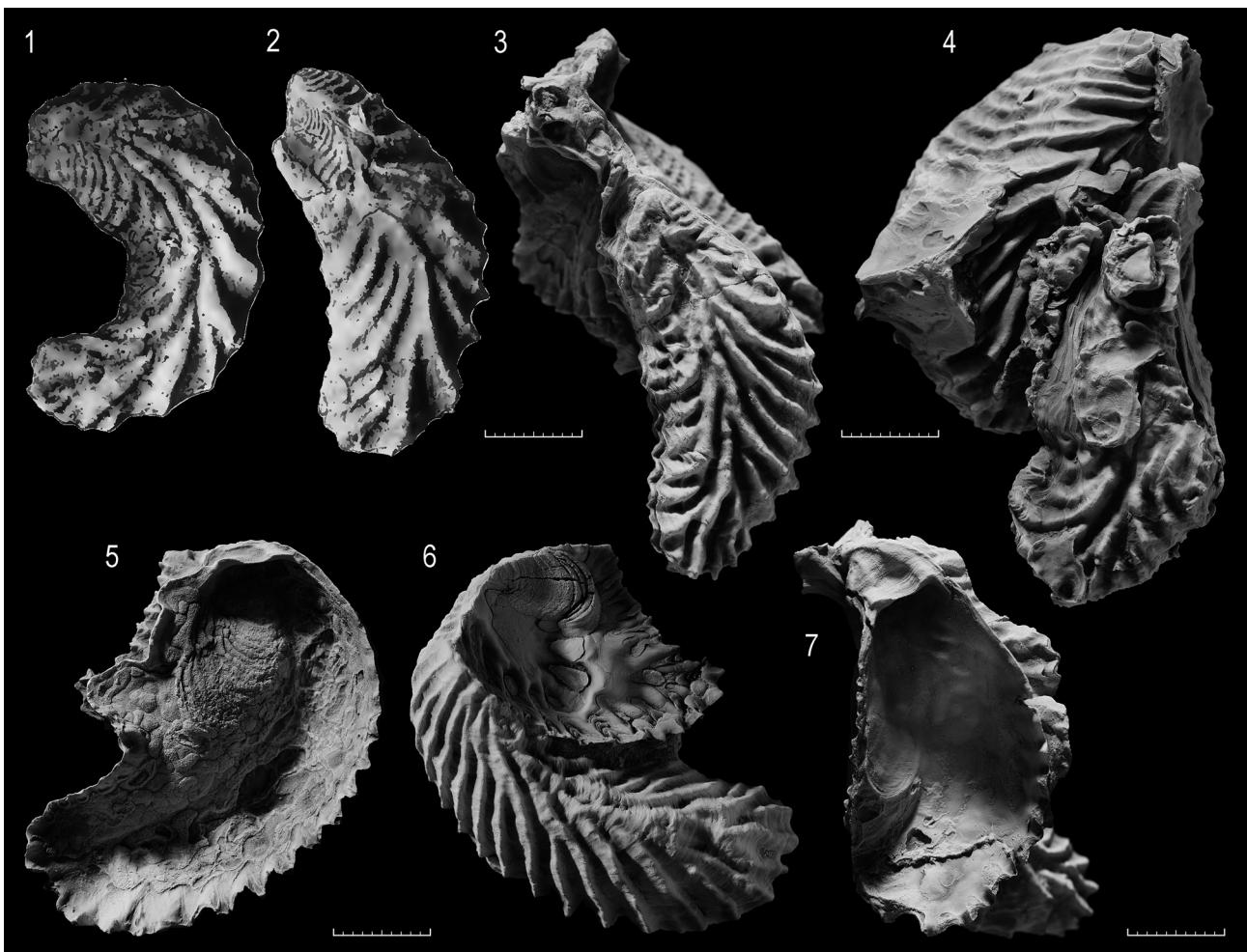


FIGURE 21. *?Rastellum rusticum* (Defrance, 1821). 1. RV, syntype of Defrance, *Ostrea rustica* Defrance, 1821, refigured from Bigot 1904, p. 72, fig. C1. 2. RV, syntype, refigured from Bigot 1904, p. 72, fig. C3; both from Gâprée, Basse-Normandie, France, Middle Callovian, Musée d' Histoire naturelle de Caen. 3–7. Specimens from Villers-sur-Mer, Calvados, France, Middle Oxfordian, FPJ collection: 3, bivalved specimen, RV, FPJ 5368a; 4, group of bivalved specimens and 2 juveniles, right specimen with prosogyrate umbo, FPJ 5370; 5–6, LV, FPJ 5369: 5, interior, with narrow, strongly curved ligament and collapsed chambers; 6, same, lateral; 7, LV, interior, with broad ligament, FPJ 5368b. Scale bars 10 mm.

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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	<i>Trichites</i> ext.	Rang Marls
MC 27E105a PL	LV	2.6	3.1	0.4	0.84	0.13	o	<i>Circunula</i> (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	<i>Isognomon</i>	Banné Marls
VTT001-3215	2V	2.65	2.35	0.8	1.13	0.34	p	<i>Isognomon</i>	Banné Marls
VTT001-3238	2V	2.6	2.7	1.0	0.96	0.37	p	<i>Costigervillia</i>	Banné Marls
VTT001-3248	LV	3.0	2.7	1.35	1.11	0.5	o	<i>Costigervillia</i>	Banné Marls
VTT001-3262	2V	3.25	3.1	0.7	1.05	0.23	o	<i>Ceratomya</i>	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	<i>Isognomon</i>	bed 70, B. M.
CRA001-25	LV	3.7	3.9	1.1	0.95	0.28	o	<i>Isognomon</i>	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	<i>Trichites</i> int.	Banné Marls
ALO009-1-II	LV	1.4	1.2	0.1	1.27	0.08	p	<i>Trichites</i> int.	Banné Marls
ALO009-1-III	LV	3.2	3.3	0.15	0.97	0.05	o	<i>Trichites</i> int.	Banné Marls
ALO009-1-IV	LV	1.75	1.6	0.12	1.1	0.08	p	<i>Trichites</i> int.	Banné Marls
ALO009-1-V	LV	1.1	1.3	0.1	0.85	0.09	o	<i>Trichites</i> int.	Banné Marls

TABLE 2. *Nanogyra (Nanogyra) nana* (J. Sowerby, 1822).

No.	shell	H	L	I	H/L	I/L	attached to	Litho./facies
VTT001-3210	2V	1.6	1.4	0.9	1.42	0.64	<i>Actinostreon?</i>	Banné Marls
VTT001-3214	LV	2.4	1.6	0.9	1.5	0.56	<i>Costigervilla</i> (LV)	Banné Marls
VTT001-3229	LV	2.32	1.11	0.9	2.09	0.82	small shell indet.	Banné Marls
VTT001-3247	LV	2.1	1.55	0.9	1.35	0.58	<i>Isognomon</i>	Banné Marls
VTT004-15	2V	2.0	1.45	0.9	1.38	0.62	heterodont bivalve	Banné Marls
TLB000-7	LV	2.2	1.4	1.1	1.57	0.79	<i>Gervillella</i>	Banné Marls
VTT001-3210	2V	1.6	1.45	1.0	1.1	0.69	<i>Actinostreon</i>	Banné Marls
VTT009-16-1	LV	1.4	1.3	0.7	1.08	0.54	<i>Isognomon</i>	Banné Marls
VTT009-16-2	LV	2.1	1.55	0.6	1.35	0.39	<i>Isognomon</i>	Banné Marls
SCR002-305	LV	2.4	1.9	1.1	1.26	0.58	<i>Gervillella</i>	L. Virgula Marl
SCR004-176-1	LV	1.8	1.4	1.2	1.29	0.86	attached on another	L. Virgula Marl
SCR004-176-2	LV	1.9	1.1	1.1	1.73	1.0	attached on another	L. Virgula Marl
SCR004-176-3	LV	1.9	1.4	1.0	1.36	0.71	attached on another	L. Virgula Marl
SCR004-176-4	LV	1.5	1.05	1.0	1.43	0.95	attached on another	L. Virgula Marl
SCR004-176-4	LV	1.5	1.2	0.9	1.25	0.75	attached on another	L. Virgula Marl

TABLE 3. *Nanogyra (Palaeogyra) reniformis* (Goldfuss, 1833)(b).

No.	shell	H	L	I	H/L	I/L	attached to	Litho./facies
VTT001-1549a	LV	1.64	1.22	0.58	1.34	0.48	<i>Actinostreon</i> (interior)	Banné Marls
VTT001-1549b	LV	1.38	1.24	0.57	1.11	0.46	RV <i>Circunula</i> (inter.)	Banné Marls
VTT006-112b	LV	1.22	0.94	0.19	1.3	0.2	RV <i>Circunula</i> (exter.)	Banné Marls
VTT006-112c	LV	1.14	1.2	0.33	0.95	0.28	<i>Actinostreon</i> (interior)	Banné Marls
VTT009-33a	LV	0.87	0.65	0.13	1.34	0.2	interior of attached shell	Banné Marls
VTT009-33b	2V	0.79	0.67	0.1	1.18	0.15	LV of <i>Actinostreon</i>	Banné Marls
VTT009-62	LV	1.75	1.52	0.57	1.15	0.38	fragment of <i>Isognomon</i>	Banné Marls
VTT001-1495	LV	0.6	0.83	0.1	0.72	0.12	LV <i>Actinostreon</i> (exterior)	Banné Marls
MC-27E38	LV	1.1	0.9	0.15	1.22	0.16	<i>Trichites</i> (interior)	Rang Marls
MC-27E40	LV	1.25	1.3	0.2	0.96	0.15	<i>Trichites</i> (interior)	Rang Marls

TABLE 4. *Nanogyra (Palaeogyra) virgula* (Deshayes, 1831).

No.	shell	H	L	I	H/L	I/L	attached to	Litho./facies
TLB001-355	LV	1.3	1.1	0.55	1.18	0.5	algae	Banné Marls
VTT001-1624	LV	1.6	1.4	0.55	1.14	0.39	stem of <i>Goniolina</i>	Banné Marls
SCR002-1787	LV	2.7	1.6	0.6	1.7	0.38	<i>N. virgula</i>	bed 2100
SCR002-1788	LV	2.3	1.8	0.8	1.28	0.44	not visible	bed 4500
SCR002-1789	LV	2.2	1.8	0.8	1.22	0.44	small shell indet.	bed 2100
SCR002-1797	LV	2.1	1.4	0.45	1.5	0.32	tiny, smooth shell	bed 2100
SCR002-1799	LV	2.1	1.6	0.7	1.31	0.44	small <i>Protocardia</i>	bed 2100
SCR002-1800	LV	2.2	1.8	0.7	1.22	0.39	smooth shell indet.	bed 2100
SCR002-1804	LV	2.4	1.8	0.8	1.33	0.44	algal stem	bed 2100
BSY009-914	2V	1.9	1.3	0.6	1.46	0.46	astartid? bivalve	bed 4500

TABLE 5. *Helvetostrea* n. gen. *sequana* (Thurmann & Étallon, 1862).

No.	shell	H	L	I	H/L	I/L	attached to	horizon, facies
SCR003-9	LV	4.5	3.55	2.1	1.23	0.47	not preserved	cou. 3500, reworked
SCR003-628a	LV	6.6	5.6	2.7	1.78	0.48	indet.	cou. 2400, high energy
SCR003-628b	LV	6.1	4.5	3.4	1.36	0.76	specimen 628a	cou. 2400, high energy
SCR003-628c	LV	2.7	2.0	1.1	1.35	0.55	specimen 628a	cou. 2400, high energy
SCR003-852	LV	6.5	4.0	3.9	1.63	0.6	not preserved	cou. 2600, high energy
SCR003-1198	LV	8.2	4.4	2.5	1.86	0.3	small object	cou. 2400, high energy
SCR003-1237	LV	7.2	5.3	2.5	1.36	0.35	not preserved	cou. 2400, high energy
SCR003-1545a	LV	4.1	2.4	2.1	1.71	0.51	RV exterior	2500-2700, high energy
SCR003-1545b	RV	2.4	2.05	0.42	1.17	0.2	LV, 1545a	2500-2700, high energy
SCR003-1552	LV	3.3	1.9	1.3	1.74	0.39	indet.	2500-2700, high energy
SCR002-177	LV	4.5	3.5	1.87	1.29	0.53	not preserved	2400, high energy
SCR002-1157	LV	5.9	3.4	2.6	1.73	0.76	indet.	cou. 2400, high energy
SCR002-1501a	LV	5.7	3.5	2.8	1.63	0.49	small object	indet., white limestone
SCR002-1501b	LV	3.5	2.1	1.0	1.67	0.29	specimen 1501a	indet., white limestone
SCR002-1501c	LV	2.1	1.2	1.1	1.75	0.52	1501a + b	indet., white limestone
TCH002-306a	LV	6.0	4.2	2.2	1.43	0.52	RV, 306b	ca. 2700, moderate
TCH002-306b	RV	4.5	2.9	0.4	1.55	0.13	isolated valve	ca. 2700, moderate
VTT001-1169b	LV	1.2	1.1	0.4	1.09	0.36	<i>Praeexogyra</i>	cou. 300?, Banné Marls

TABLE 6. *Praeexogyra dubiensis* (Contejean, 1859).

No.	shell	H	L	I	H/L	I/L	attached to	horizon, facies
MC-27E-111 PL	2V	1.3	0.95	0.72	1.37	0.76	gastropod?	oolitic marl
MC-27E-112 LT	LV	1.95	1.3	0.65	1.5	0.5	algae indet.	oolitic marl
MC-27E-113 PL	LV	1.5	1.23	0.55	1.22	0.45	small object	oolitic marl
MC-27E-116 PL	LV	2.1	1.5	1.18	1.4	0.79	other RV	oolitic marl
VTT001-1171	RV	2.6	1.6	0.3	1.63	0.18	unknown	Banné M., oolitic

TABLE 7. *Praeexogyra monsbeliardensis* (Contejean, 1859).

No.	shell	H	L	I	H/L	I/L	attached to	horizon, facies
MC 27E-141 LT	2V	3.5	3.0	1.9	1.17	0.63	unidentified shell	low energy marl
MC 27E-138 PL	LV	2.7	1.9	1.5	1.42	0.79	RV of <i>P. monsb.</i>	low energy marl
MC 27E-139 PL	LV	3.2	2.6	2.5	1.23	0.96	unidentified shell	low energy marl
MC 27E-140 PL	LV	2.2	2.3	1.6	0.96	0.69	unidentified shell	low energy marl
MC 27E-142 PL	2V	3.2	2.4	1.9	1.33	0.79	<i>Isognomon</i>	low energy marl
VTT001-3209	2V	2.7	2.1	1.2	1.29	0.57	<i>Actinostreon</i>	low energy marl
VTT001-3216	LV	2.7	2.4	2.1	1.13	0.88	<i>Costigervillia</i>	low energy marl
VTT001-3236	2V	4.0	3.3	1.5	1.21	0.45	smooth shell	coarse grained marly lst.
VTT001-3253	2V	2.9	2.15	1.5	1.35	0.70	unidentified shell	low energy marl
VTT001-3254	2V	3.5	2.6	2.4	1.35	0.92	<i>Harpagodes</i>	low energy marl
VTT001-3259	LV	3.6	2.7	1.5	1.33	0.56	<i>Isognomon</i>	low energy marl
VTT001-3261	LV	2.4	2.2	2.0	1.09	0.91	<i>Isognomon</i>	medium energy
VTT009-9a	LV	2.6	2.0	1.1	1.3	0.55	<i>Eopecten</i>	low energy marl
VTT009-9b	2V	3.9	3.5	1.1	1.11	0.31	<i>Eopecten</i>	low energy marl
VTT009-9c	LV	3.1	2.5	1.2	1.24	0.48	<i>Eopecten</i>	low energy marl
VTT009-9d	2V	2.9	2.6	1.2	1.12	0.46	<i>Eopecten</i>	low energy marl

TABLE 8. *Actinostreon gregareum* (J. Sowerby, 1815).

No.	Shell	H	L	I	H/L	I/L	plicae	attached to	Litho./facies
VTT001-1176	RV	1.9	1.6	0.3	1.19	0.19	17	tiny object	Banné Marls
VTT001-1224	RV	1.6	1.4	0.45	1.14	0.32	22	tiny object	Banné Marls
VTT001-1625	RV	1.7	1.5	0.35	1.13	0.23	24	tiny object	Banné Marls
VTT001-1630a	LV	4.1	3.8	1.3	1.08	0.34	33	<i>Costigervillia</i>	Banné Marls
VTT001-1630b	2V	3.3	2.3	1.0	1.43	0.44	23	<i>Costigervillia</i>	Banné Marls
VTT001-1653a	2V	3.4	4.0	0.6	0.85	0.15	21	<i>Isognomon</i>	Banné Marls
VTT001-1653b	2V	4.1	4.3	0.9	0.95	0.21	27	<i>Isognomon</i>	Banné Marls
VTT001-1654	2V	4.1	4.2	1.1	0.98	0.26	16	<i>Integricardium</i>	Banné Marls
VTT001-1657	2V	3.6	4.4	1.3	0.82	0.3	29	<i>Isognomon</i>	Banné Marls
VTT001-1700a	2V	3.9	4.3	1.5	0.91	0.35	24	convex shell	Banné Marls
VTT001-1700b	2V	3.6	4.0	1.6	0.9	0.4	22	convex shell	Banné Marls
VTT001-1704a	LV	3.1	2.4	0.5	1.29	0.21	26	<i>Costigervillia</i>	Banné Marls
VTT001-1704b	2V	4.0	2.8	0.7	1.43	0.25	23	<i>Costigervillia</i>	Banné Marls
VTT001-1704c	2V	3.3	3.2	1.0	1.03	0.31	26	<i>Costigervillia</i>	Banné Marls
VTT001-1705	RV	4.7	3.6	1.1	1.3	0.3	28	<i>Eopecten</i>	Banné Marls
VTT006-77	RV	5.3	6.8	1.4	0.78	0.21	33	tiny object	BM, layer 1690
VTT006-101a	2V	2.4	2.0	0.6	1.2	0.3	16	<i>Harpagodes</i>	BM, layer 1500
VTT006-101b	2V	3.9	3.2	0.8	1.22	0.25	22	<i>Harpagodes</i>	BM, layer 1500
VTT006-101c	2V	3.5	3.0	0.8	1.17	0.27	19	<i>Harpagodes</i>	BM, layer 1500
VTT006-101d	2V	3.2	2.6	0.7	1.23	0.27	21	<i>Harpagodes</i>	BM, layer 1500
VTT006-101e	2V	2.5	1.9	0.4	1.32	0.21	14	<i>Harpag.</i> , spine	BM, layer 1500
VTT006-101f	2V	3.7	3.0	0.9	1.23	0.3	21	<i>Harpagodes</i>	BM, layer 1500

PLATE 1. *Circunula* nov. gen. *cotyledon* (Contejean, 1859), Banné Marls, Reuchenette Formation, Lower Kimmeridgian, Canton Jura, Switzerland. **1a–c.** Large RV, CTD-VTT006-112, Vâ Tche Tchâ near Courtedoux (spoil material): **1a**, lateral; **1b**, interior; **1c**, dorsal view. **2.** LV, CHE-CHS009-4, Chevenez-La Scierie (attached on basal hardground of the Banné Marls), interior view. **3a–b.** Small bivalved specimen, CTD-VTT001-3215, Vâ Tche Tchâ (spoil material): **3a**, RV, lateral view, prosogyrate specimen; **3b**, ventral view of LV with regenerated shell-injury. **4 a–b.** LV, CTD-VTT001-3248, Vâ Tche Tchâ (spoil material): **4a**, anterior; **4b**, interior view. **5a–d.** Bivalved specimen, CTD-VTT001-3262: **5a**, lateral view, specimen attached to *Ceratomya excentrica* (Roemer, 1836); **5b**, lateral view, RV xenomorphic after *Ceratomya*; **5c**, anterodorsal view; **5d**, dorsal view. Specimens whitened with ammonium chloride. All scale bars 10 mm; each sub-bar 1 mm in all plates.



PLATE 2. *Circunula* nov. gen. *cotyledon* (Contejean, 1859), Reuchenette Formation, Lower–Upper Kimmeridgian. **1.** Large LV, CTD-SCR002-1049, Sur Combe Ronde near Courtedoux (layer 2100, *mutabilis* Zone), interior view, with *Cycloserpula* sp. **2a–b.** Large RV, CTD-VTT001-1546, Vâ Tche Tchâ near Courtedoux (spoil material, Banné-Marls, *cymodoce* Zone): **2a**, lateral view, showing attached spat of ca.12 LVs of *Nanogyra nana* (J. Sowerby, 1822) with similar orientation; **2b**, magnified portion of RV, with faint antimarginal riblets (left side, below *Nanogyra*) and comm marginal growth lines. **3.** RV and parts of LV, CTD-VTT006-863, Vâ Tche Tchâ (bed 70, Banné Marls), lateral view of RV, with bivalved *Nanogyra nana*. **4a–b.** Bivalved prosogyrate specimen, CTD-VTT001-3238, Vâ Tche Tchâ (spoil material, Banné Marls): **4a**, lateral view; **4b**, RV magnified, with echinoid grazing trace *Gnathichnus pentax* Bromley, 1975. **5a–b.** Bivalved prosogyrate specimen, CTD-VTT001-1196 (spoil material, Banné Marls): **5a**, RV lateral, with juvenile *Actinostreon gregareum* (J. Sowerby, 1815); **5b**, LV lateral, with antimarginal furrows and folds; **5c**, posterior view; **5d**, RV magnified, with antimarginal furrows; **5e**, LV structures magnified. **6.** RV, CTD-VTT001-3262 (same as Pl.1.5a–d), magnified, with antimarginal riblets on RV. **7a–b.** large LV, SCR002-1049, Sur Combe Ronde (hardground, bed 2000, *mutabilis* Zone): **7a**, lateral view; **7b**, magnified, with faint antimarginal furrows and growth interruptions. Scale bars 10 mm.

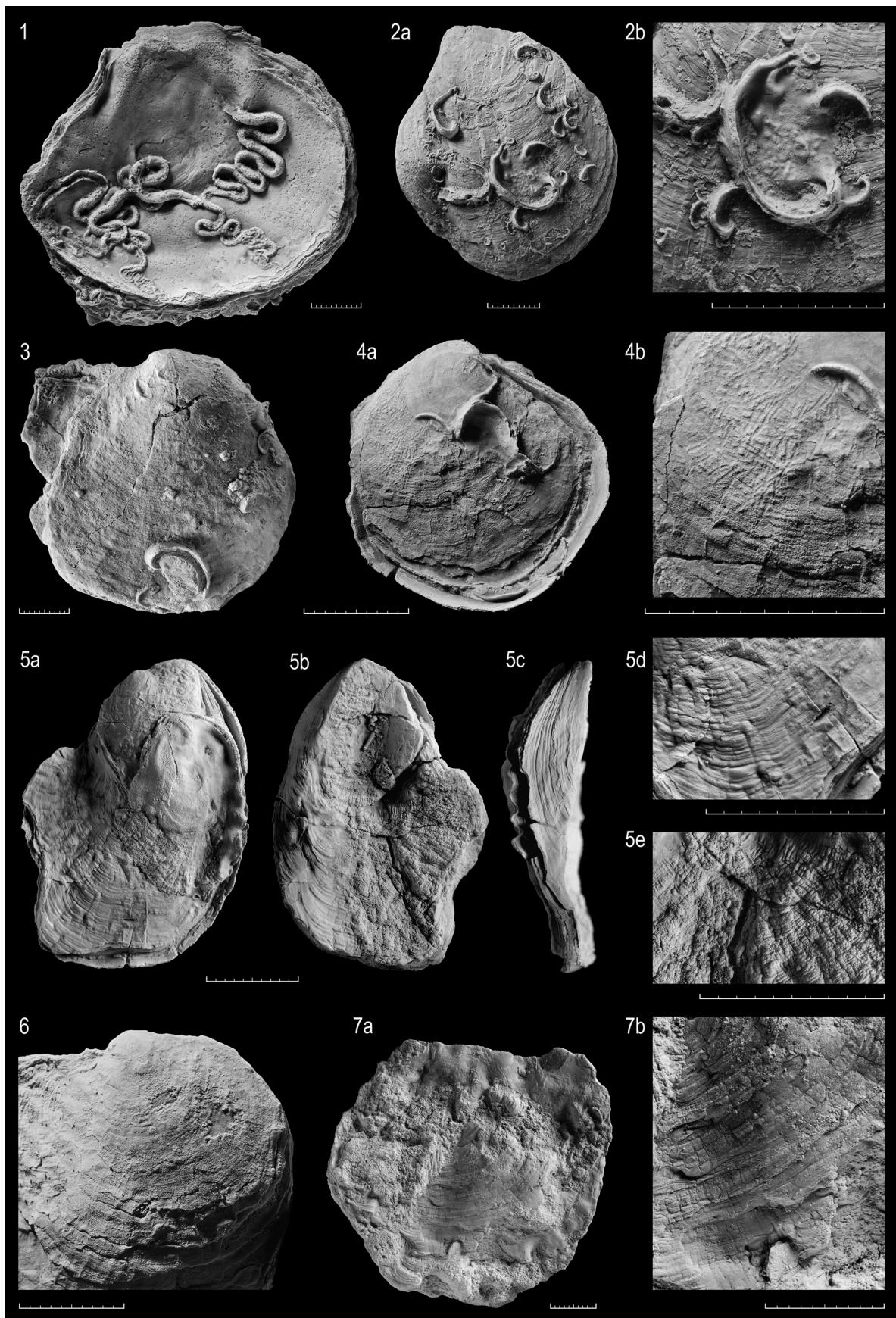


PLATE 3. *Circunula* and *Catinula*. **1–5.** *Circunula* nov. gen. *cotyledon* (Contejean, 1859). **1.** Large RV, MJSN S.1469 (A.1.10.5.7), Blauen (Canton Basel-Landschaft, Switzerland), Upper Oxfordian, RV interior, PAM = posterior adductor muscle scar. **2–3, 5.** CGN-ALO009-1, Alombre aux Vaches near Courgenay (float, Banné Marls): **2**, juvenile LVs attached on interior of a bivalved *Trichites* (at left valve close to anterior margin); **3a**, LV, ALO009-1-I, umbo opisthogyrate, dorsal margin with chomata; **3b**, prosogyrate LV, ALO009-1-II, interior pustulose (caused by exterior ornament); **3c**, LV, ALO009-1-III, with chomata and traces of external antimarginal ornament, rough inner surface caused by immurated serpulids and oysters; **3d**, LV, ALO009-1-III, hinge magnified (BLAj = base of juvenile ligament area, see arrows); **3e**, LV, ALO009-1-IV, interior pustulose; **5**, prosogyrate LV, ALO009-1-V, interior view. **4a–b.** Prosogyrate LV, CTD-VTT001-1615, Vâ Tche Tchâ (spoil material): **4a**, LV interior (ventrally damaged); **4b**, magnified, with chomata, Quenstedt muscle (QM) and PAM. **6.** *Catinula knorri* (Voltz, 1828), SMNS 67691/1, Deilingen, Baden-Württemberg, Germany, Lower Bathonian, *Knorri*-Clays, prosogyrate juvenile LV (flat stage), attached interior of adult RV, with faint relict chomata? on dorsal margin. Scale bars 10 mm (figures 1, 2, 3c), all others 5mm.

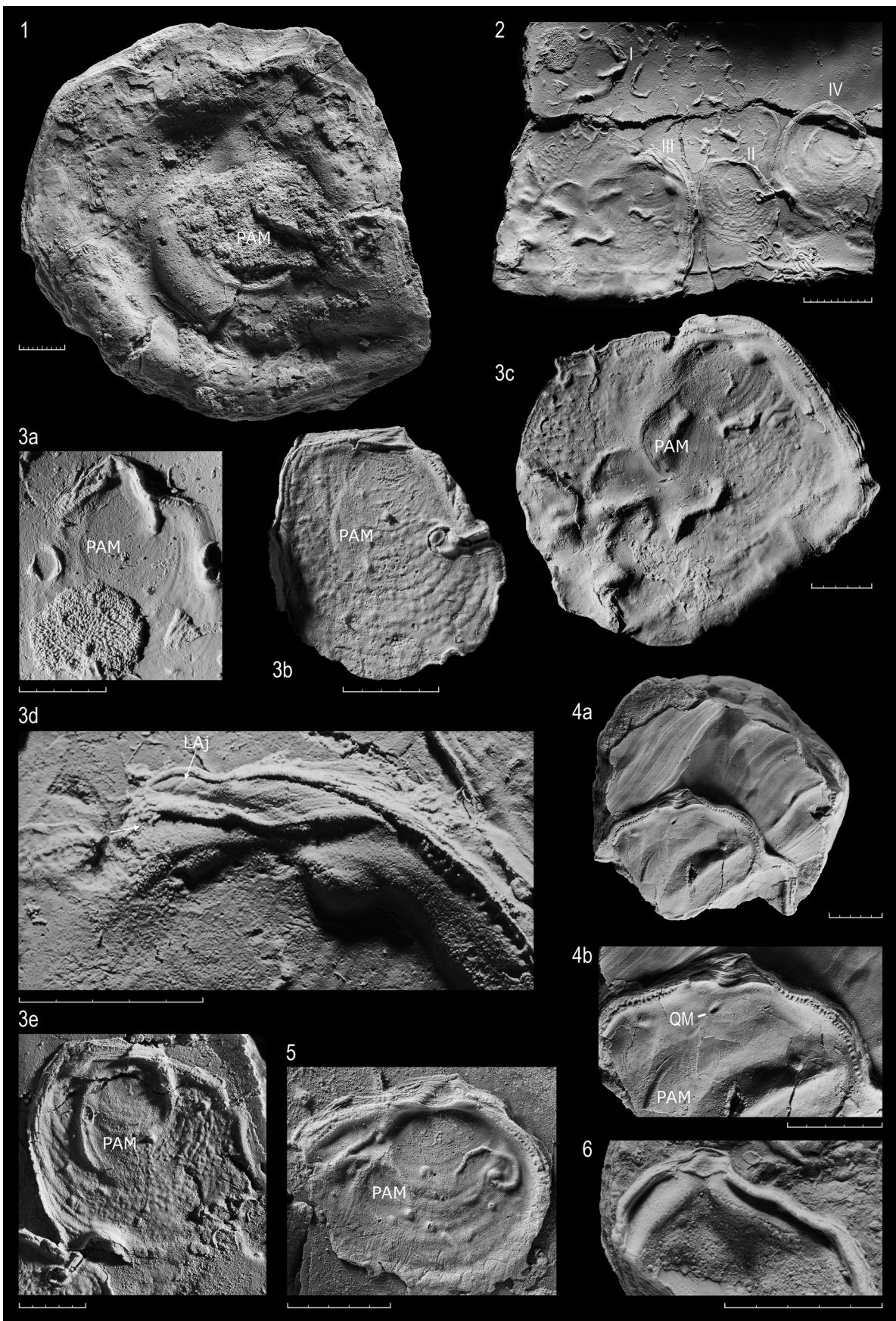


PLATE 4. *Catinula*, and *Helvetostrea*. **1, 4.** *Circunula* nov. gen. *cotyledon*, Banné Marls. **1.** Prosogyrate LV, CTD-VTT001-1615, Vâ Tche Tchâ (spoil material). **4.** LV, CTD-VTT001-3248, Vâ Tche Tchâ (spoil material), dorsal view. **2–3, 5–6.** *Catinula knorri* (Voltz, 1828), Lower Bathonian, zigzag Zone, Knorri-Clays, Baden-Württemberg, Germany. **2.** Prosogyrate RV, SMNS 67691/5, Deilingen, lateral view. **3a–b.** Bivalved specimen, SMNS 67691/4, Deilingen: **3a**, LV lateral; **3b**, RV lateral. **5a–b.** LV, SMNS 67692/2, Geisingen a. d. Donau: **5a**, lateral; **5b**, interior. **6.** RV, SMNS 67691/3, Deilingen, interior view. **7–9.** *Helvetostrea* n. gen. *sequana* (Thurmann & Etallon, 1862), Reuchenette Formation, Upper Kimmeridgian (*mutabilis* Zone), Sur Combe Ronde near Courtedoux, Canton Jura, Switzerland. **7a–c.** Large LV, CTD-SCR003-1198 (bed 2400), elongated morphotype: **7a**, LV interior; **7b**, lateral view; **7c**, ventral view, with deep umbonal cavity. **8.** Small cluster of specimens, CTD-SCR003-628 (bed 2400), poorly preserved, with boreholes (*Gastrochaenolites* isp.) of *Lithophaga*. **9a–b.** LV, CTD-SCR002-1157 (bed 2150): **9a**, lateral view; **9b**, details of irregular squamous shell surface. Scale bars 10 mm; and for small specimens and magnified portions 5mm.

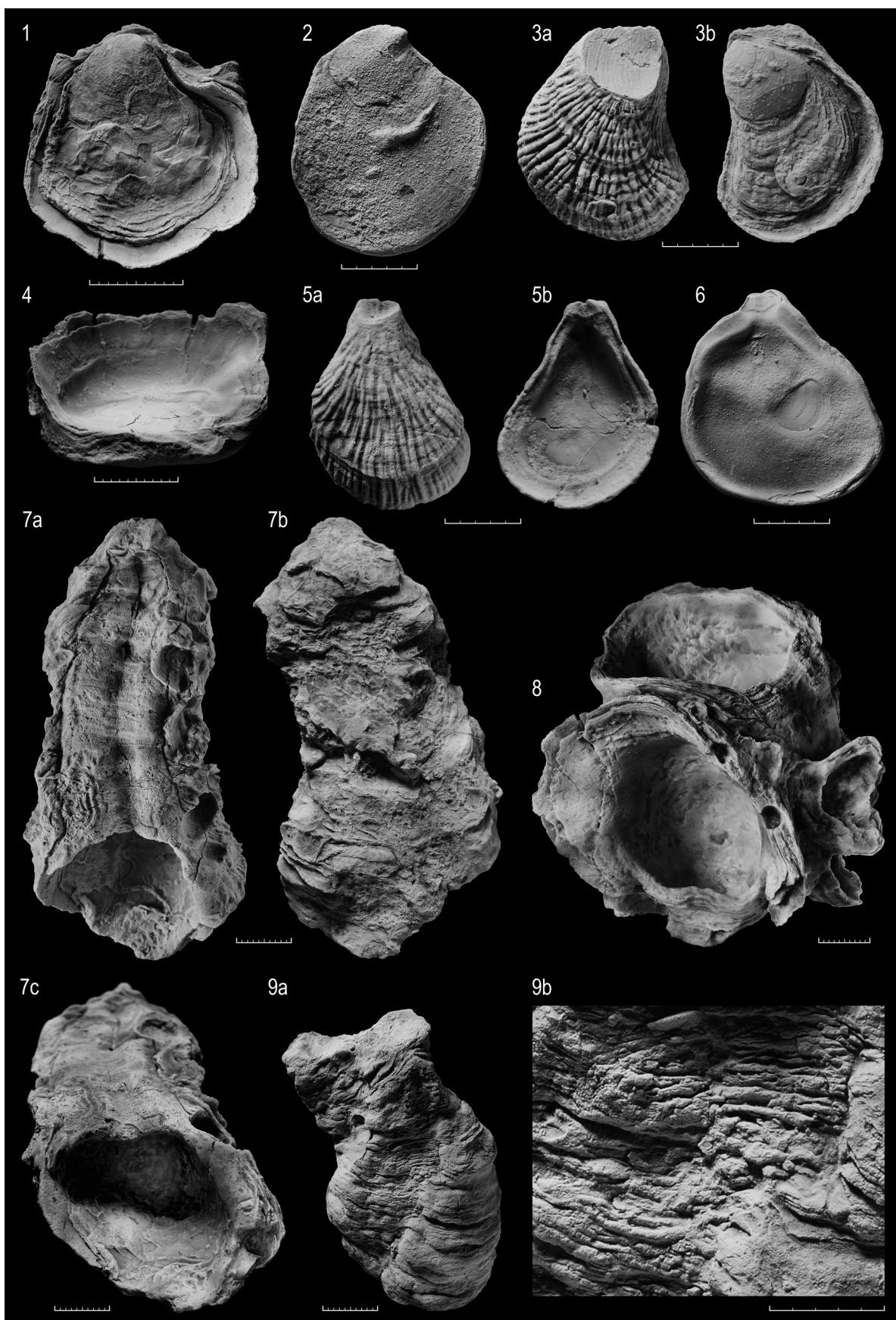


PLATE 5. *Nanogyra (Nanogyra) nana* (J. Sowerby, 1822), **1–4, 7–8**, Vâ Tche Tchâ near Courtedoux, Banné Marls. **1a–d**. Bivalved specimen, CTD-VTT001-3210 (spoil material): **1a**, RV (with part of LV), lateral view; **1b**, LV, posterodorsal view, with xenomorphic ornament; **1c**, LV, lateral; **1d**, LV, anterior view. **2a–b**. LV, CTD-VTT001-3214 (spoil material): **2a**, interior view; **2b**, anterior view. **3a–c**. RV, CTD-VTT001-144 (spoil material): **3a**, lateral view; **3b**, posterior; **3c**, interior, with grooves marking gill-position. **4a–c**. Bivalved specimen, CTD-VTT004-15 (spoil material): **4a**, LV, lateral view; **4b**, RV, lateral view; **4c**, LV, posterior view, with antimarginal, xenomorphic furrows. **5**. RV, MJSN S1067, labelled as *Ostrea (Exogyra) bruntrutana* var. *portlandica* Thurm. (Thurmann coll.), Reuchenette Formation, Banné (hill in Porrentruy), “Lower Virgula Marl”, Upper Kimmeridgian, *eudoxus* Zone, lateral view. **6**. Large RV, CTD-SCR002-1367, Sur Combe Ronde near Courtedoux, “Lower Virgula Marl” (bed 4500), lateral view. **7**. Bivalved specimen, CTD-VTT006-645 (bed 1680), part of oyster-cluster with *Actinostreum gregareum* and *Nanogyra nana* (see Pl.5.8, Pl. 19.2a–d), LV and RV, lateral view. **8**. Group of LVs, CTD-VTT006-645, 4 LV, interior view. Scale bars 5 mm, except for fig. 7 (3 mm).

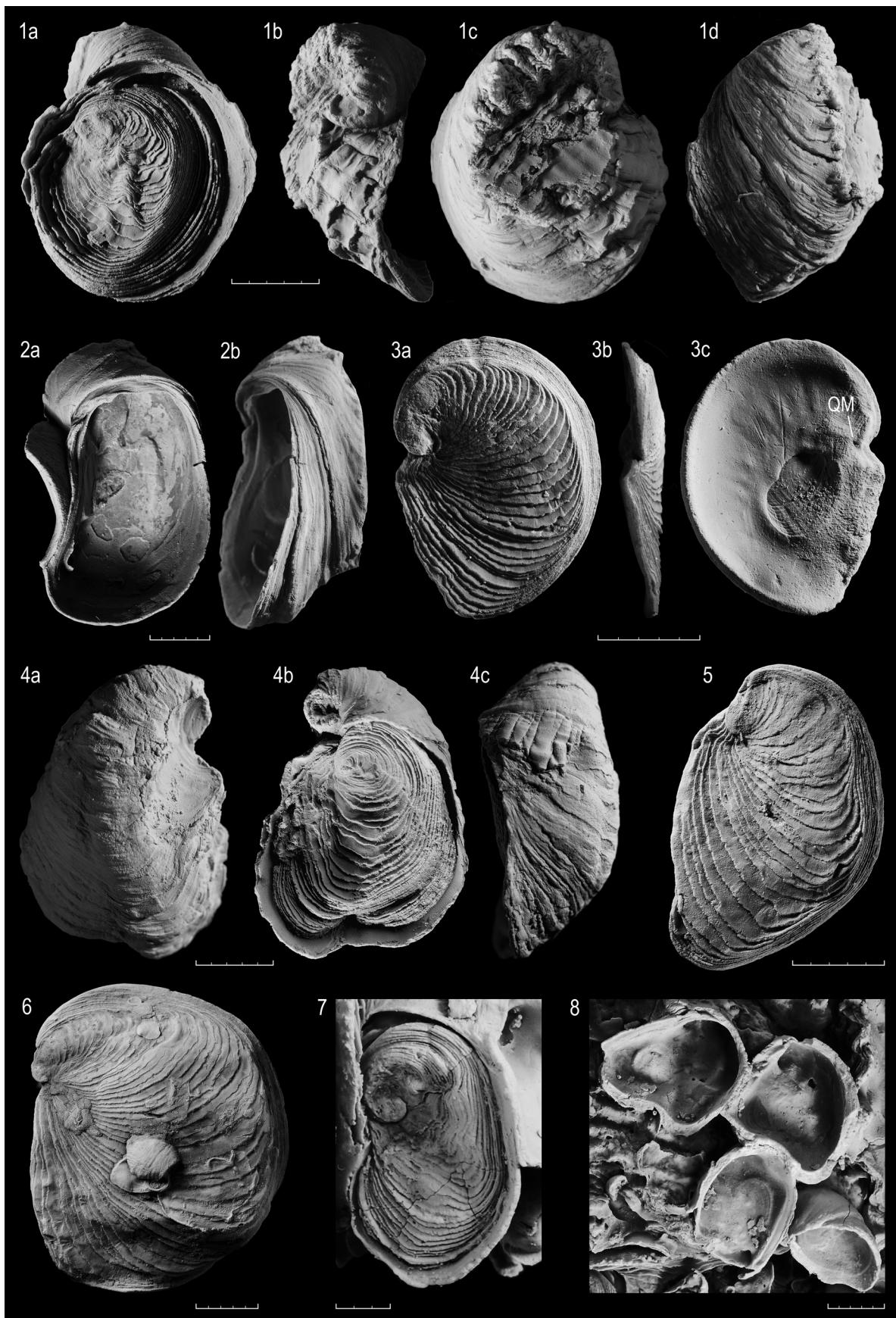


PLATE 6. *Nanogyra* (*Nanogyra*) and *?Praeexogyra*. **1–4.** *Nanogyra* (*N.* Sowerby, 1822), Reuchenette Formation, Lower–Upper Kimmeridgian. **1a–c.** Group of similar oriented specimens, CGN-ALO009-1, Alombre aux Vaches near Courgenay (Banné Marls), Lower Kimmeridgian: **1a**, numerous juvenile specimens attached at umbonal end of *Trichites* (LV, see Pl. 3.2–3); **1b**, part of population (rotated, from middle left of fig. 1a); **1c**, 2 bivalved specimens (lower left of fig. 1a). **2a–c.** Bivalved specimen, CTD-VTT004-15, Vâ Tche Tchâ (spoil material), Banné Marls, Lower Kimmeridgian: **2a**, RV (same specimen as Pl. 5.4b), umbo; **2b**, RV, prismatic layers of ventral margin; **2c**, juvenile stage magnified, with internal mould of dissolved prodissococonch. **3a–b.** Juvenile RV, CTD-VTT001-7974, Vâ Tche Tchâ (spoil material), Banné Marls: **3a**, lateral view; **3b**, internal calcitic mould of prodissococonch, dimensions L = 300 µm, H = 285 µm. **4a–c.** 2 RVs, CTD-BSY009-917, Bois de Sylleux near Courtedoux (bed 4500), “Lower Virgula Marl”, Upper Kimmeridgian: **4a**, lateral view; **4b**, umbo magnified, dimensions of prodissococonch (calcitic mould): L = 283 µm, H = 241 µm; **4c**, juvenile RV, found on the larger specimen below the centre, dimension of prodissococonch L = 296 µm, H = 268 µm. **5.** *?Praeexogyra* aff. *sandalinoides* (de Loriol, 1901), juvenile RV, GG 382-3, Langhagen, erratic boulder (Langhagen 97/7, author collection, leg. Mäschker), Lower or Middle Callovian, Mecklenburg, Northern Germany, lateral view, aragonitic prodissococonch preserved, dimension of prodissococonch L = 208 µm, H = 244 µm. Scale bars 10 mm, 5 mm and 3 mm, SEM samples with own scale bars.

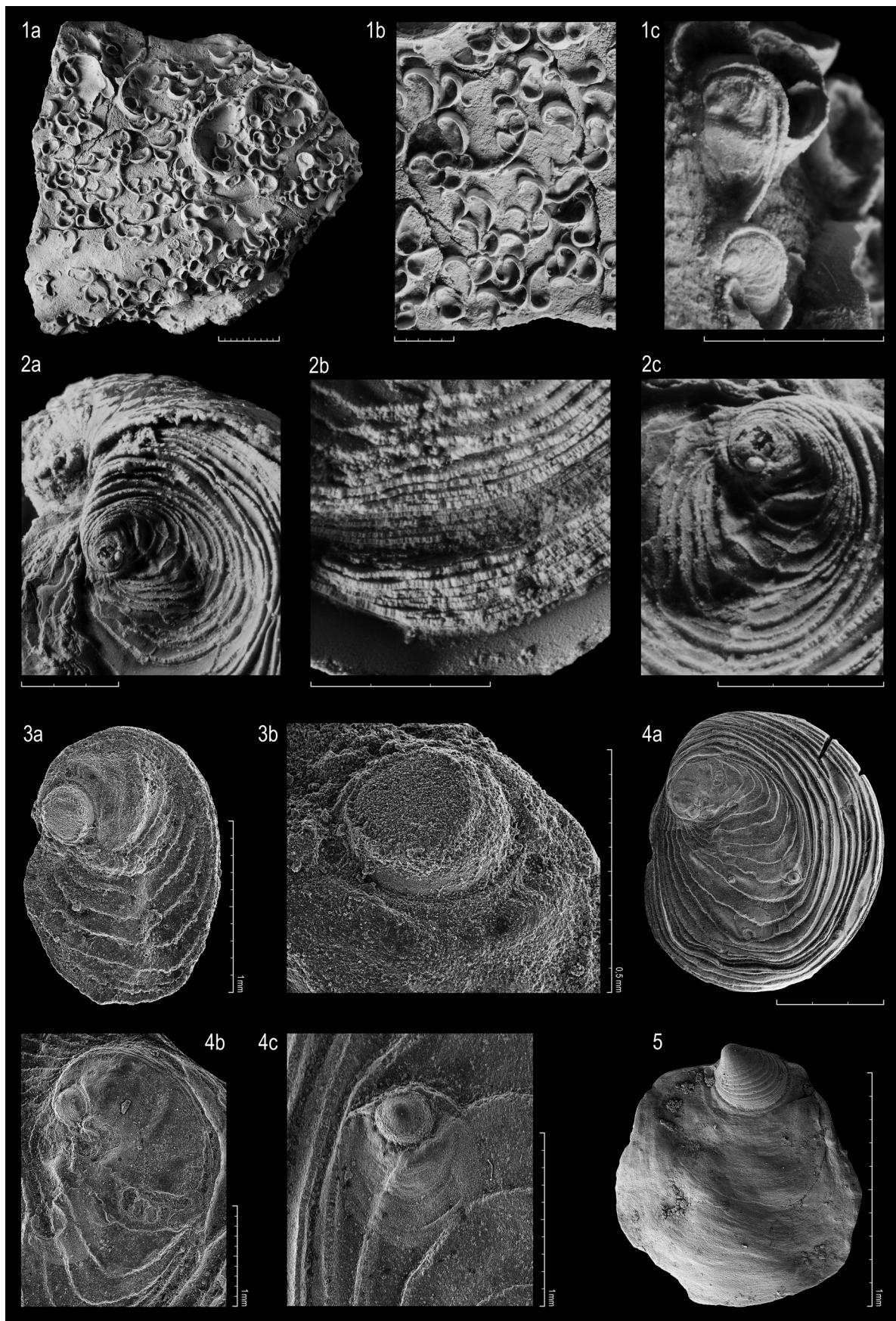


PLATE 7. *Nanogyra*. **1a–d.** *Nanogyra* (N.) sp., LV, CTD-VTT001-3233, Vâ Tche Tchâ (spoil material), Banné Marls, Lower Kimmeridgian: **1a**, lateral view, with fine antimarginal furrows; **1b**, anterior view, tiny attachment area (gastropod?); **1c**, interior view; **1d**, dorsal view, **2–4.** *Nanogyra (Palaeogyra) reniformis* (Goldfuss, 1833)(b), Vâ Tche Tchâ (spoil material), Banné Marls. **2a–c.** 2 specimens, CTD-VTT009-33: **2a**, LV with chomata and small bivalved specimen, attached to inner shell of *Isognomon*; **2b**, bivalved specimen, RV, lateral view; **2c**, umbo with remains of prodissoconch. **3a–c.** 2 LV, CTD-VTT001-1549: **3a**, interior view, specimens attached to the inner side of *Actinostreon gregareum* (RV, with traces of *Gnathichnus pentax*); **3b**, same, magnified, with relict chomata on posterodorsal commissural shelf; **3c**, ventral and dorsal view. **4a–b.** LV, CTD-VTT001-3218: **4a**, interior view, attached to inner side of *Circumula cotyledon* (RV); **4b**, same, magnified, with chomata at dorsal margin. Scale bars 10 mm, 5 mm and 3 mm.

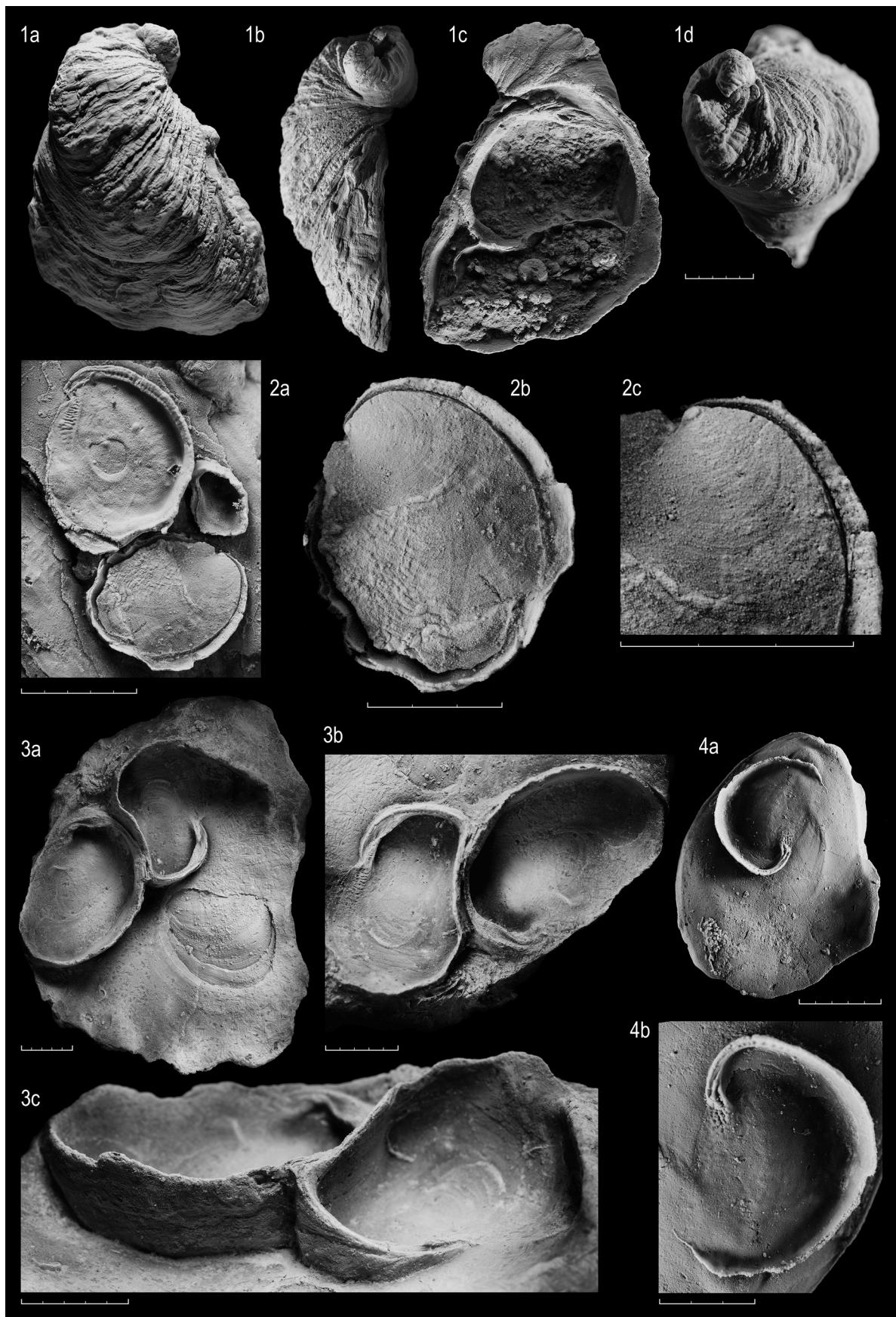


PLATE 8. *Nanogyra* (*Palaeogyra*). **1–2.** *Nanogyra* (*P.*) *reniformis* (Goldfuss, 1833), Vâ Tche Tchâ near Courtedoux, Banné Marls (spoil material), Lower Kimmeridgian. **1a–b.** Group of specimens, CTD-VTT001-1186: **1a**, several LVs, interior view, attached to xenomorphic RV of *Actinostreon gregareum*; **1b**, 2 LV (centre of host shell), interior view. **2.** LV, CTD-VTT001-3218, same as Pl. 7.3a–c, posterodorsal view, with weak antimarginal furrows at ventral margin. **3–8.** *Nanogyra* (*P.*) *virgula* (Deshayes, 1831), Reuchenette Formation, Lower–Upper Kimmeridgian. **3.** Juvenile LV, CTD-VTT001-1173, Banné Marls, Lower Kimmeridgian, interior view, with weak chomata, specimen attached to umbo of *Actinostreon gregareum* (RV), **5.** LV, POR-TLB001-303, "Tunnel du Banné" (spoil material, temporary exposure, tunnel through Banné hill), Banné Marls, lateral view, fine ribbed phenotype. **6a–c.** Bivalved specimen, CTD-VTT001-1624, Vâ Tche Tchâ (spoil material, probably bed 300), Banné Marls: **6a**, LV, anterior view, attached to stem of calcareous algae (probably *Goniolina geometrica*); **6b**, lateral view, coarse ribbed phenotype; **6c**, RV, lateral view. **4, 7–8.** 3 LV, MJSN S294 (Thurmann collection), Banné (hill in Porrentruy), "Lower Virgula Marl" (bed 4500), Upper Kimmeridgian, *eudoxus* Zone. **4a–b.** LV, MJSN S294-10: **4a**, interior view, with chomata; **4b**, lateral view. **7a–d.** LV with juvenile specimens, MJSN S294-11: **7a**, LV, interior view; **7b**, lateral view, attached to *Grammatodon*; **7c**, juvenile LVs, attached to umbo of adult LV; **7d**, interior view, with chomata. **8.** LV, MJSN S294-1, lateral view, finely ribbed variant. Scale bars 5 mm and 3 mm.

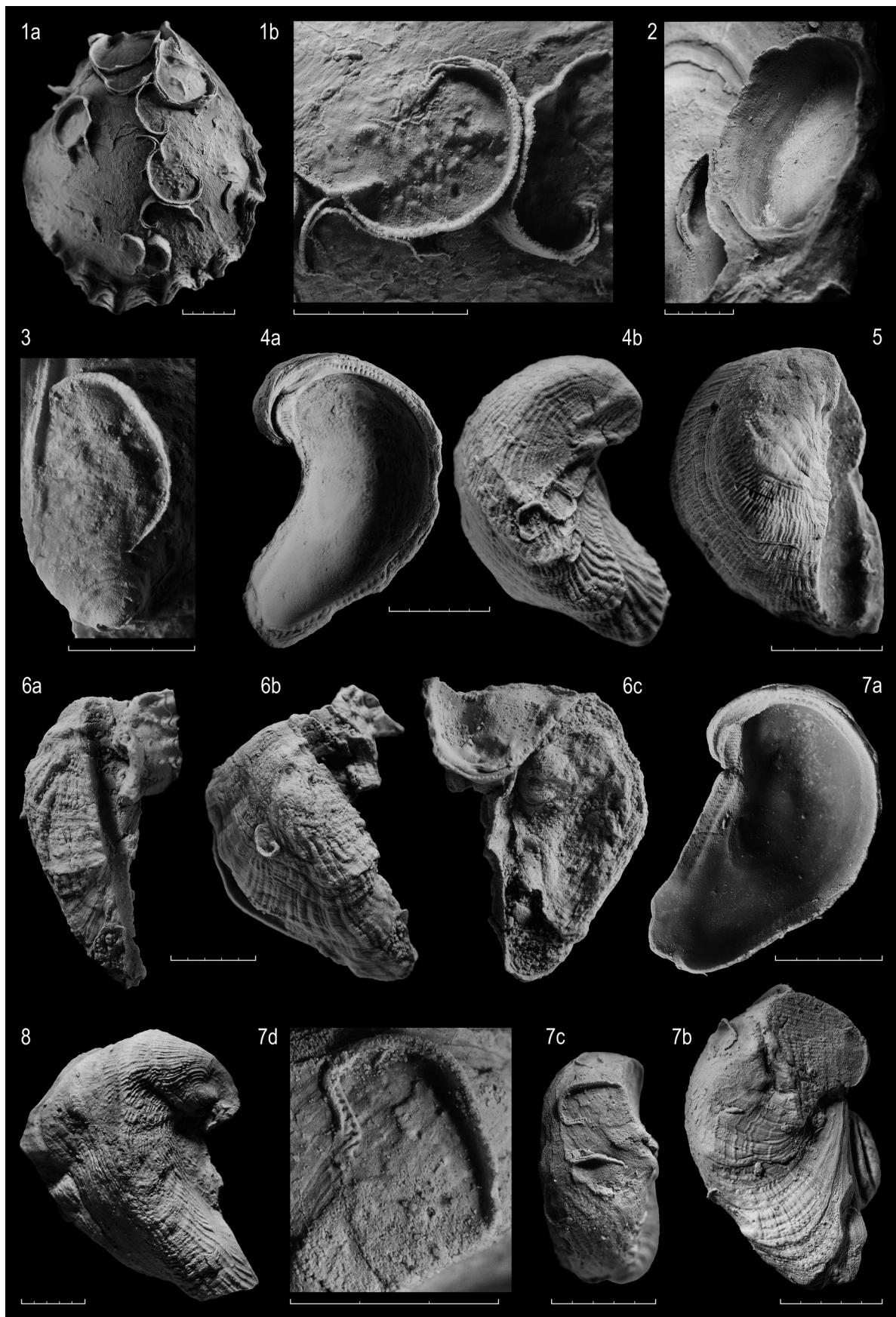


PLATE 9. *Nanogyra (P.) virgula* (Deshayes, 1831). **1–9.** Variation of shape and ornament, MJSN S294-2–9, 12, Banné (hill in Porrentruy), Thurmann collection, “Lower Virgula Marl” (bed 4500), Reuchenette Formation, Upper Kimmeridgian, *eudoxus* Zone, 8 LV in lateral view. **1.** S294-2, with eroded posterior flank. **2.** S294-6, weakly striated. **3.** S294-8. **4.** S294-5. **5.** S294-3. **6.** S294-9. **7.** S294-7. **8.** S294-4. **9a–c.** RV, S294-12: **9a**, lateral view; **9b**, interior view, with well-developed chomata; **9c**, posterior view. **10a–e.** Bivalved specimen, CTD-BSY009-915, Bois de Sylleux near Courtedoux, “Lower Virgula Marl” (bed 4500), Upper Kimmeridgian, *eudoxus* Zone: **10a**, LV, lateral view; **10b**, anterior view; **10c**, RV, dorsal half; **10d**, RV, umbo magnified, with remains of prodissococonch; **10e**, RV, lateral view. **11.** Juvenile LV, CTD-SCR002-1367-1, Sur Combe Ronde near Courtedoux, “Lower Virgula Marl” (bed 4500), lateral view, SEM. Scale bars 5 mm and 3 mm, SEM sample 1 mm.

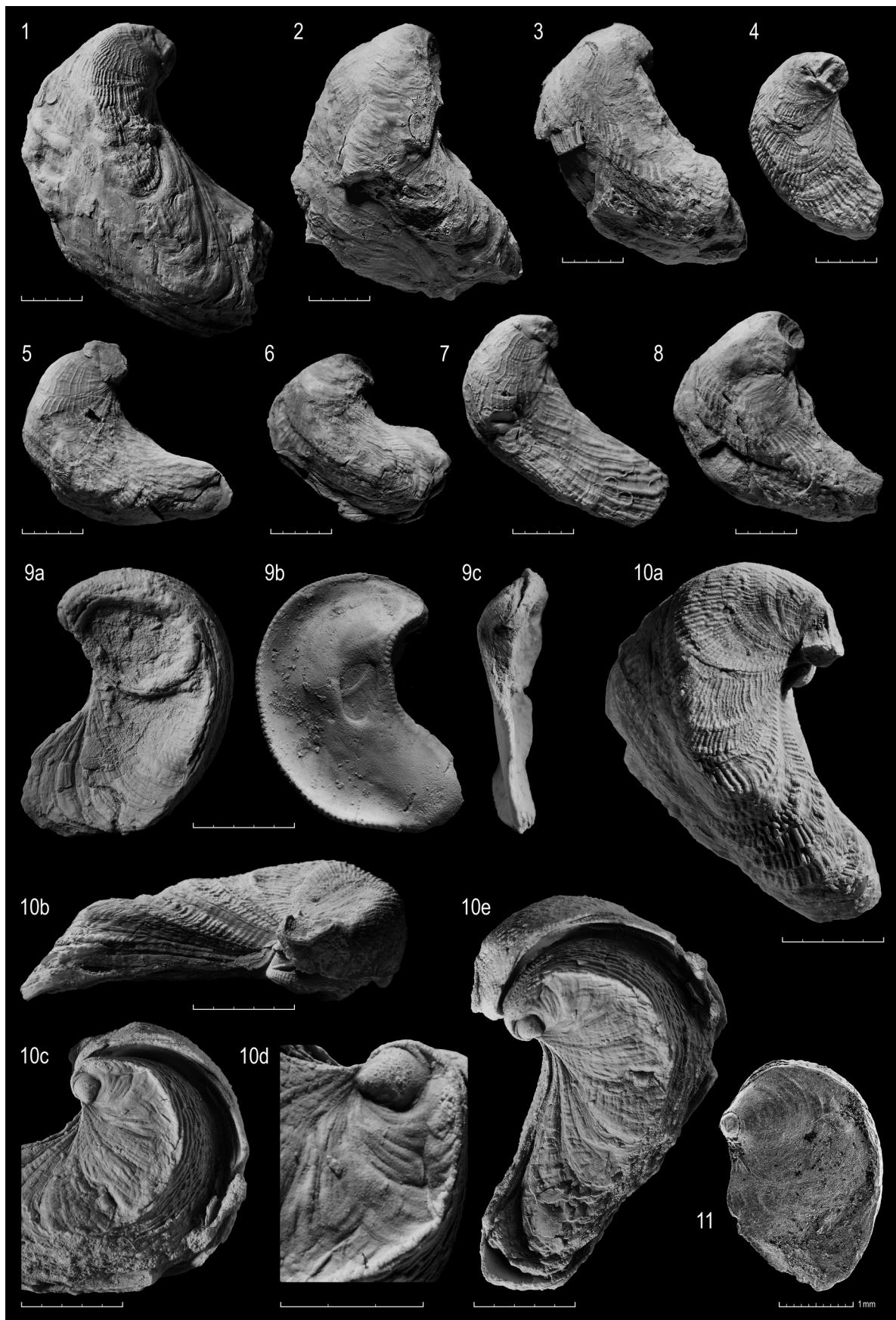


PLATE 10. *Nanogyra* and *?Praeexogyra*. **1a–f.** *Nanogyra (P.) virgula* (Deshayes, 1831), juvenile RV, SCR002-1367-1, Sur Combe Ronde near Courtedoux, “Lower Virgula Marl” (bed 4500), Reuchenette Formation, Upper Kimmeridgian, *eudoxus* Zone: **1a**, umbo (see Pl. 9.11); **1b**, internal calcite mould of prodissoconch; **1c**, posterior margin with weak chomata; **1d**, interior view; **1e**, anterodorsal margin with chomata; **1f**, outer prismatic layer. **2a–d.** *Nanogyra (N.) cf. auricularis* (Münster in Goldfuss, 1833), SMNS 67694/1, Stuttgart-Vaihingen (university area, leg. M. Urlich), “Angulatenton-Formation”, Upper Hettangian, *angulata* Zone, Baden-Württemberg, Germany, Lower Jurassic: **2a**, RV, prodissoconch (recrystallized aragonite, calcite-pseudomorph); **2b**, umbo magnified; **2c**, nepioconch with prodissoconch; **2d**, prodissoconch, crassostreine/liostreine type. **3a–b.** *?Praeexogyra* aff. *sandalinoides* (de Loriol, 1901), GG382-4, Langhagen, erratic boulder (Langhagen 97/7, author collection, leg. Mäschker), Lower or Middle Callovian, Mecklenburg, Northern Germany: **3a**, juvenile RV, with liostreine prodissoconch (aragonite preserved); **3b**, postlarval shell, with slightly reclined prismatic layer. Scale bars as labelled, for 2a = 5 mm.

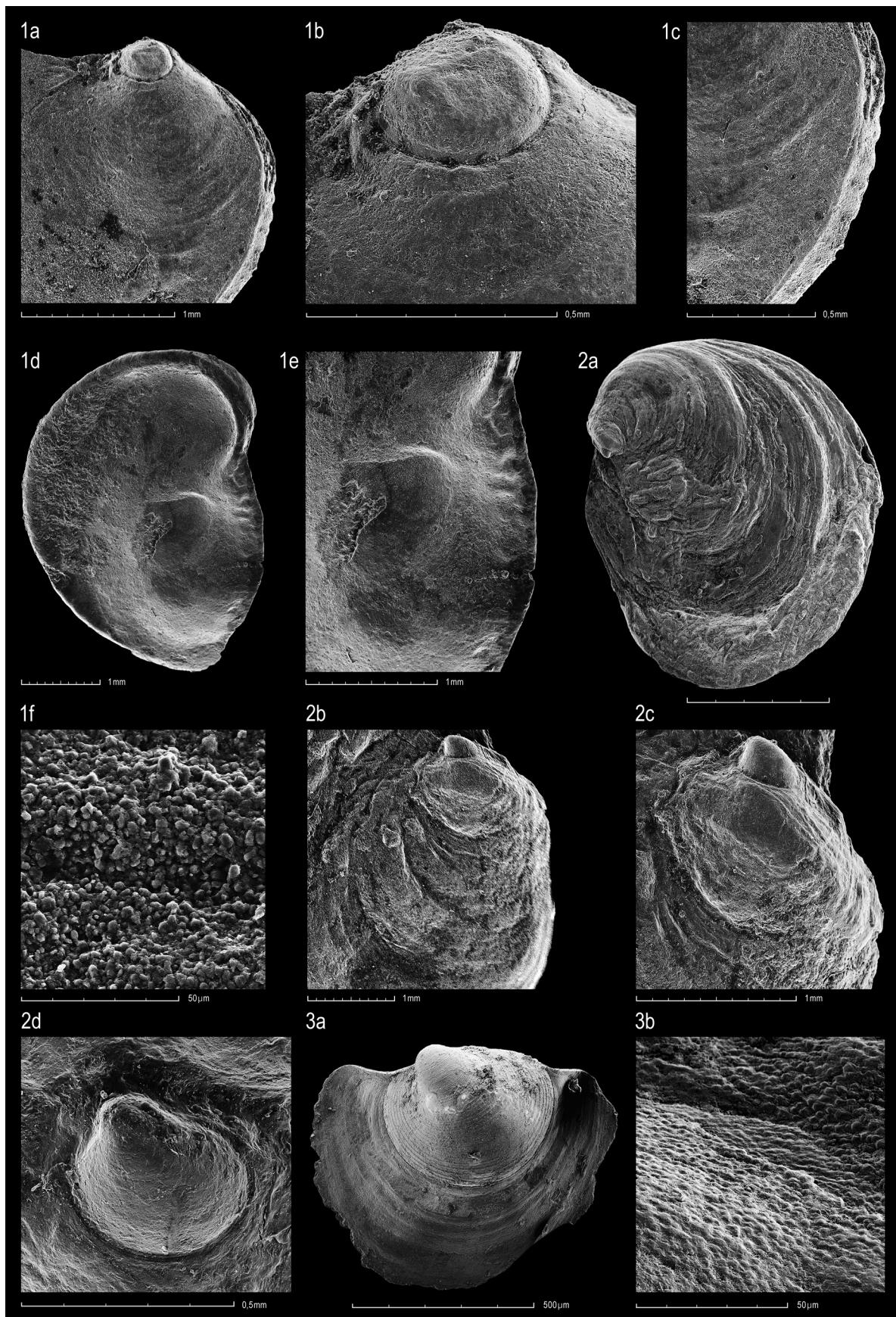


PLATE 11. *Helvetostrea n. gen. sequana* (Thurmann & Etallon, 1862), Reuchenette Formation, Lower–Upper Kimmeridgian. **1a–d.** Both valves, CTD-TCH002-306, Tchâfouè near Courtedoux (spoil material, marly horizon, *mutabilis* Zone): **1a**, LV interior view; **1b**, RV interior, attached by LV; **1c**, LV, anterior view; **1d**, LV anteroventral, magnified, shell strong bioeroded. **2.** LV, CTD-SCR002-1157, Sur Combe Ronde near Courtedoux (bed 2150, *mutabilis* Zone), LV interior view. **3a–c.** Juvenile LV, VTT001-1171, Vâ Tche Tchâ near Courtedoux (bed 300, Banné Marls), Lower Kimmeridgian: **3a**, LV, interior view (parallel with commissure); **3b**, view parallel with ligament area; **3c**, ventral view. **4a–b.** LV, CTD-SCR003-1198, Sur Combe Ronde (bed 2400): **4a**, posterior view, with oblique angle between commissure and ligament; **4b**, bioeroded ligament area, magnified. **5a–d.** LV, CTD-SCR003-9, Sur Combe Ronde (bed 3500): **5a**, lateral view; **5b**, detail of reworked, strongly eroded shell; **5c**, interior view; **5d**, ligament area, with chomata-like structures at anterior dorsal margin. Scale bars 10 mm; and for small specimens and magnified portions 5 mm.

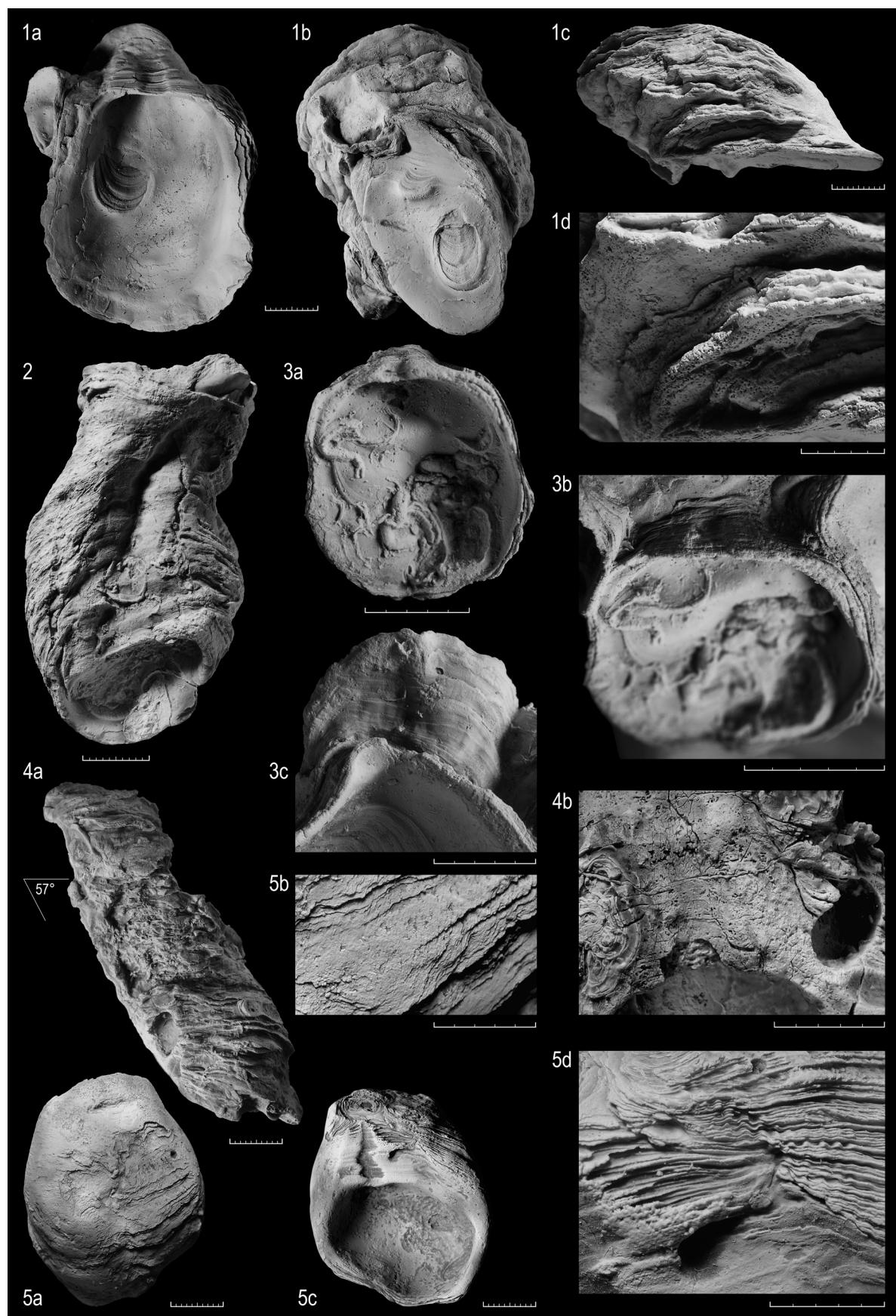


PLATE 12. *Helvetostrea* and *Praeexogyra*. **1–2.** *Helvetostrea n. gen. sequana*, Reuchenette Formation, Upper Kimmeridgian, *mutabilis* Zone (*lallierianum* Subzone). **1.** LV, CTD-SCR003-852, Sur Combe Ronde near Courtedoux (bed 2600): **1a**, lateral view, bioeroded by algae or fungi, with boreholes of *Lithophaga* sp.; **1b**, dorsal view, internal hollow chambers exposed. **2a–d.** Rock sample with several LVs (*Helvetostrea*-ostreolith), CTD-SCR004-265 (bed 2700): **2a**, weathered cross-section; **2b**, tube-shaped juvenile LV, with cross-foliated shell and thick, previously hollow chambers (filled with blocky sparitic calcite); **2c**, LV (specimen in the centre), magnified anteroventral cross-section, with layers of regular foliate and thick cross-foliated structure; **2d**, same specimen as 2c, chambers (left, filled with sparite) and ventral margin (right), thin shell with regular foliated structure separating chambers. **3–4.** *Praeexogyra monsbeliardensis* (Contejean, 1859), Banné Marls, Lower Kimmeridgian, **3a–b.** Group of 4 specimens, CTD-VTT009-9, Vâ Tche Tchâ (spoil material): **3a**, 2 bivalved specimen and 2 LV, attached with *Nanogyra nana* to *Eopecten velatus* (LV, not visible); **3b**, RV (on the right), detail of umbonal region, heavily bioeroded by regular echinoids producing the trace fossil *Gnathichnus pentax*. **4a–e.** Bivalved specimen, CTD-VTT001-3254, Vâ Tche Tchâ (spoil material): **4a**, LV, anterior view; **4b**, LV, lateral view, with strong commarginal swellings; **4c**, RV, detail of bioeroded surface (near ventral margin), with fine traces of *Gnathichnus pentax*; **4d**, RV, lateral view; **4e**, both valves, dorsal view. Scale bars for 1, 2a, 3a = 10 mm, all others = 5 mm.

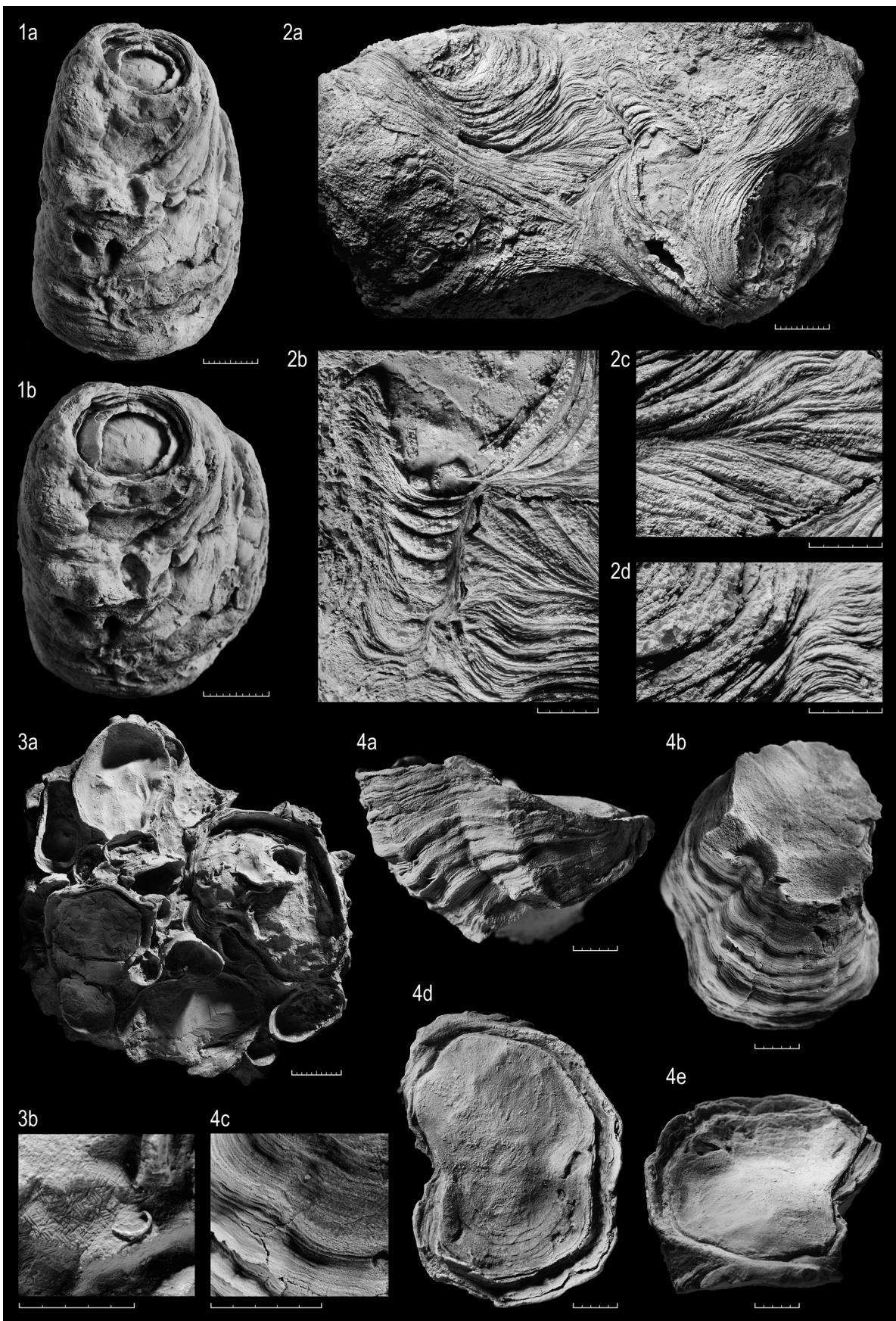


PLATE 13. *Praeexogyra monsbeliardensis* (Contejean, 1859), Banné Marls, Lower Kimmeridgian. **1a–c.** CTD-VTT001-3261, Vâ Tche Tchâ near Courtedoux (spoil material): **1a**, 2 LV, lateral view; **1b**, interior of larger specimen (with *Nanogyra nana*); **1c**, LV, hinge magnified. **2a–c.** RV, CTD-VTT001-1211, Vâ Tche Tchâ: **2a**, lateral view; **2b**, posterior; **2c**, interior. **3.** Juvenile LV, FPJ Glov. 5.2.98 MB/3-60, Glovelier, interior view, specimen attached to LV of *Camptonectes (C.) auritus* (Schlotheim, 1813). **4a–d.** LV, CTD-VTT001-3236, Vâ Tche Tchâ: **4a**, bivalved specimen, RV lateral view; **4b**, LV lateral view, attached to the gastropod *Harpagodes*; **4c**, anterior view; **4d**, LV, ventral margin magnified, with few antimarginal furrows. **5a–d.** Prosogyrate RV, CTD-VTT001-3222, Vâ Tche Tchâ: **5a**, lateral view; **5b**, ventral margin magnified, with antimarginal furrows and thin plicae; **5c**, interior view; **5d**, hinge magnified. **6a–b.** Opisthogyrate RV, CTD-VTT001-3225, Vâ Tche Tchâ: **6a**, lateral view, near umbo with LV of *Nanogyra (P.) reniformis* (Goldfuss, 1833); **6b**, interior view, with imprint of Quenstedt muscle (QM). Scale bars 5 mm.

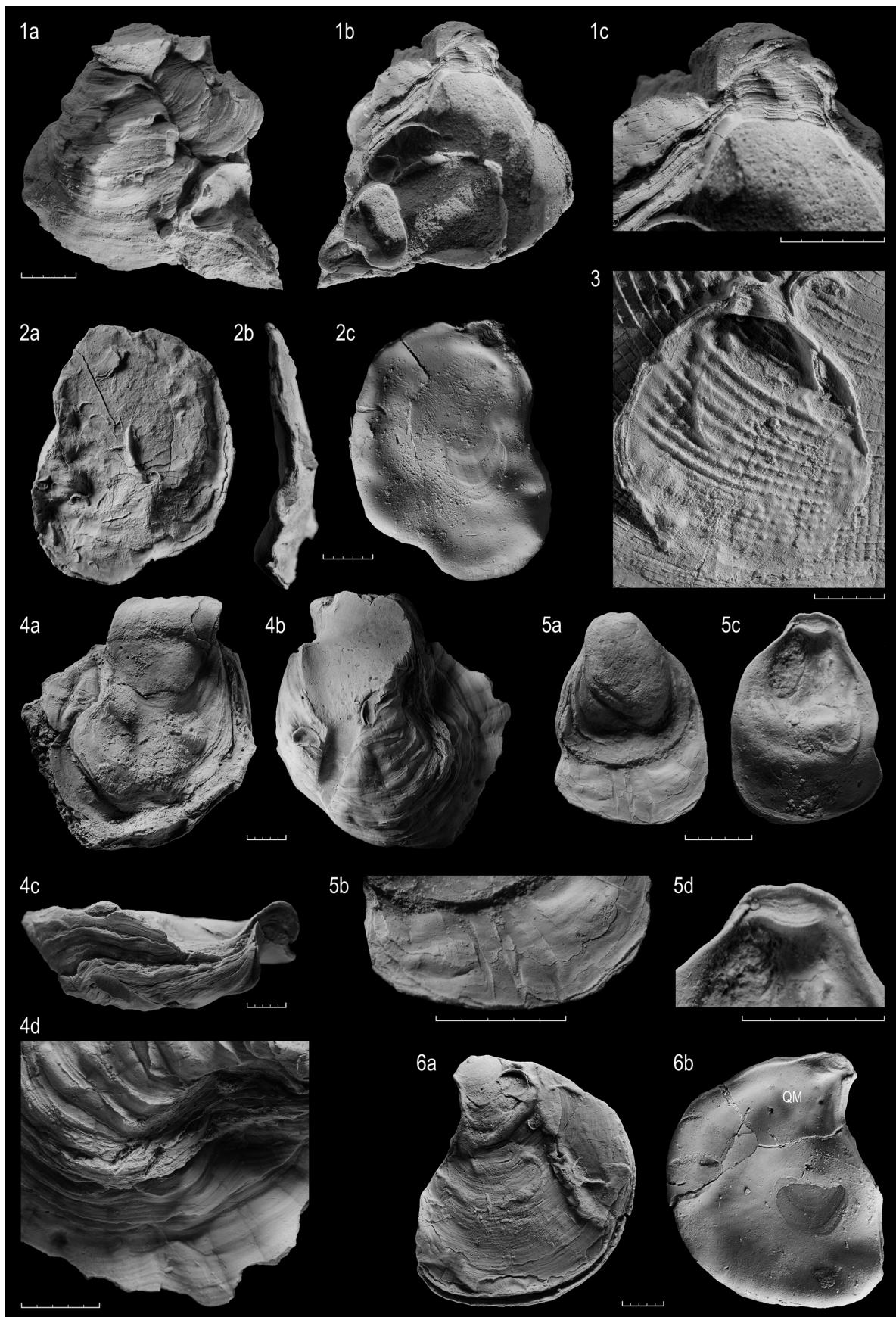


PLATE 14. *Praeexogyra*. **1–4.** *Praeexogyra monsbeliardensis* (Contejean, 1859). **1a–b.** LV, MC-27E-140, paralectotype (figured in Contejean 1859, pl. 26, fig. 4), Côte de Rôce in Montbéliard, "Marnes à Ptérocéres", Lower Kimmeridgian, Department Doubs, France: **1a**, LV, lateral view; **1b**, ventral view. **2–4.** From Vâ Tche Tchâ, Banné Marls, Lower Kimmeridgian, Canton Jura, Switzerland. **2a–b.** Prosogyrate LV, CTD-VTT009-9 (spoil material): **2a**, interior view (from oyster group, see Pl. 12.3a, upper specimen); **2b**, hinge magnified. **3a–b.** Bivalved specimen, VTT001-3209: **3a**, RV, lateral view; **3b**, umbo magnified, RV with antimarginal riblets. **4a–b.** RV, VTT006-644 (bed 1680): **4a**, lateral view, unusual convex (with 4 associated LV of *Nanogyra reniformis*); **4b**, RV, interior view (with attached LVs of *Nanogyra nana* and cyclostome bryozoans). **5–6.** *Praeexogyra dubiensis* (Contejean, 1859), from Vâ Tche Tchâ (spoil material), Banné Marls. **5a–b.** Juvenile prosogyrate LV, VTT001-3238: **5a**, interior view (attached on RV of *Circumula cotyledon*, figured on Pl. 2.4a) with *Gnathichnus pentax*; **5b**, hinge and deep umbonal cavity. **6a–c.** Large RV, VTT001-1171 (bed 300): **6a**, interior view; **6b**, xenomorphic RV, lateral view, with attached *Helvetostrea sequana* (figured in Pl. 11.3a –c) and *Nanogyra nana*; **6c**, posterior view. Scale bars 5 mm, except for fig. 5b with 3 mm.

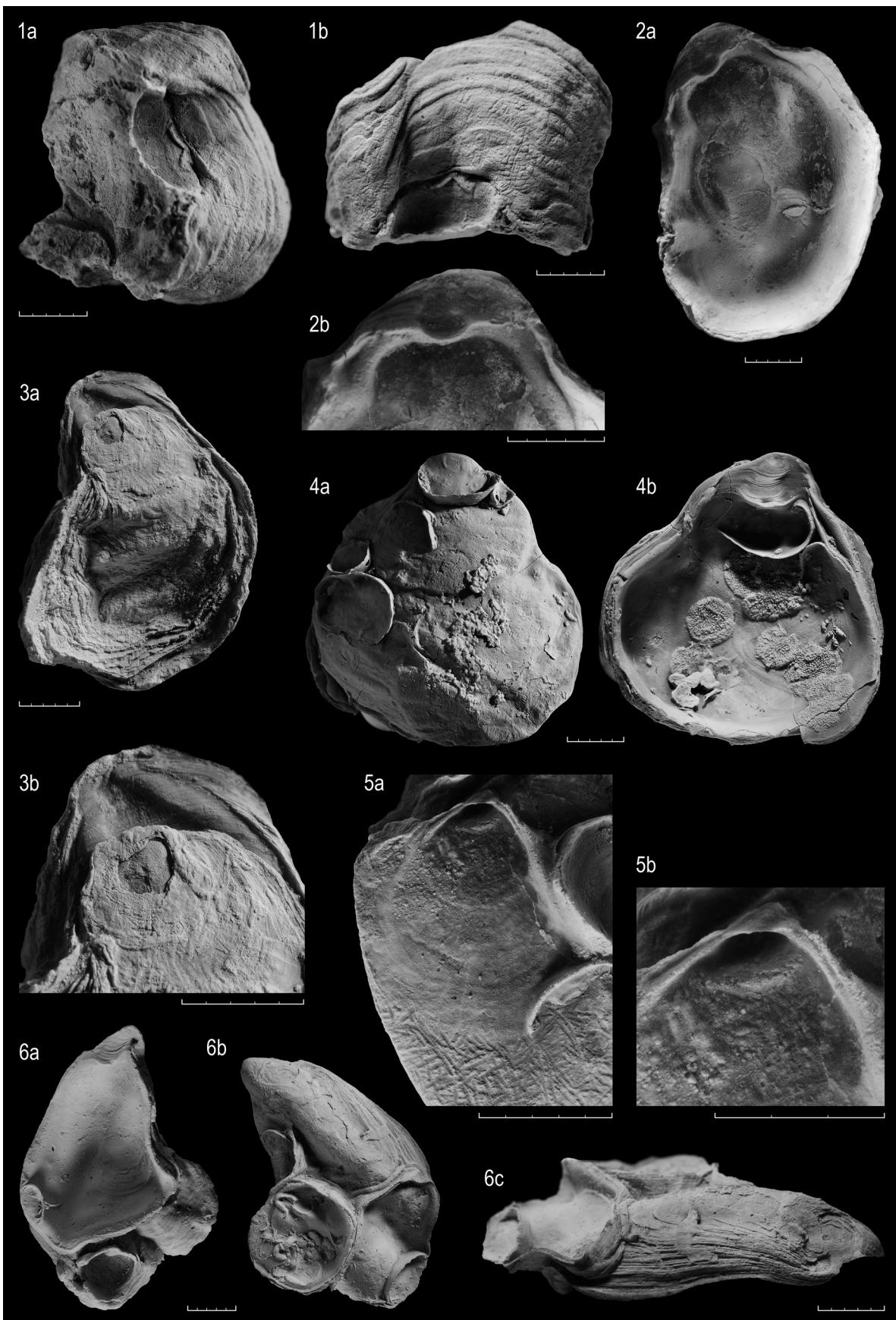


PLATE 15. *Praeexogyra*. **1–2.** *Praeexogyra dubiensis* (Contejean, 1859), from Bussurel near Montbéliard, "Calcaire à Natices", Upper Oxfordian, Department Haute-Saône (Franche-Comté), France. **1a–f.** LV with attached RV, MC-27-E-116, paralectotype: **1a**, LV, interior view; **1b**, anterior; **1c**, oblique anteroventral view, with adductor scar; **1d**, lateral; **1e**, hinge; **1f**, RV, interior view. **2a–b.** RV, MC-27-E-114, paralectotype (figured in Contejean 1859, pl. 21, fig. 10): **2a**, interior; **2b**, lateral view. **3–4.** ?*Praeexogyra sandalinoides* (de Loriol, 1901), Vierow near Lubmin, glacial erratic boulder, Middle Callovian, *jason* Zone, Western Pomerania, Northern Germany. **3a–b.** Bivalved specimen, GG 382-1: **3a**, LV, lateral view, attached to a serpulid; **3b**, RV, lateral view. **4a–b.** GG 382-2: **4a**, RV, interior view; **4b**, hinge. Scale bars are 5 mm, except for fig. 4 (3 mm).

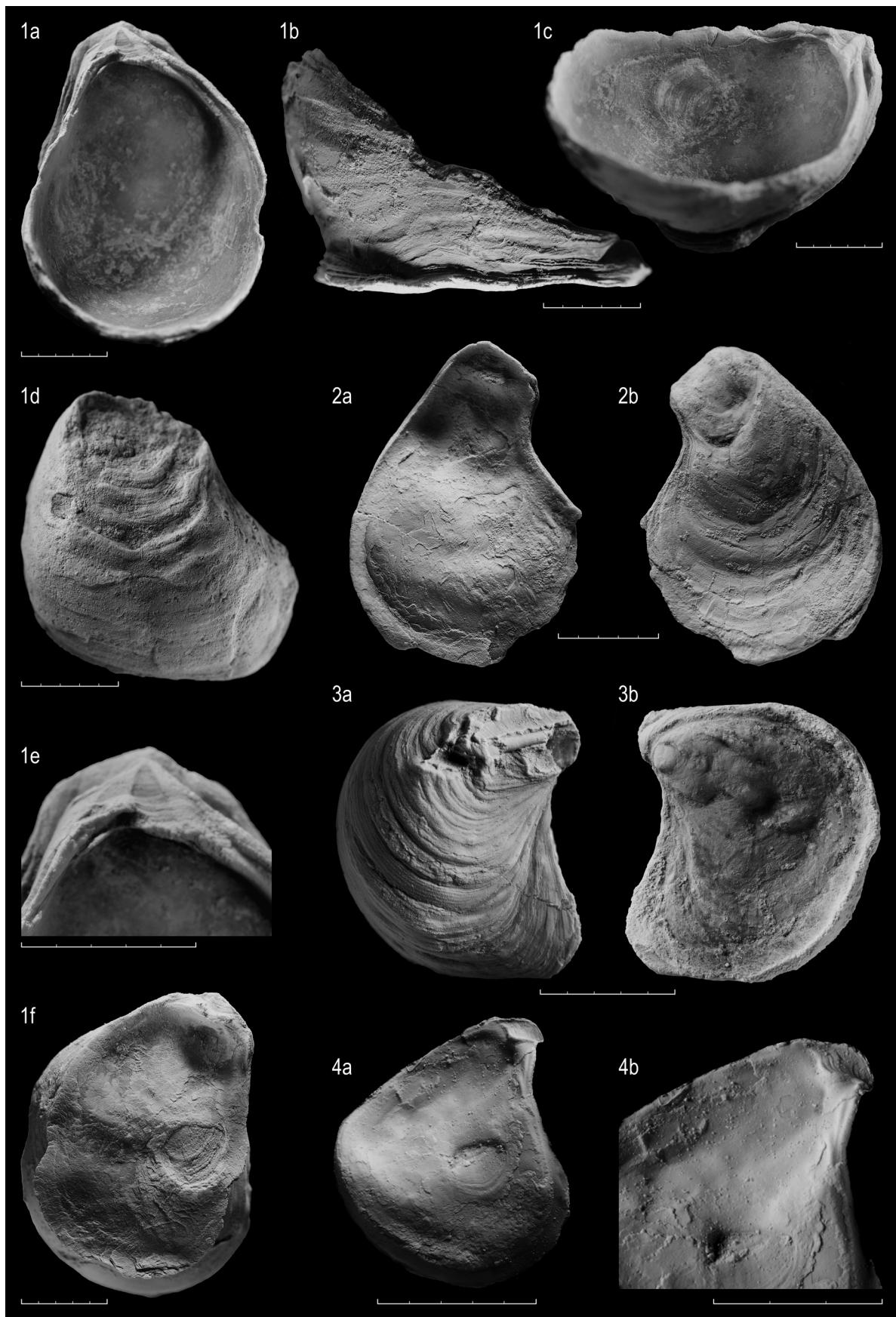


PLATE 16. *Actinostreon gregareum* (J. Sowerby, 1815), Vâ Tche Tchâ, Banné Marls. **1.** Large RV, CTD-VTT006-77 (bed 1690), lateral view. **2a–b.** 3 specimen (2 bivalved, 1 LV) attached on RV of *Costigervillia gesneri* (Contejean, 1859), CTD-VTT001-1704 (spoil material): **2a**, 2 RV, 1 LV, lateral view, with attached LV (and 1 RV) of *Nanogyra (N.) nana* (J. Sowerby, 1822); **2b**, LVs, lateral view, with imprint of *Costigervillia* (main body and posterior wing). **3a–b.** Bivalved specimen, CTD-VTT001-1327 (spoil material, probably bed 300): **3a**, LV, attached to algal stem with encrusting serpulid *Glomerula gordialis* (Schlotheim, 1820); **3b**, xenomorphic RV, lateral view. **4.** RV, CTD-VTT001-1705 (spoil material, after lithology upper part of the section), lateral view, xenomorphic after *Eopecten velatus* (Goldfuss, 1833). **5a–d.** Prosogyrate RV, CTD-VTT001-1225 (spoil material, probably bed 300): **5a**, lateral view, xenomorphic after *?Modiolus*; **5b**, interior view, with strong chomata at dorsal margin; **5c**, lethal predation, shell showing naticid-like drillhole (see Harper & Kelley, 2012); **5d**, hinge. **6a–d.** Opisthogryrate RV, CTD-VTT009-18 (spoil material): **6a**, interior view, with juvenile *N. nana*; **6b**, lateral view, encrusted with *N. nana*; **6c**, hinge, ligament strong curved; **6d**, interior, posterior adductor scar (posteroventral buttressed) and echinoid gnawing traces (*Gnathichnus pentax*). Scale bars are 10 mm, 5 mm, 4 mm and 3 mm.

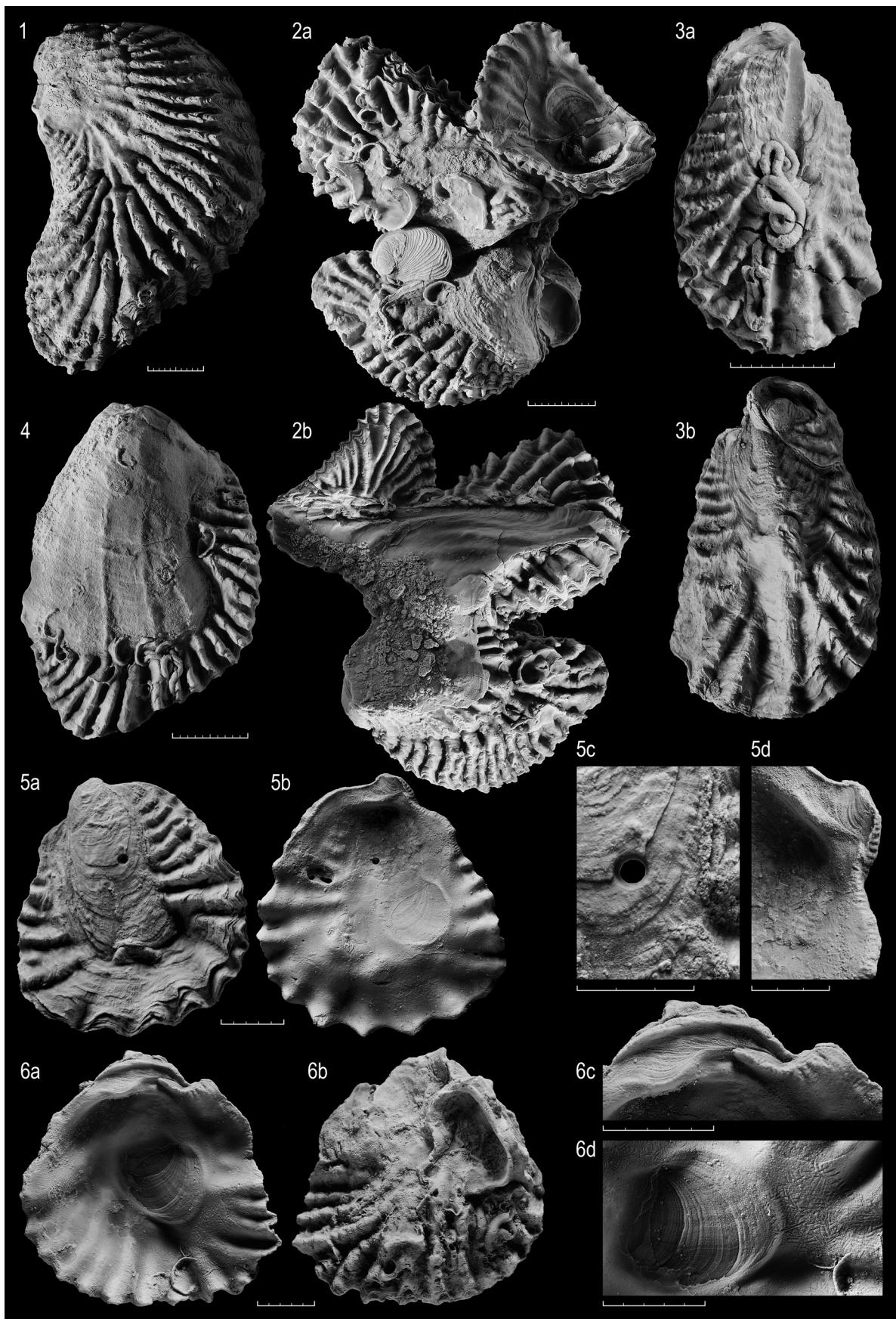


PLATE 17. *Actinostreon gregareum* (J. Sowerby, 1815), Reuchenette Formation, Vâ Tche Tchâ, Banné Marls, Lower Kimmeridgian. **1a–e.** Bivalved specimen, CTD-VTT001-2455 (spoil material), valves separated by preparation: **1a**, RV, lateral view, xenomorphic umbo; **1b**, RV, interior view; **1c**, LV, lateral view, attached to *Isognomon*; **1d**, LV, interior view, with collapsed internal chambers; **1e**, both valves, posterior view. **2a–b.** 2 bivalved specimens, CTD-VTT001-1700 (spoil material): **2a**, lateral view; **2b**, ventral view. **3a–e.** Bivalved specimen, CTD-VTT009-41 (spoil material), shells separated: **3a**, RV, lateral view; **3b**, RV, interior view; **3c**, LV, interior view, with collapsed chambers; **3d**, both valves, dorsal view; **3e**, LV, lateral view. **4a–b.** RV, CTD-VTT001-1597 (spoil material, probably bed 300): **4a**, interior view, with chomata and attached specimens of *Nanogyra nana*; **4b**, lateral view. **5.** RV, CTD-VTT001-1210 (spoil material), lateral view, umbo unusually smooth. Scale bars 10 mm and 5 mm.

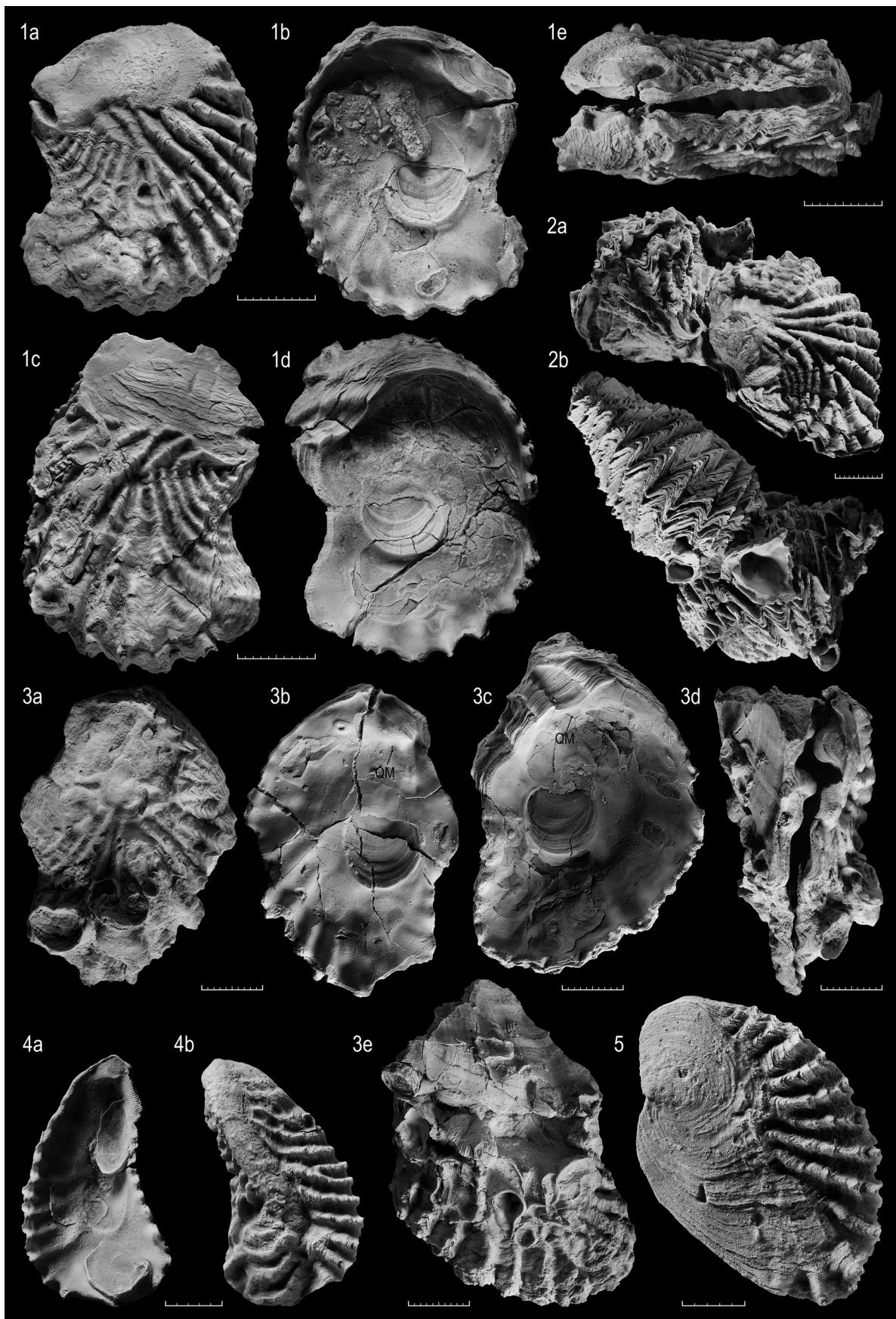


PLATE 18. *Actinostreon gregareum* (J. Sowerby, 1815), Vâ Tche Tchâ, Banné Marls, Lower Kimmeridgian. **1a–e.** Xenomorphic RV, VTT001-1173 (spoil material, probably lower third of Banné Marls): **1a**, RV, lateral view, with bulging area reproducing the alga *Goniolina geometrica* (Roemer, 1839); **1b**, posterodorsal view; **1c**, interior, with twisted juvenile hinge; **1d**, anteroventral margin; **1e**, interior view. **2a–c.** Bivalved specimen, VTT001-1602 (spoil material, probably bed 300): **2a**, LV, lateral view, with imprint of bioimmured calcareous alga *Goniolina geometrica*; **2b**, magnified, with minute details of the former thallus surface; **2c**, RV, lateral view, xenomorphic bulge after *Goniolina*. **3a–b.** LV, VTT001-1205 (spoil material): **3a**, lateral view, with imprint of *Goniolina*; **3b**, interior, with strong chomata. **4a–b.** RV, VTT001-1352 (spoil material): **4a**, lateral view, large xenomorphic area, probably depicting crenulated ventral margin of a heterodont bivalve; **4b**, opisthograte umbo. **5.** Juvenile LV, VTT001-1196 (spoil material), interior view, attached to *Circunula n. gen.* (Pl. 2.5a,c), ventral with xenomorphic structures. **6.** LV, VTT009-41 (spoil material), interior view, hinge (see Pl. 17.3c). Scale bars 5 mm.

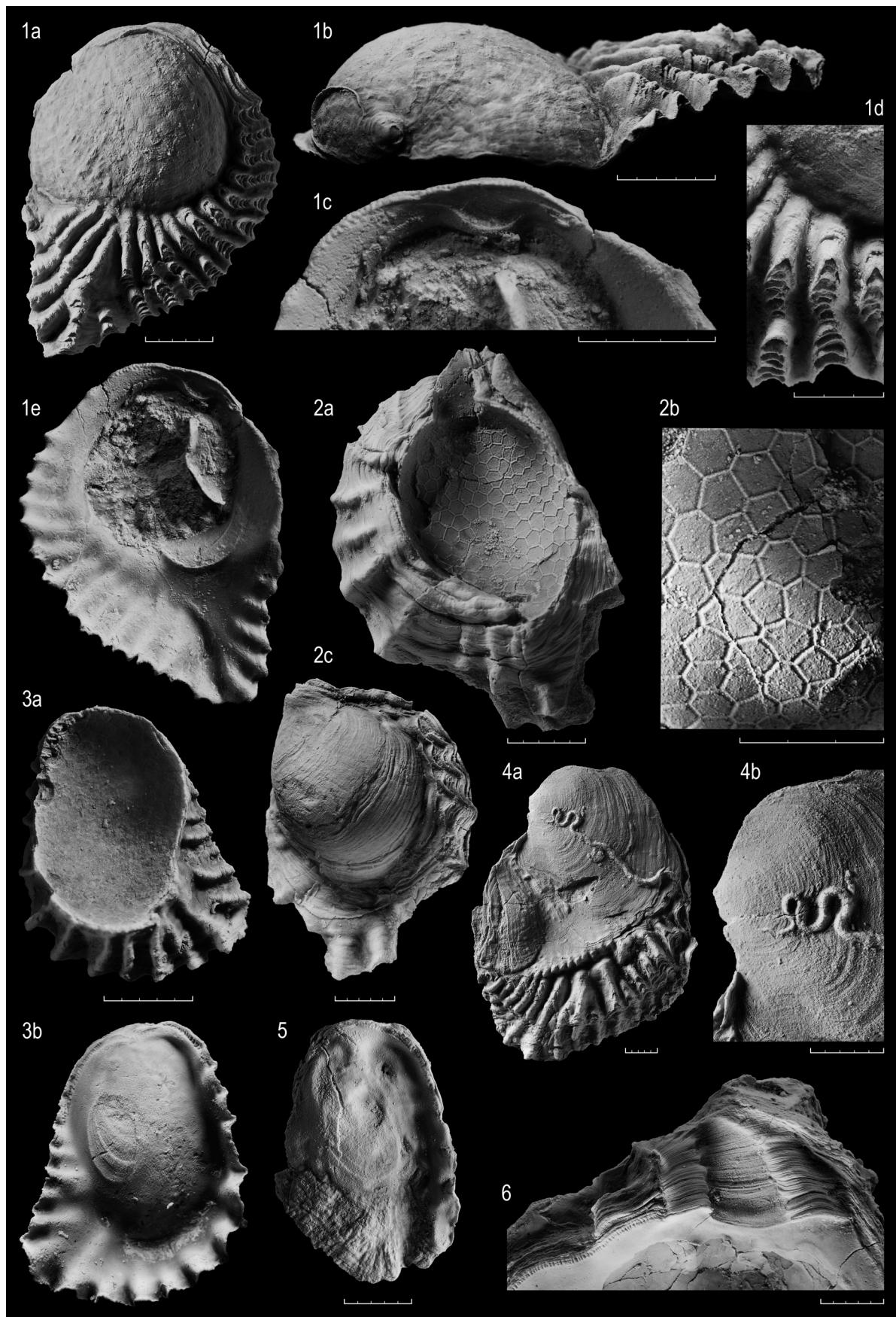


PLATE 19. *Actinostreon gregareum* (J. Sowerby, 1815), **1–2.** Vâ Tche Tchâ near Courtedoux, Banné Marls, Lower Kimmeridgian, **1a–b.** 2 LV, VTT001-4013 (spoil material): **1a**, ventral margins of 2 LV, attached post mortem to the interior of *Ceratomya excentrica* (Roemer, 1836), LV of *Ceratomya* encrusted with *Nanogyra cf. reniformis*; **1b**, magnified ventral end of *Ceratomya*. **2a–d.** Small oyster build-up, VTT006-645 (bed 1680): **2a**, 3 specimens of *A. gregareum* encrusted with numerous *Nanogyra nana* (bivalved specimen of *N. nana* figured on Pl. 5.7); **2b**, ventral margin of *A. gregareum*; **2c**, left side of fig. 2a; **2d**, back side of fig. 2a. **3–4.** *Actinostreon marshii* (J. Sowerby, 1814), Middle Callovian, *Erymnoceras coronatum* Zone, Lithuania. **3a–b.** Bivalved specimen, Rotkyte coll. (nr. 2402, Vilnius university), Papartiné near Papile (Popilani): **3a**, RV, lateral view; **3b**, ventral margins. **4a–d.** Juvenile RV, GG 382-5 (authors coll., University Greifswald), Papile (Popilani): **4a**, lateral; **4b**, umbo with nepioconch; **4c**, prodissococonch lateral view; **4d**, juvenile shell, posterior view. Scale bars 10 mm, 5 mm, 1 mm and 300 µm.

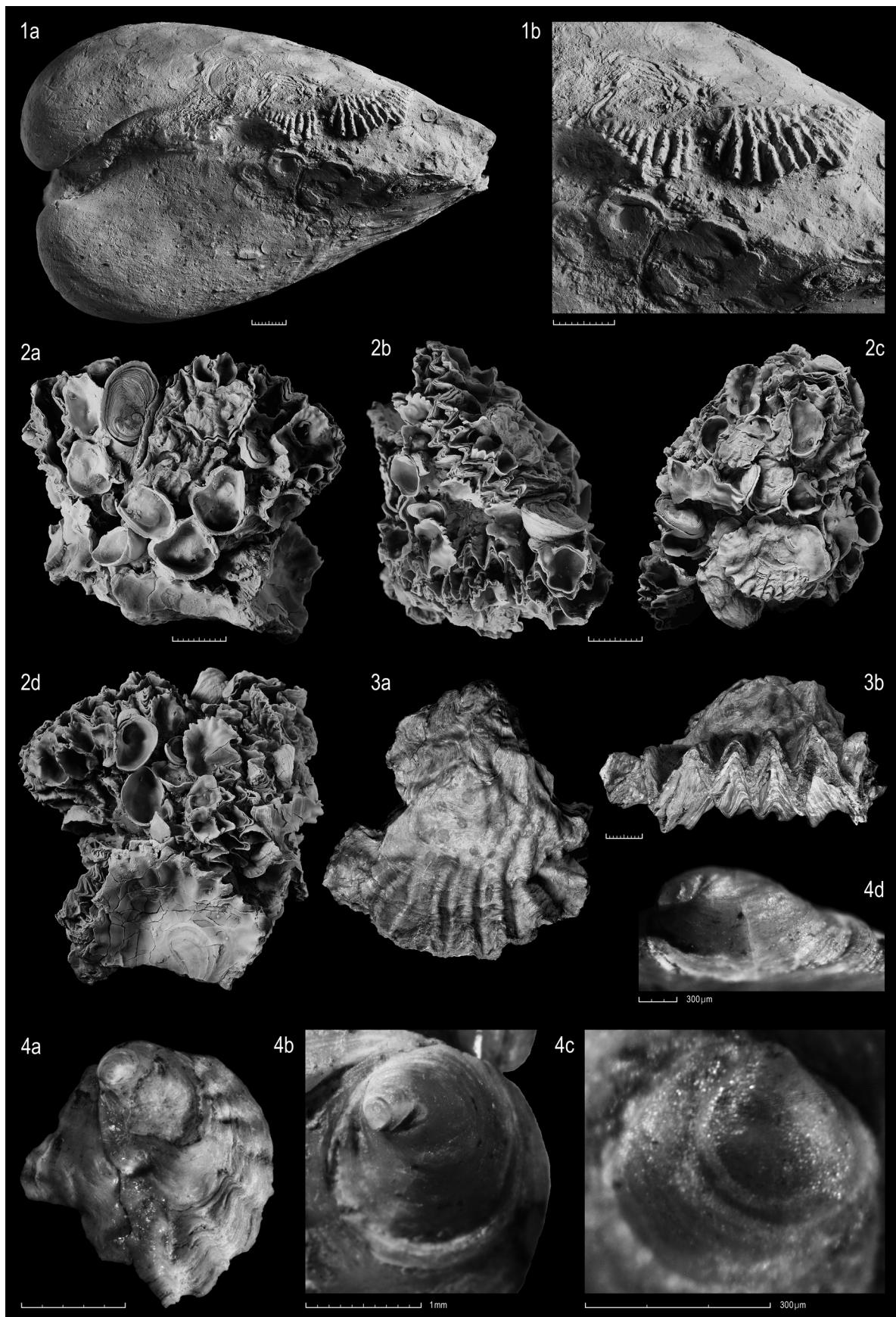


PLATE 20. Shell microstructures. **1a–c.** *Circunula n. gen. cotyledon* (Contejean, 1859), Banné Marls, Lower Kimmeridgian, thin section of RV, CTD-VTT001-1550, Vâ Tche Tchâ near Courtedoux (spoil material): **1a**, dorsoventrally cut, ventral margin (VM, right side); **1b**, ventral half magnified, (1) slightly dorsally reclined, regular simple prismatic microstructure (SP, up to 170µm), (2) irregular complex cross-foliated (CCF) structure, lower part and (3) homogeneous CCF, (4) regular foliated structure (RF); **1c**, dorsal magnified, (1) regular SP, (2) irregular dorsal reclined CCF, below dashed line and (3) with homogeneous “mosaic” to cone CCF, (4) RF structure, (5) band of thin crystalline calcite (myostracum?). **2a–d.** *Helvetostrea n. gen. sequana* (Thurmann & Etallon, 1862), Courtedoux Member, Reuchenette Formation, Upper Kimmeridgian, Canton Jura, Switzerland. Cross-section of 4–5 attached LV (Pl. 12.2a–d), CTD-SCR004-265, Sur Combe Ronde near Courtedoux: **2a**, scanned thin section, rectangles mark positions of figs. 2b–d; **2b**, LV dorsal, (1) large chamber, filled with limestone matrix, (2) septum-like, complex cross foliated structure (CCF), (3) large chamber, with blocky sparite, (4–5) complex cross-foliated structure, (4) coarse, (5) finer structured, (6) outer shell with homogeneous “mosaic” to cone CCF, at scale with *Lithophaga borehole* (*Gastrochaenolites*); **2c**, limit between 2 LV, view rotated, (1) smaller LV with CCF, middle layer, (2) outer shell, homogeneous “mosaic” to cone CCF, (3) upper larger LV, outer shell, homogeneous “mosaic” to cone CCF, (4) area of regular foliated structure fading into mosaic CCF, (5) young shell-parts with CCF; **2d**, small LV, rotated view, (1) thick septum with coarse CCF, partly recrystallized?, (2) strong bioeroded outer shell (chlorophycean borings?), (3) regularly foliate (left) and CCF (right), (4) outer shell, CCF.

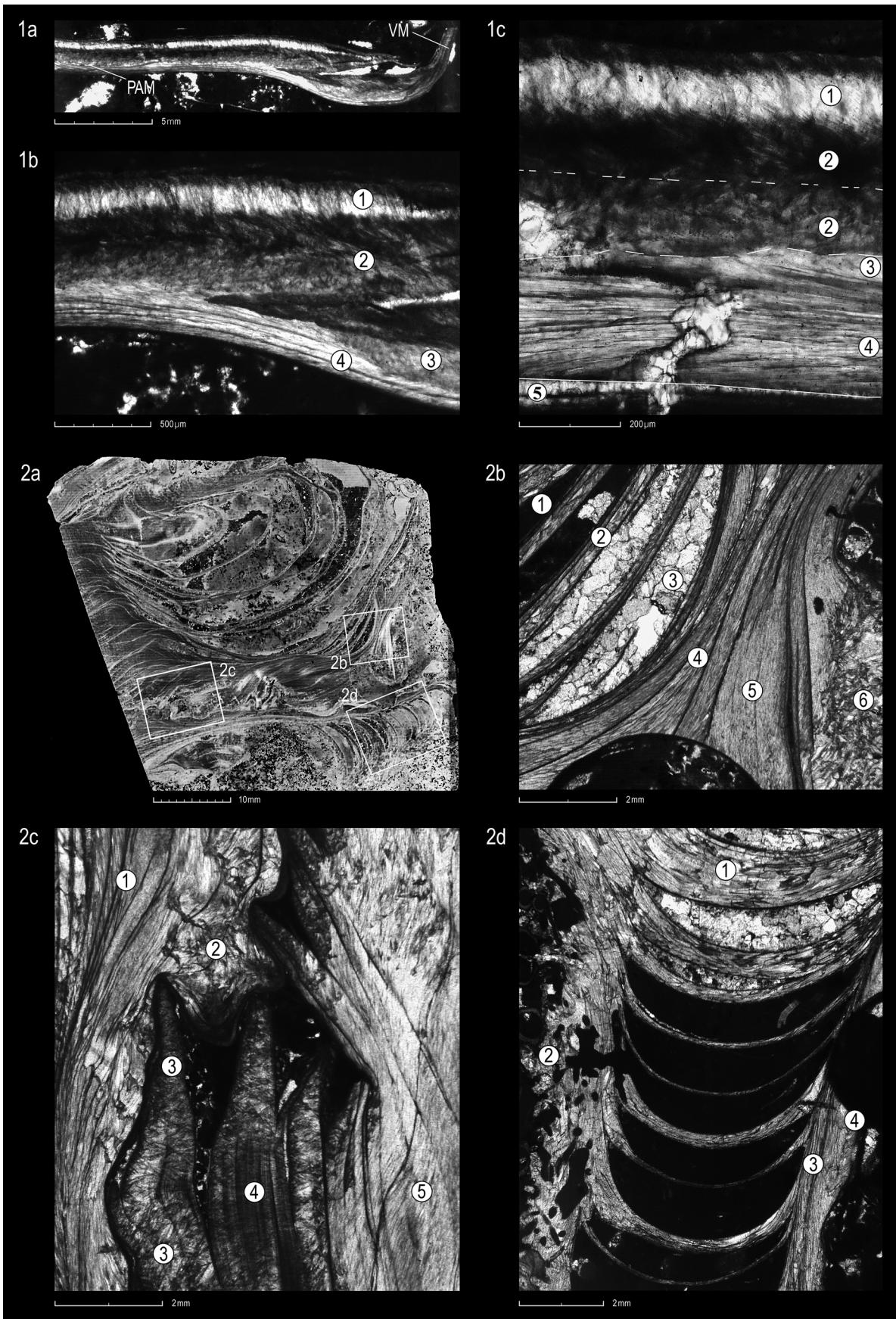


PLATE 21. Shell microstructures. **1a–h.** *Praeexogyra monsbeliardensis* (Contejean, 1859), Banné Marls, CTD-VTT001-3252, Vâ Tche Tchâ near Courtedoux: **1**, vertical cross-section of bivalved specimen (LV below, umbo damaged, right); **1a**, ventral third, (1) two thin calcitic bands (probably former aragonite); **1b**, RV, ventral third (position as in fig. 1), (1) internal sparitic calcite layer (100 µm thick), former recrystallized aragonite?, not myostracum, (2) regularly foliated structure below, grade into irregular CCF structure (3); **1c**, LV, lower ventral margin, (1) diffuse, thin (ca. 50 µm thick) regular simple prismatic structure (SP), dark layer above (= intruded sediment?), (2) thin homogeneous “mosaic” to cone CCF structure (250 µm), (3) middle shell layer, regularly foliated (RF, 500 µm thick), (4) sparitic calcite layer (100–220 µm thick), (5) thin, irregularly foliated CCF structure (ca. 100 µm), partially homogeneous; **1d**, LV, middle of ventral margin, with positions of Figs. 1f–h; **1e**, LV, same layer-numeration as in Fig. 1c, (3) bright lenses with sparitic calcite; **1f**, LV interior, (1) RF, (2) thin calcitic band (10–20 µm), (3) end of the sparitic calcite layer, grading into a diffuse portion of shell, (4) CCF, inwards regular foliated; **1g**, LV, middle/inner shell with micro-borings; **1h**, LV, outer shell, (1) diffuse RF, (2) thin homogeneous “mosaic” to cone CCF (100 µm), (3) RF.

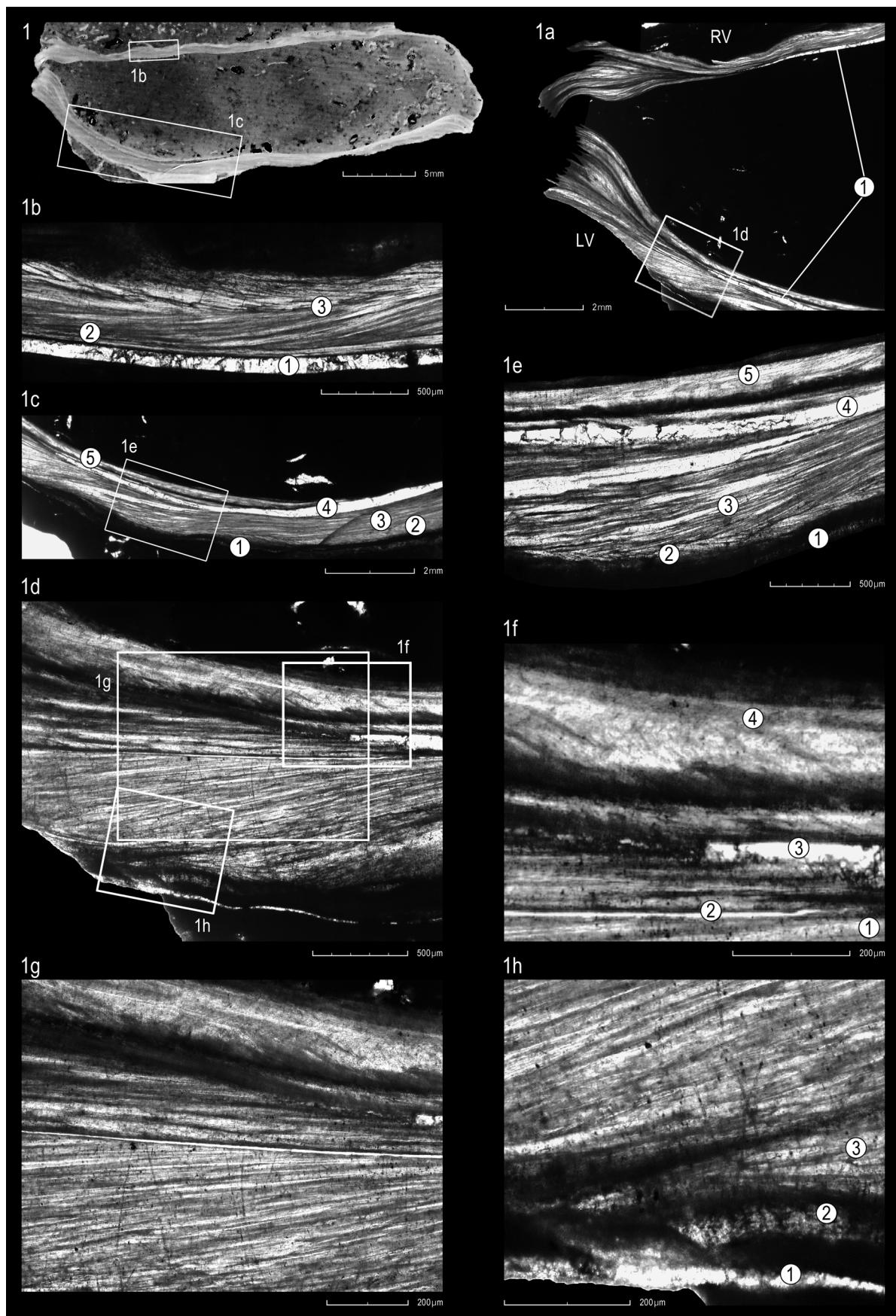


PLATE 22. Shell microstructures of *Actinostreon gregareum* (J. Sowerby, 1815), Banné Marls, Vâ Tche Tchâ near Courtedoux, Canton Jura, Switzerland. **1a–c.** Bivalved specimen, transverse cross section (ventral third), CTD-VTT001-1634: **1**, scanned thin section, LV below; **1a**, LV, anterior half, large lensoid chambers (with sparitic calcite), middle shell mainly regularly foliated, outer layers with irregular to homogeneous CCF, no prismatic outer shell preserved; **1b**, LV interior, anterior margin with regularly foliated structure and dipping laminae (10° with respect to depositional surface); **1c**, ventral margin, middle, (1) outer shell homogeneous “mosaic” CCF, (2) transitional between irregular CCF and homogeneous “mosaic” CCF, (3) middle and inner shell regular foliated, (4) middle, thin dark-grey layer with RF. **2a–c.** Bivalved specimen, vertical section, CTD-VTT001-1445: **2**, scanned thin section, LV below, umbo left; **2a**, LV, 180° rotated view (ventral left), central inner shell regular foliated (RF), laminae dipping dorsal (40° to depositional surface), many small lensoid chambers subparallel to depositional surface (chambers close to umbo destroyed by calcite crystals); **2b**, umbo, mostly LV (RV upper right), (1) LV, transition between RF and homogeneous “mosaic” CCF grading into irregular CCF, (2) folia dipping perpendicular to ligamental surface, (3) RV supporting buttress (resilifer), irregular CCF to homogeneous “mosaic” CCF; **2c**, LV (upper left), (1) lensoid chamber, with sparite cement, right side with early diagenetic, tooth-like calcite crystals, (2) RF, (3) homogeneous “mosaic” CCF.

