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Pinnidae (Bivalvia) from the Reuchenette Formation (Kimmeridgian, Upper Jurassic) of northwestern Switzerland

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ABSTRACT:

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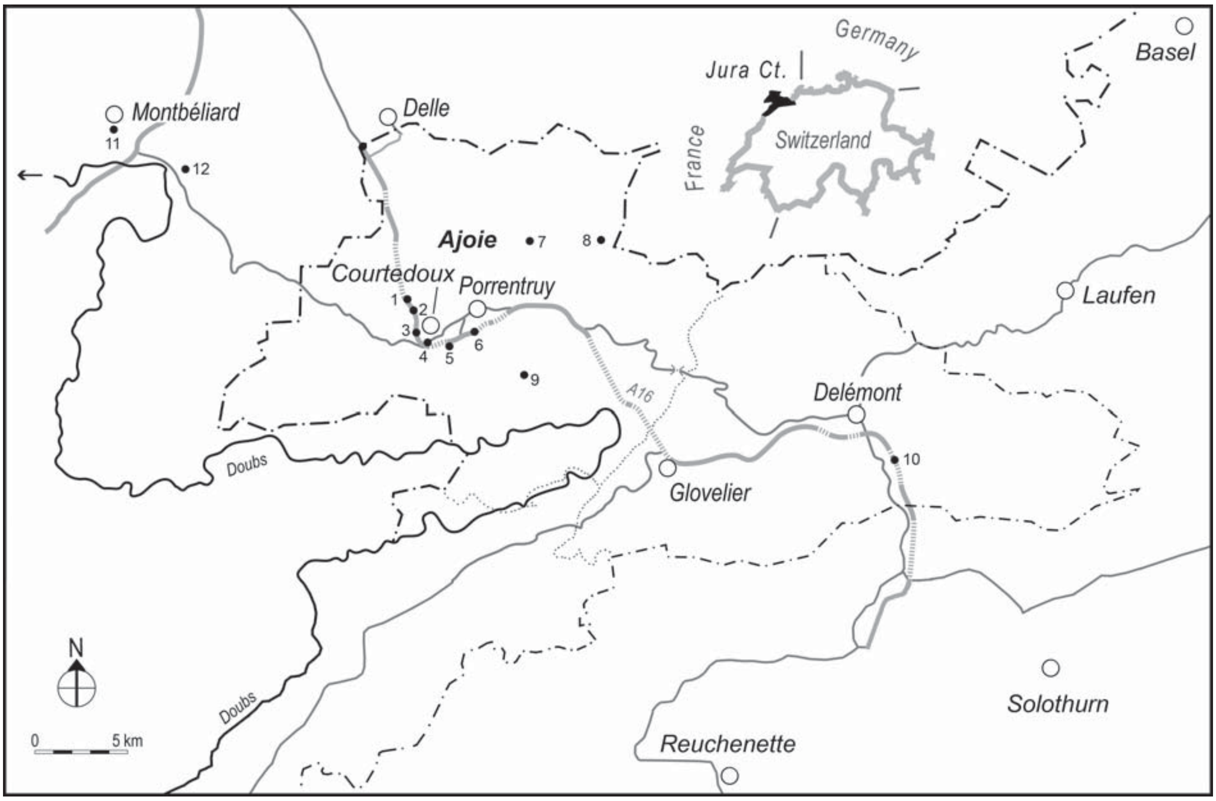
The shallow-marine carbonate deposits of the Reuchenette Formation (Kimmeridgian, Upper Jurassic) in northwestern Switzerland and adjacent France yield highly diverse bivalve associations, but only rarely contain remains of pinnid bivalves. The three occurring taxa *Pinna* (*Cyrtopinna*) *socialis* d'Orbigny, 1850, *Stegoconcha granulata* (J. Sowerby, 1822) and *Stegoconcha obliquata* (Deshayes, 1839) have been revised. A lectotype for *Pinna* (*C.*) *socialis* was designated and the taxon is assigned herein to *P.* (*Cyrtopinna*) Mörch, 1853, the first record of the subgenus from the Jurassic. A brief review of *Stegoconcha* Böhm, 1907 revealed two species groups within the genus. Species close to the type species *S. granulata* are characterized by a nearly smooth anterior shell, followed posteriorly by deep radial furrows and rows of pustules covering the dorsal flank. Another group comprises radially ribbed species related to *S. neptuni* (Goldfuss, 1837). It includes among others the Paleogene species *S. faxensis* (Ravn, 1902), extending the known range of *Stegoconcha* from the Middle Jurassic into the Paleogene. The paper suggests a relationship between *Stegoconcha* and the Cretaceous *Plesiopinna* Amano, 1956, with *S. obliquata* as a possible intermediate species leading to *Plesiopinna* during the Early Cretaceous. Furthermore, a possible relationship between *Stegoconcha* and *Atrina* Gray, 1842 is discussed.

Key words: Taxonomy, Bivalvia, Pinnidae, Pinna (Cyrtopinna), Stegoconcha, Kimmeridgian, Jurassic, Switzerland.

INTRODUCTION

The Upper Jurassic strata of the Jura Mountains in the border region between France and Switzerland have been a classic region for geological and palaeontological research since the early 19th century (Thurmann 1832). This activity is well reflected by many publications and monographs describing rich invertebrate associations, including numerous bivalve species (e.g., Agassiz 1840, 1842–1845; Contejean 1859, 1866; de Loriol 1886−1888, 1892, 1895, 1896, 1897; Thurmann and Etallon 1861−1864). With the multi-volume edition of Rollier (1911−1917) ended the classical era of studies related to Upper Jurassic bivalves from Switzerland. A new phase of palaeontological research started with the construction of the Transjurane highway (A16) in the Canton Jura and the related work of the "Paléontologie A 16" research group (PAL A16) and associated scientists. Large temporary outcrops in the Ajoie region (Text-fig. 1) exposing the Upper Jurassic Reuchenette Formation were accessible for studies between 2000 and 2012. Scientists of the PAL A16 (including the author) and members of the "Fondation paléontologique jurassienne" (FPJ) explored and excavated numerous sites along the highway, in the nearby quarries and in temporary road cuts. The main focus of the PAL A16 research group have been several spectacular dino-



Text-fig. 1. Map of studied localities in the Upper Jurassic of northwestern Switzerland and adjacent France. **1-8**; Kimmeridgian sites in the Ajoie region (Porrentruy district, Canton Jura), on the Transjurane highway (A 16) and nearby; 1 – Vâ Tche Tchâ near Courtedoux (A16, CTD-VTT, Banné Marls); 2 – Bois de Sylleux (A16, CTD-BSY, Coral limestone); 3 – Sur Combe Ronde (A16, CTD-SCR); 4 – Creugenat (CTD-CRE, Creugenat beds); 5 – Bressaucourt-Chalembert (BRE-CLB); 6 – Tunnel du Banné (A16, POR-TLB, tunneling the Banné hill, Banné Marls); 7 – Cras de Coeuve (Creugenat beds); 8 – Vendlincourt-Ecorchevez (VEN-ECO, Banné Marls, abandoned quarry); 9 – Alombre aux Vaches near Courtedoux (quarry, Banné Marls); 10 – Tunnel de Choindez near Courrendlin (A 16, Canton Jura, lower Callovian); **11-12**. Sites in the Montbéliard region, France: 11 – Petite Hollande (Upper Oxfordian, "Calcaires à *Cardium*"); 12 – La Baume, east of Audincourt (Kimmeridgian, "Calcaire à *Corbis*")

saur track sites discovered in the Courtedoux area (Marty 2008) and the remains of vertebrates, such as turtles, crocodilians and fishes from the "Lower *virgula*-Marls" (Marty and Billon-Bruyat 2004; Billon-Bruyat 2005; Anquetin *et al.* 2014; Püntener *et al.* 2014; Comment *et al.* 2015).

Invertebrate fossils such as bivalves and gastropods are common throughout the whole Reuchenette Formation. They can be found in enormous quantities in the Lower Kimmeridgian Banné Marls, which have therefore been in the focus for excavation and sampling of invertebrates. Ammonites are generally rare due to the unfavourable environmental conditions of a shallow-marine and often lagoonal carbonate platform. Those ammonites that were recovered are elements typical of the Subboreal Realm and allow for a refined biostratigraphy of the area (Comment *et al.* 2015).

Bivalves represent the most diverse and abundant fossils of the Reuchenette Formation, represented by more than 110 species (own data). Roughly 15,000 specimens of bivalves have been collected by the PAL A16 research group, among them several thousand oysters, which have been studied and revised by Koppka (2015). Additional research using the PAL A16 material was already done by Heinze (2007), who revised species of the bivalve family Pectinidae. Unpublished master theses of Hicks (2006) and Richardt (2006) had their main focus on the palaeoecological aspects of bivalve associations found in the Banné Marls of the A16 road cut at Vâ tche Tcha (Text-fig. 1).

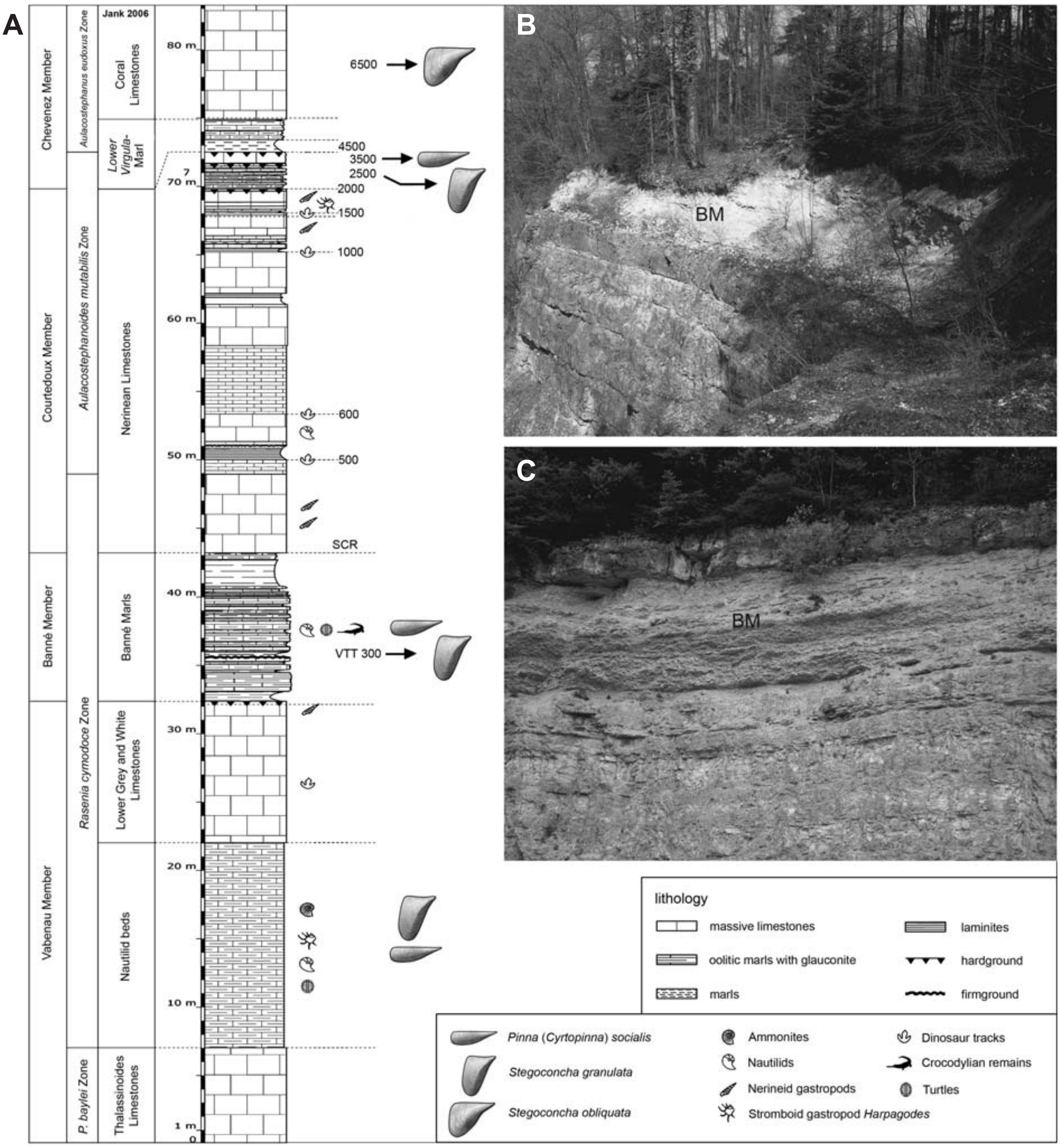
Only two genera of the bivalve family Pinnidae Leach, 1819, i.e., *Pinna* Linnaeus, 1758 and *Stegoconcha* Böhm, 1907, occur in the Reuchenette Formation. They are relatively rare and their occurrence is restricted to a few horizons (Text-fig. 2A). The Pinnidae, commonly known as razor, wing or pen shells, are a morphologically conservative family of large wedge-shaped bivalves with a long evolutionary history. They are already known from the Lower Carboniferous, display little change over time, and in the past appear to have occupied similar niches as today. Recent species live semi-infaunally in muds and sands of subtidal and coastal environments, and are found most commonly in sea-grass or sea-weed beds, where they may occur in large quantities (Lemer *et al.* 2014).

It has to be mentioned here that remains of the large thick-shelled genus *Trichites* Voltz in Thurmann, 1832 are relatively common in the Reuchenette Formation, e.g., in grey or white limestones and particularly in marly horizons of the Lower Kimmeridgian. However, the rich material, which includes three species of *Trichites*, was not included into this study. *Trichites* has been traditionally assigned to the Pinnidae (Cox and Hertlein 1969), but is excluded here because of its divergent internal morphology. The thick shell, the presence of a long ligamental area, a large buttressed posterior adductor scar, and a myofringing crest are features unknown from any member of the Pinnidae. A revision of the genus *Trichites*, together with a description of the species from the Reuchenette Formation and Oxfordian strata, will be presented by the author in a separate study.

GEOLOGICAL SETTING

The focus of the current study is the Reuchenette Formation of the Ajoie region (Text-fig. 1) in northwestern Switzerland (Canton Jura). During the Late Jurassic, the area was located in a distal position at the northwestern rim of the Helvetic shelf. During the Kimmeridgian, most of south-central Western Europe was covered by an epicontinental sea and situated in a subtropical climate belt at around 27° northern palaeolatitude (Frakes *et al.* 1992; Thierry and Barrier 2000). The structurally complicated, shallow-marine carbonate platform and ramp system of the Swiss Jura was oriented in an NE–SW direction, following Variscan structures in the basement (Jank *et al.* 2006b, c; Comment *et al.* 2015). The northwestern side of the platform was open towards the Paris Basin and graded in the south-east into the Helvetic rim basin, which itself continued towards the Ligurian Tethys (Marty 2008; Koppka 2015, fig. 1). In the north-east the platform bordered the southern German Jura sea (Swabian marl basin) and faced in the north and north-west a large land area that was part of the Rhenish and London–Brabant Massifs (Jank *et al.* 2006c; Comment *et al.* 2015). Sea-level fluctuations during the *Rasenia cymodoce* and *Aulacostephanus mutabilis* ammonite biozones (Text-fig. 2A) caused the emergence of large tidal flats along the platform margins, allowing dinosaurs to transit between the Central Massif in the southwest and the big northern landmass mentioned above.

The platform topography is not well understood yet. Lateral facies changes in the study area are particularly recognisable in NW-SE oriented transects (Jank *et al.* 2006c) and suggest a gentle NW-dip of the carbonate platform. This model is supported by the observed thickness reduction of the Lower Kimmeridgian Banné Marls from the depocentre in the Porrentruy region (up to 12 m) to merely 1 m or even by their absence towards the south-east in the direction of Reuchenette and Solothurn (Jank *et al.* 2006c, fig. 13; Text-figs 1, 2). A basin-and-swell morphology, as suggested by Jank *et al.* (2006c) for the lowermost part of the Reuchenette Formation, was apparently still present during the time interval of the Banné Member (*R. cymodoce* Biozone, *R. chatelaillonensis* Subzone; Comment *et al.* 2015). This unit is also known from southwestern Switzerland in the Vallée de Joux in the Canton Vaud (Aubert 1943) and can also be correlated with the French "Marnes à ptérocères" (Contejean 1859, 1866; Contini and Hantzpergue 1973) or the "Marnes de Rang" (Chevallier 1986, p. 145, fig. 61). The French equivalent of the Banné Member can be followed for at least 180 km in a NE–SW direction between Montbéliard (Franche-Comté) and Nantua (Rhône-Alpes). A large northern basin of the "Marnes de Rang" with up to 10 m in thickness is situated between Montbéliard, Besançon and Gray (Chevallier 1986, fig. 61) and was connected with a smaller basin of the Ajoie region. As in Switzerland, the marls are bound towards the south to NE–SW and NW–SE oriented swells or uplifted areas. Synsedimentary tectonic movements related to reactivated Variscan structures in the basement appear to have had an important influence on the platform morphology and explain the numerous local facies differences and rapid thickness changes as suggested by Jank *et al.* (2006c, pp. 256–258, figs 12, 13). Due to a high subsidence rate, the thickness of the Kimmeridgian deposits is about 155 m (Comment *et al.* 2015) in the Porrentruy-Courtedoux area. Towards the south-east, the thickness of the Reuchenette Formation is reduced to only 52 m in Solothurn (Jank *et al.* 2006b, c; Gygi 2013). The reduction and finally absence of transgressive units such as the Banné Marls and the "Lower *virgula*-Marls" indicate hiatuses in a more



Text-fig. 2. A – Generalised section of the Reuchenette Formation in the Ajoie area (based mainly on the Vâ tche Tchâ, VTT and Sur Combe Ronde, SCR sections); B – Banné Marls (*c.* 5 m in thickness) in the abandoned Vendlincourt-Ecochevez quarry (VEN-ECO), C – Banné Marls (*c.* 6 m) in Alombre aux Vaches; B, C – photographs of the author

central and shallower area of the platform. This is the case in the region between Balsthal and Solothurn and the area has therefore been interpreted by Jank *et al.* (2006c) as an uplifted block bounded from the west by the NNE–SSW-striking Rhenish Lineament and the neighbouring faults.

Pinnid bivalves (*Pinna* and *Stegoconcha*) are usually rare in the shallow-marine deposits of the Reuchenette Formation, but they are characteristic elements of highly fossiliferous marls and limestones deposited in subtidal, open lagoonal environments.

Most of the finds are restricted to transgressive marl units such as the “Nautilid Beds” (“Couches de Creugenat”) or especially the “Banné Marls” and the “Lower Virgula Marls” (Jank *et al.* 2006a, b, c; Comment *et al.* 2015; Koppka 2015; Text-fig. 2). Occurrences of *Stegoconcha granulata* and *S. obliquata* appear to have been ecologically linked to a few layers with characteristic lithologies, such as biodetritic marly limestones for *S. granulata* and pure, white chalky limestones for *S. obliquata*.

The Banné Member (Gygi 2000a, b) of the Lower Kimmeridgian of the *Rasenia cymodoce* Biozone contains the highest abundance of pinnid bivalves and is therefore briefly introduced here. The Member, usually referred to as the Banné Marls (“Marnes du Banné”) in local literature (Comment *et al.* 2015; Koppka 2015), is named after the Banné hill located south-east of Porrentruy (Canton Jura). Many informal names have been given to this unit such as “Marnes kimméridgiennes ou du Banné” (Marçou 1848), “Marnes à ptérocères” (Contejean 1859; Contini and Hantzpergue 1973), “Zone ptérocérienne” (Thurmann 1852), and “Zone strombienne” (Thurmann and Etallon 1861–1864). The latter terms refer to the spiny stromboid gastropod *Harpagodes thirriae* (Contejean, 1859), which is very abundant in these marls and a characteristic index fossil of the Lower Kimmeridgian. The gastropod was assigned in the 19th century to genera such as *Strombus* Linnaeus, 1758 or *Pterocera* Lamarck, 1799 and only more recently has been determined as *Harpagodes* Gill, 1870.

Only a few additional finds of pinnid bivalves have been made, and these came from a slightly older unit locally known as the “Couches à Creugenat” (Comment *et al.* 2015) or a few younger beds of the *Aulacostephanus mutabilis* and *A. eudoxus* ammonite biozones (see section in Text-fig. 2).

PREVIOUS RESEARCH

Recent pinnids have been revised amongst others by Schultz and Huber (2013) using a morphological approach. They recognised 55 species, a view that was challenged by Lemer *et al.* (2014), who provided the first molecular phylogenetical study of the family. They found evidence for numerous additional cryptic species and suggested a higher specific diversity than previously thought. However, phenotypic plasticity, morphologic stasis, and hybridization are key problems for taxonomists working on Recent pinnids (Liu *et al.* 2011; Lemer *et al.* 2014).

Despite this progress in Recent pinnid taxonomy, much less attention has been paid to fossil members of the family. This is especially true for the numerous Jurassic pinnids, which were mostly described in the 19th century, but have not undergone a much needed modern revision. The number of Jurassic pinnids known already is hard to estimate. Probably more than 100 Jurassic species have been described worldwide. Preservational problems, numerous synonyms for each species and the lack of revisions make it difficult to percieve the real diversity of the family.

An important work for early descriptions of Jurassic pinnids is “The Mineral conchology of Great Britain”, published by James Sowerby (1812–1822) and later continued by James de Carle Sowerby (1822–1846). Numerous Upper Jurassic pinnids from Jurassic strata in France were named and briefly described by d’Orbigny (1850) in the second volume of his “Prodrome de Paléontologie Stratigraphique”. However, due to the short nature of the descriptions and the lack of plates depicting the existing material (now housed in the “Salle d’Orbigny” of the Muséum de Paris), many species have become the subject of dispute and misinterpretation. Subsequently, Thevenin (1906–1923) and Cottreau (1913–1932) revised and figured d’Orbigny’s type material from the Upper Jurassic, including *Pinna socialis* d’Orbigny, 1850 in Cottreau (1932). Rollier (1914) in Rollier (1911–1917) gave an overview of most of the pinnid taxa known from Switzerland and neighbouring countries. Dechaseaux (1941) introduced the French pinnids from the Paris Basin. The revision of the English Corallian bivalve fauna by Arkell (1929–1937) contains valuable information about Upper Jurassic pinnids (Arkell 1933, 1934), including a description of the type species of *Stegoconcha*. Cox (1940) made the first revision of the genus *Stegoconcha* in his work about the bivalves from the Jurassic of Kachchh, India. A couple of modern papers containing descriptions of species of European Upper Jurassic pinnids provides supplementary references and information (e.g., Duff 1978; Kelly 1984; Fürsich and Werner 1988; Delvene 2000).

Kimmeridgian bivalves in the area around Porrentruy have been first studied by Thurmann (1832, pp. 12, 13). The presence of *Pinna* sp. was mentioned by him in 1832, without any further information. That species was described much later, after Thurmann’s early death, as *Pinna banneiana* Thurmann *in* Thurmann and Etallon (1862). However, Contejean (1859), who was a friend of Jules Thurmann, used several of Thurmann’s manuscript names (sometimes with a slightly different spelling!) and described a probably not conspecific species with a much wider umbonal angle as *Pinna bannesiana* Th. from the Upper Kimmeridgian of the nearby Montbéliard region in France. Further species of Thurmann and Etallon (1862) found in the Kimmeridgian of Porrentruy are *Pinna ampla* J. Sowerby, 1812 [revised here as *Stegoconcha granulata* (J. Sowerby, 1822)] and *Pinna intermedia* Thurmann and Etallon, 1862 [= *Stegoconcha obliquata* (Deshayes, 1839)].

MATERIAL AND METHODS

Jurassic pinnids are generally difficult to study because of their often poor preservation. The material of the Reuchenette Formation lacks the aragonite internally present and exhibits only the thin and brittle, prismatic outer shell. Internal moulds occasionally reveal weak imprints of the dissolved dorsal and ventral nacre lobes. Nevertheless, the preservation allows the observation of the position of the posterior adductor muscle scar (Text-figs 3D, 7). Because of their thin shells, all pinnids are vulnerable to any form of reworking, and transport leads to instant damage or even complete destruction. Nearly all the specimens studied are preserved articulated, but shells found in marls are often deformed due to sediment compaction. Furthermore, the fragile shells tend to shatter during sampling, which makes collecting and preparation labour-intensive. Hence, it was not possible to find any undamaged specimens in the studied material. Reworked but still articulated shells found on bedding planes are missing their anterior and posterior ends. Representatives of *Pinna*, being semi-infaunal mud stickers in the sense of Seilacher (1984), their posterior ends were exposed and probably already disintegrated shortly after the death of the individual or broke off due to current activities. Strongly deformed specimens have been found in life position (embedded perpendicular to the bedding plane) in the thin marly limestone layers of the Banné Marls. These specimens have no posterior end preserved; they are strongly compressed in length and have become artificially curved during diagenetic compaction of the sediment.

Material of the following institutions and collections has been included into the study:

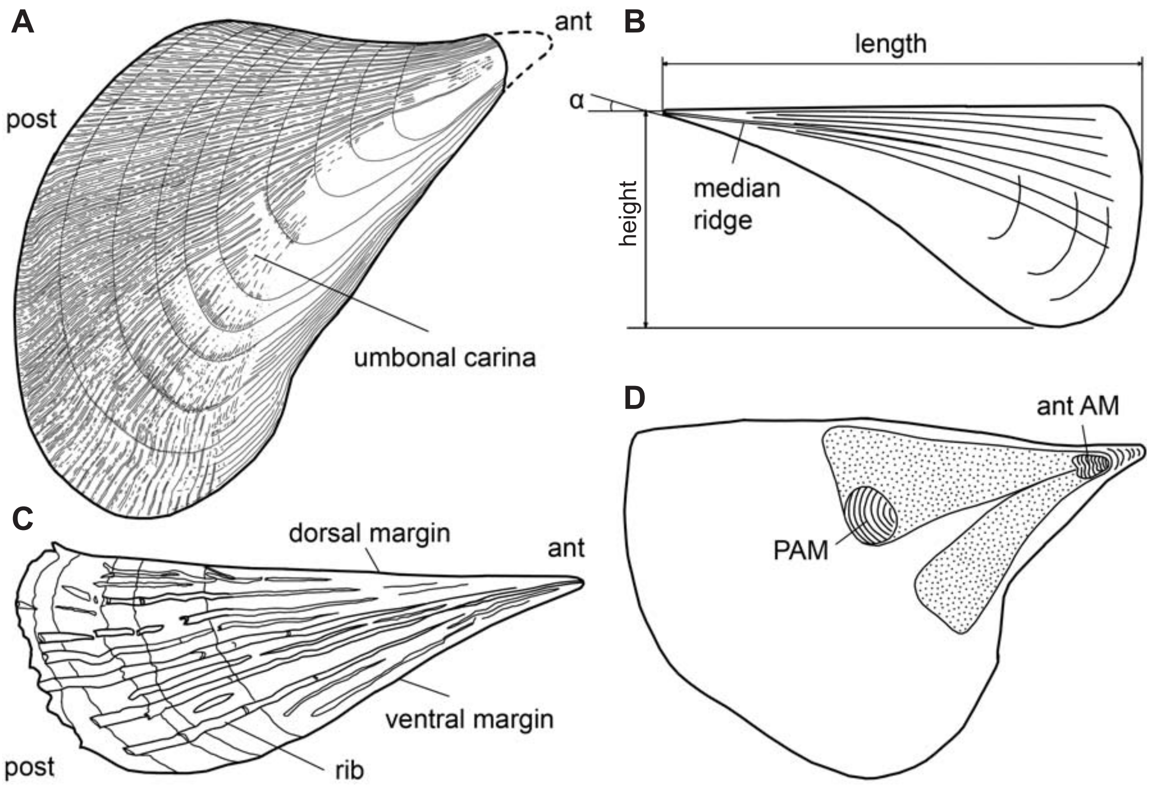
“*Paléontologie A16*” *(PAL A16) (Switzerland).* All of the observed specimens and especially the figured material are part of the taxonomic bivalve collection assembled by the author and now housed in the collections of the Jurassica Museum in Porrentruy (Canton Jura). The majority of the material has been found in the Banné Marls (*R. cymodoce* Biozone, Lower Kimmeridgian) of the Vâ Tche Tchâ (VTT) near Courtedoux and Tunnel du Banné (TLB) in Porrentruy localities. Additional material comes from the boundary of the *A. mutabilis*/*eudoxus* biozones (horizons: 2300, 3500, 6000) around 25–30 m above the Banné Marls in the Courtedoux area (Text-figs 1, 2). Only one specimen of *Stegoconcha obliquata* has been found in the white limestones above the “Lower *Virgula* Marl” (*A. eudoxus* Biozone, Upper Kimmeridgian). Samples of the PAL A16 collection are coded alphanumerically, consisting of three letters for the municipality, three letters for the site, sampling year (three digits), and sample number (e.g., CTD-SCR009-1234 refers to Courtedoux – Sur Combe Ronde – 2009 – no. 1234). In the text, an abbreviated code without the first letters is used, but complete site codes can be found in Text-fig. 1.

“*Jurassica*” *(MJSN) (Switzerland).* The “Jurassica” Museum is the former “Musée jurassien des sciences naturelles (MJSN)” in Porrentruy, Switzerland. It hosts several, but unfortunately not all, types and topotypes of the “Lethea bruntrutana” published by Thurmann and Etallon (1861–1864). All available specimens of Upper Jurassic pinnids from the collections of J. Thurmann, F.L. Koby, and G.A. Scheurer have been studied.

“*Fondation paléontologique jurassienne*” *(FPJ) (Switzerland).* One well-preserved specimen (FPJ 21621) of *Stegoconcha plotii* (Arkell, 1933) from the Lower Callovian Ifenthal Formation of the “Tunnel de Choindez” (A 16) at Courrendlin (Canton Jura, Switzerland) has been included in order to introduce the microstructure of *Stegoconcha* and for comparison (Text-fig. 5).

PREPARATION AND DOCUMENTATION

The material of the PAL A16 collection has been partly prepared by Fritz Furrer (PräpGem, Zuzwil) and by the author using pneumatic airscribes and air abrasives. Photographic imaging has been done together with Bernard Migy at the PAL A16 facilities using a Nikon D300 with a MicroNikkor 60 mm lens, except for a few specimens photographed by the author with private equipment (Canon EOS 1000D, Canon EFS 60 mm macro lens). Most of the specimens have been coated with ammonium chloride before photographing for a homogeneous appearance, a better contrast, and to enhance the surface details. The illustrations (Text-figs 4, 6–8) were prepared by P. Roeschli (PAL A16) in cooperation with the author after discussion and explanation of taxonomically important details. Due to the incomplete material, the reconstructions are often based on several specimens.



Text-fig. 3. Orientation and terminology. **A** – *Stegoconcha ampla* (J. Sowerby, 1812), right valve (RV), modified after holotype figure; Middle Jurassic, England; **B** – *Pinna* (*Cyrtopinna*) sp., Upper Jurassic, left valve (LV), α – umbonal angle; **C** – *Pinna* (*P.*) *rudis* Linnaeus, 1758; Recent, Barbados; ant – anterior, post – posterior; **D** – *Pinna* (*Exitopinna*) *deltodes* Menke, 1843; Recent, Australia; left valve interior, stippled fields – lobes of nacre, PAM – posterior adductor muscle scar, ant AM – anterior adductor muscle scar

TERMINOLOGY

Shell-orientation and terminology (Text-fig. 3) follows Cox and Hertlein (1969), Duff (1978), Kelly (1984), and Fürsich and Werner (1988). Some special morphological features need a brief explanation. The median ridge (Text-fig. 3B; Pl. 1, Figs A, C–K) separates the dorsal and ventral flank of the shell and works in *Pinna* as a pseudoligament (Chinzei *et al.* 1982) or flexure zone, allowing flexing of the shell centre. With contraction of the posterior adductor muscle the middle shell bends inwards and the gaping posterior end closes (Text-fig. 4B). This ridge is prominent in Jurassic members of the genus but less common in Recent taxa of *Pinna* (*Pinna*). A rounded ridge, here referred to as the umbonal carina (Fürsich and Werner 1988), is characteristic of *Stegoconcha*. It is a concave rounded edge, running close to the ventral margin from the umbo towards the posteroventral end.

Abbrevations used for measurements: H – height; L – length; I – inflation of single valve; LV – left valve; RV – right valve; PAM – posterior adductor muscle.

SYSTEMATIC PALAEONTOLOGY

Class Bivalvia Linnaeus, 1758
Superorder Ostreiformii Férussac, 1822
Order Ostreida Férussac, 1822
Suborder Malleidina Gray, 1854
Superfamily Pinnoidea Leach, 1819
Family Pinnidae Leach, 1819
Genus *Pinna* Linnaeus, 1758

TYPE SPECIES: *Pinna rudis* Linnaeus, 1758; subsequent designation by Children (1823, p. 34); Recent, Barbados (Antilles, Caribean Sea).

DIAGNOSIS: Equivalve, wedge-shaped; umbones at extreme anterior end, ventral margin straight to concave; median ridge well-defined, especially anteriorly; sculpture of radial ribs or rows of scales and/or ventral growth folds; posterior margin gaping; nacre of interior divided medially by a groove into two lobes (after Cox and Hertlein 1969, p. *N*283; Fürsich and Werner 1988, p. 133).

OCCURRENCE: Cosmopolitan, ?Lower Carboniferous–Recent.

REMARKS: Cox and Hertlein (1969, p. *N*283) noted a stratigraphic range of *Pinna* (*Pinna*) from the Lower Carboniferous to Recent, which contradicts Turner and Rosewater's (1958, p. 297) claim that the earliest record of *Pinna s.s.* is Jurassic. In the view of the latter authors, the first "true" *Pinna* in the Jurassic has a more derived morphology. Particularly, the presence of a well-developed median ridge (or medial shell carina) is an important difference and corresponds with a deep division of the internal nacreous layer into two lobes, producing a zone of shell flexure. As stated by Waller and Stanley (2005, p. 29), this contradiction is based on the uncritical use of the genus name *Pinna*, by applying this name to Palaeozoic pinnids, which miss even a demonstrable median carina. An example is "*Pinna* (*Pinna*) *costata* Philipps" as figured in Cox and Hertlein (1969, fig. *C*23.2c). However, this Carboniferous species is, according to these authors, a synonym of *P. flexicostata* McCoy, 1844, which is the type species of *Sulcatopinna* Hyatt, 1892. The latter genus was included by Cox and Hertlein (1969) in their broad concept of *Pinna*, but should better be used as a separate genus rather than a subgenus of *Pinna* as suggested by Hoare (2007) and Schulz and Huber (2013).

Subgenus *Cyrtopinna* Mörch, 1853

TYPE SPECIES: *Pinna incurva* Gmelin, 1791 (Gmelin 1791, p. 3366; by monotypy); Jurassic–Recent; fossil species cosmopolitan, Recent species restricted to the Indo-Pacific.

DIAGNOSIS: Long, narrow, slightly curved, very thin-shelled; median ridge well defined; radial ribbing weak (Cox and Hertlein 1969, p. *N*283).

REMARKS: Jurassic species of *Pinna* have been traditionally assigned to *Pinna* or when specified to the subgenus *Pinna* (*Pinna*). However, the suggestion of Cox and Hertlein (1969, p. *N*283) that the subgenus *P.* (*Cyrtopinna*) already existed in Jurassic times was overlooked or not applied by subsequent authors. The relatively flat but strongly plicate and even spinose type species *Pinna rudis* (see Text-fig. 3C) shows little similarities with the Jurassic representatives of the genus. They have usually inflated shells with a rhomboidal, in some cases also a quadrate cross-section, a weakly developed radial sculpture without spines, and a well defined median ridge. However, the type species of *Pinna* (*Cyrtopinna*) is the Recent *P.* (*C.*) *incurva*, which is morphologically very close to the Jurassic *P.* (*C.*) *socialis*. The prominent median ridge of *P.* (*Cyrtopinna*) (see Text-figs 3B, 4) was also described as a "cracking keel" (Chinzei *et al.* 1982) and is of functional importance in fossil and Recent species, allowing flexing of the shell to close the gaping posterior end.

Pinna (*Cyrtopinna*) *socialis* d'Orbigny, 1850
(Text-fig. 4A–G; Pl. 1, Figs A–M)

* 1850. *Pinna socialis* d'Orb. 1847; d'Orbigny, vol. 2, p. 53, no. 148.
? 1859. *Pinna Bannesiana* Th.; Contejean, p. 218, pp. 296, 297, pl. 18, fig. 3.
v 1861. *Pinna Banneiana*, Th.; Thurmann and Etallon, pp. 45, 53, 55, 56, 61, 66.
v 1862. *Pinna Banneiana*, Th.; Thurmann and Etallon, p. 217, pl. 28, fig. 1.
1914. *Pinna Bannéiana* (Thurm.); Rollier, pp. 292, 293.
1914. *Pinna socialis* d'Orbigny, 1850; Rollier, p. 394.
? 1915. *Pinna quadrata* n. sp.; Schneid, p. 408, pl. 29, fig. 4.
1932. *Pinna socialis* d'Orb.; Cottreau, p. 200, pl. 66, figs 16, 17 (refigured syntypes).
1933−34. *Pinna sandsfootensis* n. sp.; Arkell, p. 223 (1933), pl. 29, figs 4, 4a (1934).
1964. *Pinna* (*Pinna*) *quadrata* Schneid 1915; Wellnhofer, p. 32, pl. 2, figs 1−3; text-fig. 18a−f.
1966. *Pinna suprajurensis* d'Orb.; Zakharov, p. 69, pl. 20, figs 1, 2.
? 1966. *Pinna romanikhae* Zakh. sp. nov.; Zakharov, p. 73, pl. 18, fig. 7; pl. 21, fig. 1; pl. 22, figs 1, 2; text-fig. 12.
1973. *Pinna bannesiana* Th.; Contini and Hantzpergue, p. 150.
1974. *Pinna* aff. *romanikhae* Zakharov; Zakharov and Mesezhnikov, p. 137, pl. 29, fig. 1.
2000. *Pinna* (*Pinna*) cf. *socialis* d'Orbigny 1850; Delvene, p. 91, pl. 1, fig. 15a, b.
2003. *Pinna* (*Pinna*) cf. *socialis*; Delvene, p. 524.
v 2006. *Pinna* cf. *lanceolata*; Hicks, p. 36.
v 2006. *Pinna* cf. *lanceolata* (J. Sowerby 1821); Richardt, pp. 9, 18.

LECTOTYPE (designated herein): *Pinna socialis* d'Orbigny, 1850 (p. 53, no. 148); MNHN-F-R09004 (no. 4704 of the d'Orbigny Collection, Muséum national d'histoire naturelle, Paris), description and figure in Cottreau (1932, p. 200, pl. 66, figs 16, 17) and Pl. 1, Fig. C herein; Châtelaillon-Plage (department Charente-Maritime), Kimmeridgian, Upper Jurassic, France.

MATERIAL: Numerous articulated specimens of the PAL A16 collection from Vâ Tche Tchâ (VTT001-6–8, 10, 450, 3977, VTT006-228, 568, 637) near Courtedoux and Vendlincourt-Ecorchevez Quarry (VEN-ECO009-16). All specimens are from the Banné Marls (*R. cymodoce* Biozone, Lower Kimmeridgian, Reuchenette Formation). Only one additional younger find (SCR011-1168, Pl. 1, Figs G, H, M) is known from horizon 3500 (*Orthaspidoceras schilleri*-horizon, *O. lallierianum* Subzone, *A. mutabilis* Biozone) of Sur Combe Ronde (SCR) near Courtedoux. Six specimens (determined as *Pinna* cf. *lanceolata* J. Sowerby, 1821) from layer 800 of Vâ Tche Tchâ (see Pl. 1, Fig. F) collected by Simone Hicks and Fabian Richardt (Würzburg/Erlangen) and now stored in the MJSN collection. Three specimens (MJSN S 412a, b) from the Banné Marls of Porrentruy (labeled as *Pinna banneiana* Thurmann) from the Thurmann collection, Jurassica Museum (figured in Pl. 1, Figs D, E). Three additional specimens from Cras de Coeuve (determined as *Pinna banneiana* Thurmann, MJSN S 382a–c) from the Koby collection (Jurassica Museum, Porrentruy). The label noted Banné Marls as the find horizon, which is misleading. The locality is known for lithologically similar, but older strata of the "Nautilid Beds" (lower *R. cymodoce* Biozone) or the upper part of the "Couches du Creugenat", respectively (Jank *et al.* 2006b; Comment *et al.* 2015, p. 168).

The material comprises mostly isolated internal moulds of articulated specimens, with few or no shell remains preserved. All specimens are fragmentarily preserved and miss small or larger parts of their posterior and anterior ends. Brackets indicate measurements based on graphically reconstructed outlines with estimated length and/or inflation.

Dimensions (in cm):

Specimen	H	L	I	H/L	α
VTT001-6	3.4	(9.1)	0.9	0.37	27°
VTT001-7	3.2	(11.9)	0.98	0.27	25°
VTT001-8	1.55	(5.4)	0.58	0.29	21°
VTT001-10	1.2	(3.9)	0.54	0.31	24°
VTT001-450	1.7	(6.5)	0.77	0.26	20°
VTT001-3977	1.5	(5.1)	0.63	0.29	24°
VTT006-228	2.27	(8.0)	1.0	0.28	20°
VTT006-568	2.85	(9.3)	0.97	0.31	21°
VTT006-637	2.05	(6.0)	(0.6)	0.34	25°
ECO009-16	1.45	4.3	(0.5)	0.34	22°
SCR011-1168	1.83	(5.5)	0.67	0.33	24°
MJSN S382a	1.9	(7.7)	0.9	0.25	20°
MJSN S382b	2.8	(10.0)	0.81	0.28	20°
MJSN S382c	2.15	(7.0)	(1.1)	0.3	20°

DESCRIPTION: **Shape, size** – Small- to moderate-sized, wedge-shaped (cuneiform), distinctly lanceolate and subequivalve, moderately inflated; umbones straight and pointed, situated at extreme anterior end (but usually not preserved); narrow byssal gape present anteroventrally (Text-fig. 4B; Pl. 1, Fig. B); anterior half with nearly straight dorsal and ventral margins, diverging regularly with an umbonal angle between 20° and 30°, ventral margin slightly convex towards posterior end, dorsal margin straight, but occasionally slightly concave close to umbo; with sharp median carina separating dorsal and ventral parts of shell, forming an angle of 110° to 120° (in undistorted specimens); ventral half slightly higher than dorsal one, with dorsal half of LV up to 30% higher than the same area on RV; cross-section of closed shell subcircular close to umbo and more rhomboidal to lanceolate towards the posterior end (Text-fig. 4; Pl. 1, Figs H, K). Maximum length estimated from reconstructed specimen 11.9 cm (Text-fig. 4A), but average length usually between 5 and 8 cm.

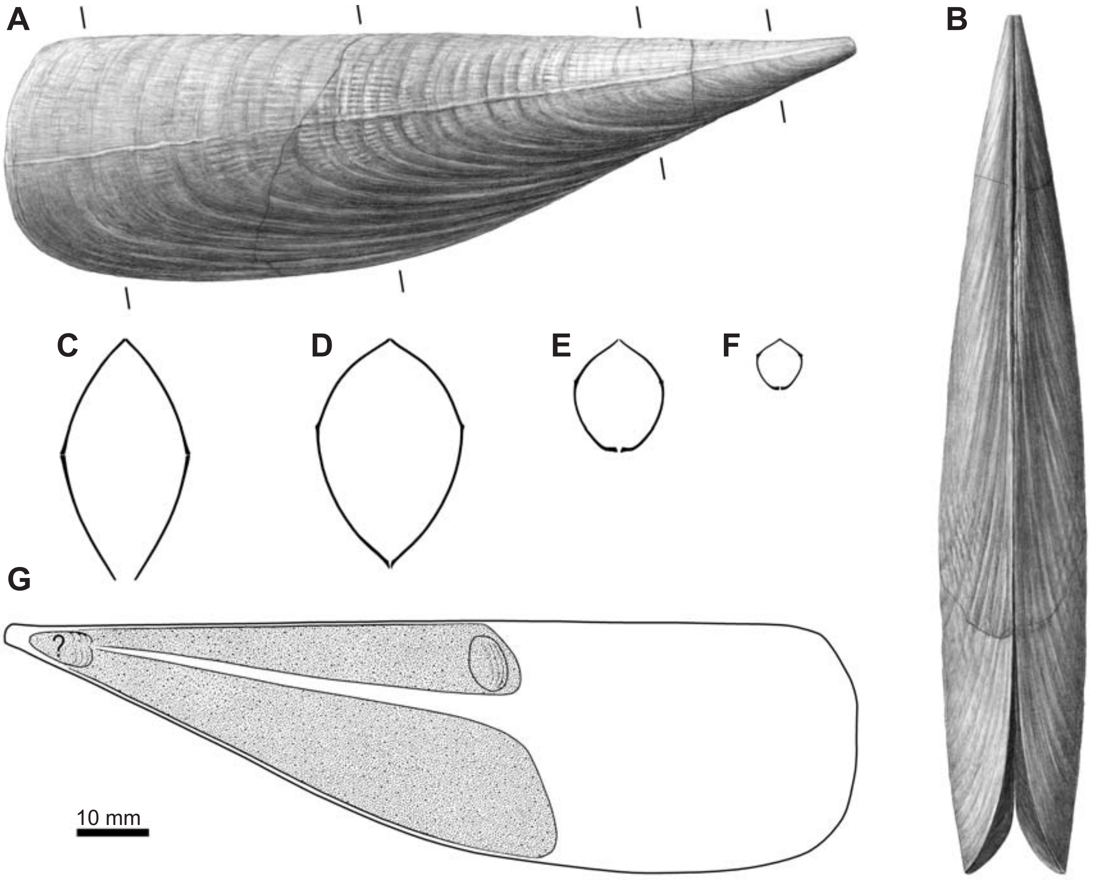
Sculpture – Shells weakly ornamented, usually with few radial ribs on dorsal flank; some specimens nearly smooth, especially anteriorly; average specimens with eight weakly developed radial ribs on dorsal flank (Pl. 1, Fig. D), which become more numerous in larger specimens (up to 15; Pl. 1, Figs F, J) and more distinct towards the posterior margin; ribs rarely continue ventral of median carina and then only in strongly ornamented adults; commarginal growth folds present but usually weak and developed only on ventral flank, becoming more prominent near to median carina and anteriorly.

Internal shell characters – Usually poorly or not preserved due to dissolution of internal nacre and fragmentary preservation; posterior adductor scar small, of oval shape and situated on dorsal flank at about two-thirds of total length; anterior adductor scar not seen (Text-fig. 4G).

Microstructure – Only thin outer calcitic shell preserved, comprising of simple prismatic structure, usually < 0.5 mm thick; median ridge flanked on both sides by brown coloured thicker shell, whereas other shell parts are lighter; internal aragonite always dissolved, but weak imprints of two lobes of nacre occasionally present (Text-fig. 4G).

OCCURRENCE: Oxfordian of England and Spain; Kimmeridgian of Switzerland and France; ?Tithonian of Germany; Middle Volgian to Valanginian (Lower Cretaceous) of Russia.

REMARKS: *Pinna banneiana* Thurmann and Etallon,



Text-fig. 4. *Pinna* (*Cyrtopinna*) *socialis* (d'Orbigny, 1850). A-G –Reconstruction based mainly on VTT001-7, Vâ Tche Tchâ (Banné Marls, Lower Kimmeridgian); A – RV lateral view; B – both valves, ventral view; C-F – dorso-ventral cross-sections; G – RV, interior view (schematic), reconstruction of anterior and posterior adductor scars and former (dissolved) nacreous lobes (dotted area, based on faint imprints on internal moulds)

1862 was described on the basis of material found in the Banné Marls in the area around Porrentruy. The figured specimen of Thurmann and Etallon (1862, pl. 28, fig. 1a, b) is somewhat idealised and shows a curved dorsal margin, indicating diagenetic deformation. However, syntypes from the Thurmann collection agree well with the material from the Banné Marls. *Pinna bannesiana* Th. *sensu* Contejean (1859, pl. 18, figs 3, 4) is based on a fragmentary specimen. Its reconstruction shows a rather large reconstructed *Pinna* with an umbonal angle of *c.* 40° and a wide posterior end. It is hard to interpret Contejean's (1859) figure, which may show an unusually broad specimen or even a different species. However, the figured specimen appears to be lost and another, uncharacteristically strongly ribbed and fragmentary specimen (labeled as *P. bannesiana* in the Contejean collection at Montbéliard) is too poorly preserved to allow determination at species level. Both specimens appear not to be conspecific with the material of *P. banneiana* Thurmann and Etallon [= *Pinna* (*Cyrtopinna*) *socialis* d'Orbigny, 1850] as introduced in this paper. However, the observed Kimmeridgian material from Switzerland shows a relatively wide range of variation (Pl. 1, Figs A, D–J). Most specimens have narrow umbonal angles between 20° and 30°, which results in a rather lanceolate shape as reconstructed in Text-fig. 4A. This is in contrast with the lectotype of *P.* (*C.*) *socialis,* which has a rather wide umbonal angle of about 40° (Pl. 1, Fig. C) and is more similar to Contejean's (1859) figure. However, the lectotype lacks its posterior end and the final adult shape is therefore not observable, but may be narrower and not as broad as drawn by Contejean (1859).

Several more narrow and weakly ornamented species have been described from the Upper Jurassic of Europe and are here seen as possible synonyms of *Pinna* (*C.*) *socialis* d'Orbigny, 1850. *Pinna sandfootensis* Arkell, 1933 is known from the Upper Oxfordian "Calcareous Grit" [=Sandsfoot Grit] of

Sandsfoot, Weymouth, England. Compared with the Lower Kimmeridgian material from Switzerland only the completely straight ventral margin of *P. sandfootensis* (Arkell 1934, pl. 29, figs 4, 4a) appears to be different, whereas the ornamentation, general morphology, and size are identical. The Tithonian limestones of Neuburg (southern Germany) yield *Pinna quadrata* Schneid, 1915. The material of that species is usually strongly compressed in length, but its morphology and sculpture agree well with *P.* (*C.*) *socialis*. The large and almost complete specimens of *Pinna romanikhae* Zakharov, 1966 (Zakharov 1966, p. 73, pl. 18, fig. 7; pl. 21, fig. 1a, b; pl. 22, figs 1, 2) from the Lower Valanginian (Lower Cretaceous) of Siberia and the Volgian (*Eosphinctoceras magnum* ammonite Biozone) of the Urals in Russia (Zakharov and Mesezhnikov 1974, p. 137, pl. 29, fig. 1) fit perfectly in the species concept of *P.* (*C.*) *socialis* and are seen here as the youngest known representatives of a variable and long-ranging species.

COMPARISONS: As mentioned by Fürsich and Werner (1988), many Jurassic species of *Pinna* are ill-defined. Determinations on species level are therefore difficult, especially when only fragmentary or poorly preserved material is available and necessary revisions of many species are still lacking. Some of the better-known species occurring in the Upper Jurassic are here briefly introduced and compared in alphabetic order.

Pinna (*Pinna*) *lanceolata* J. Sowerby, 1821 (J. Sowerby 1821, p. 145, pl. 281) – This species was originally described from the Lower Oxfordian of Scarborough (Yorkshire, England). The holotype appears to be lost and therefore Arkell (1933, p. 222, pl. 28, fig. 5) chose one of Sowerby's topotypes from the "Lower Calcareous Grit" of Oliver's Mount at Scarborough as the neotype (SM J511). This species is morphologically close to *P. socialis*, but differs in being larger (maximum length 17 cm; Duff 1978, p. 45) and in having an anteriorly curved shell with a concave dorsal margin and a convex ventral margin (Duff 1978, fig. 12a). The radial ornament in *P. lanceolata* is stronger and covers most of the shell including the umbonal region. In the dorsal half are 8–10 sharp, wire-like radial ribs and also the ventral half carries 3–5 ribs. On the contrary, *P. socialis* is nearly smooth close to the umbo and ventral radial ribs are only occasionally present on the posterior half of large specimens.

Pinna (*Pinna*) *mitis* Phillips, 1829 (Phillips 1829, pl. 5, fig. 7) – The holotype (YM 2192, figured in Arkell 1933, pl. 26, fig. 7, and Duff 1978, pl. 3, fig. 11) of this species comes from the Upper Oxford Clay (*Quenstedtoceras mariae* Biozone, Lower Oxfordian) of Scarborough (Yorkshire, England). It is similar in size to *P. socialis* but differs in being less inflated and in having a distinct concave-curved anteroventral margin. The ornament differs in being much more pronounced and particulary in having 13–22 dorsal radial ribs and up to seven well-developed radial ribs on the ventral part of the shell (Duff 1978, p. 43). The ribs are present close to the umbo and continue towards the posterior end, wheras *P. socialis* is nearly smooth anteriorly.

Pinna (*Pinna*) *subcuneata* Eichwald, 1865 (Eichwald 1865, p. 55, pl. 23, fig. 6; nomen novum pro *Pinna cuneata* Eichwald, 1861; non Bean, 1839) – According to Kelly (1984, p. 35), the type specimen cannot be traced and is believed to be lost. The species was originally found in the "grès néocomien supérieur de Khoroschovo" near Moscow, Russia. Material from the same site was dated by Gerasimov (1955, p. 100) as belonging to the *Garniericeras catenulatum* Biozone (Upper Jurassic, Volgian). The species differs from *P. socialis* by its wider umbonal angle of 30° to 40°, numerous well-developed concentric folds on the whole ventral flank and by the presence of up to 20 radial riblets, which cover the complete dorsal flank and the dorsal third of the ventral flank (Kelly 1984, pl. 5, fig. 13).

Pinna (*Pinna*) *suprajurensis* d'Orbigny, 1850 [d'Orbigny 1850, vol. 2, p. 60, no. 47, nomen novum pro *Pinna obliquata* Deshayes *sensu* Leymerie (Leymerie 1846, p. 232, pl. 9, fig. 2), non *Stegoconcha obliquata* (Deshayes, 1839)] – Leymerie's type specimen comes from the Upper Kimmeridgian or Lower Tithonian of Marolles-sous-Lignières (Department l'Aube) in France. *Pinna socialis* and *P. suprajurenis* have a similar shape, but the latter species is larger (shells up to 20 cm long) and on the dorsal flank and parts of the ventral flank bears a much stronger ornament of up to 12 comparably thick radial, wire-like riblets (Kelly 1984, p. 36, pl. 4, fig. 18; pl. 5, figs 10–12, 14, 15).

PALAEOECOLOGY: Most of the material belongs to bivalved specimens, which are usually found parautochthonous in a horizontal position, within or on top of fossil-rich limestone beds alternating with marls. Occasionally, a group of specimens has been found close together on a bedding plane. All observed specimens lack their posterior ends, with at least one-third of the total shell length not preserved. The damage was probably the result of heavy storms which reworked the shells and caused breakage of articulated specimens. This indicates that the bivalves were still alive when being reworked. Some strongly deformed specimens have been found in life position in a thin marly limestone layer (field observation of dumped material of the Banné Marls), with the long axis perpendicular to the bedding plane. These specimens are strongly compressed in length, often somewhat curved, and their posterior end is not preserved.

Genus *Stegoconcha* Böhm, 1907

TYPE SPECIES: *Pinna granulata* J. Sowerby, 1822; subsequent designation by Cox (1940, p. 133); Oxfordian–Kimmeridgian, England, UK.

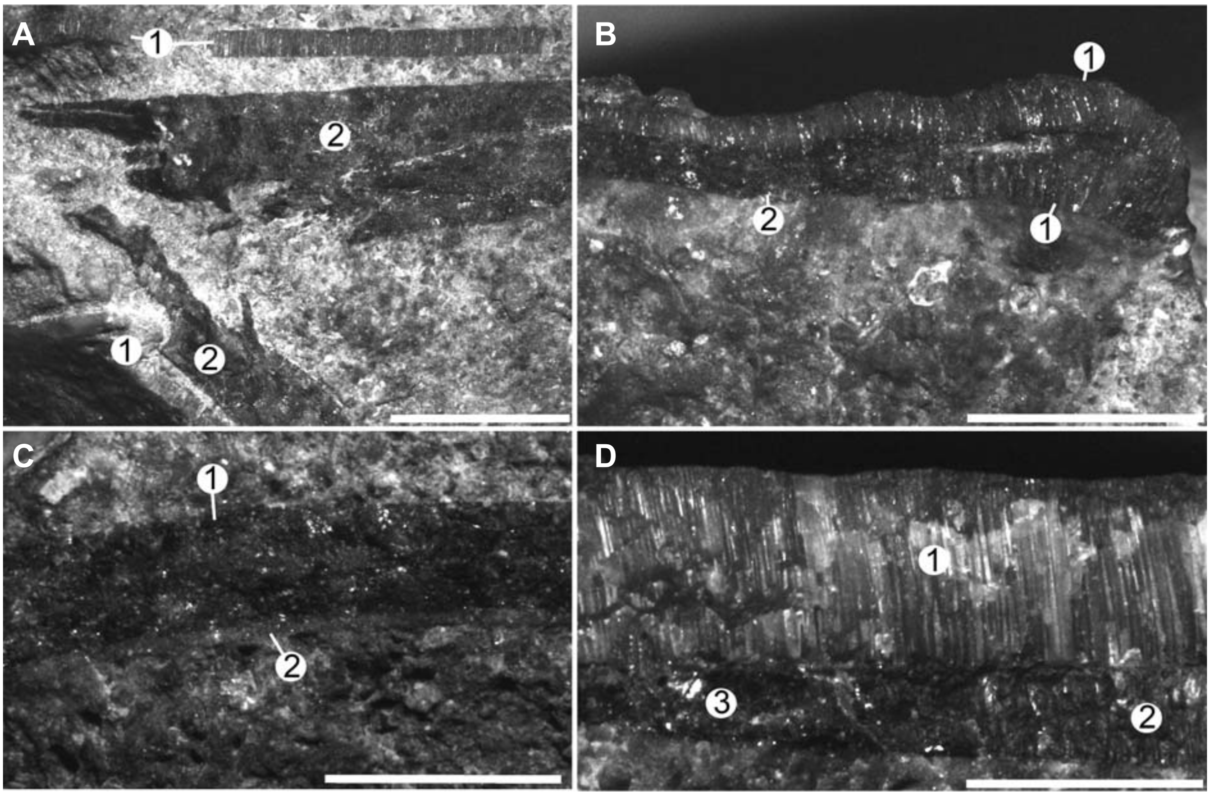
DIAGNOSIS: Equivalve, large, mytiliform, gibbose, most inflated along rounded ridge (umbonal carina) passing from umbo to posteroventral angle; height usually exceeding length; posterior end closed; anteroventrally concave; ornament consisting of irregularly distributed radial furrows and depressed radial ribs or threads, commonly broken up posteriorly into rectangles or granules, and confined to, or most conspicuous on the dorsal side of umbonal carina (with the exception of dorsally and ventrally ribbed Cretaceous and Paleocene species); occasionally nearly smooth with radial ornament and granules absent anteriorly and more prominent towards posterior end; shell moderately thick (usually 3–5 mm, max. 8 mm) and without median flexure zone; weak internal median ridge may be present anteriorly (fading towards umbo) but restricted to calcitic simple prismatic outer shell layer, covered by a continuous nacreous middle shell layer; ridge (furrow on internal moulds) diverges into narrow chevron towards shell centre, dividing the internal nacreous layer into two lobes (modified after Böhm 1907, p. 148; Cox 1940, p. 133; Cox and Hertlein 1969, *N*283 and own data).

MICROSTRUCTURE: *Stegoconcha* occurs usually in facies unsuitable for the preservation of aragonite, leaving in most cases only the calcitic simple prismatic outer shell intact. A rare exception is the specimen of *Stegoconcha plotii* (Arkell, 1933) from the Lower Callovian of Switzerland (Text-figs 5 and 9), where the internal aragonite is mostly preserved but recrystallised into dark bituminous calcite. The unique specimen is not available for thin-sectioning. It was broken dorsoventrally and in an anteroposterior direction (Text-fig. 9), allowing at least a microscopic study of the different shell layers and thickness changes before the pieces were glued back together. Despite the preservational limitations, the observed structures can be interpreted by comparison with the microstructure known from the relatively simply constructed shells of Recent pinnids. Their outer simple prismatic shell layer is the only calcitic component and all other internal layers are composed of aragonite (mostly nacre). Furthermore, Carter (1990) already mentioned the presence of internal nacre and aragonitic prismatic shell layers in fossil pinnids from the Upper Carboniferous.

The microstructure of the shell of *Stegoconcha* was so far unknown and the following description is based on microscopic observations of the mentioned specimen of *S. plotii*. At up to 4 mm, the former aragonitic shell is particularly thick along the dorsal margin where a relatively thick ligament (*c.* 2–3 mm wide) was attached (Text-fig. 5A). The aragonitic shell is overlain by a thin outer calcitic, columnar, regular simple prismatic shell layer (SP) of about 0.7 mm in thickness. The SP-layer is missing in most parts of the anterior shell. The articulated but posteriorly damaged specimen was already somewhat degraded and the outer shell layer got partially lost due to reworking (Text-fig. 5A, SP-layer separated from internal nacre), before the final deposition took place. In Recent *Atrina* Gray, 1842 (Carter 1990, p. 213; Carter *et al.* 2012, fig. 230) the lamellar ligament is attached to a very thin layer of ligostracum, which separates it from the nacreous middle shell layer. However, neither the ligament nor an aragonitic fibrose ligostracum is preserved in *S. plotii* and the recrystallisation of the aragonite does not allow for a clear observation of the microstucture of the former nacreous layer.

The anteroventral margin of the RV shows an inward fold of the calcitic simple prismatic shell layer, which is between 0.2 mm and 0.7 mm thick, and encloses a *c.* 0.2 mm thick aragonitic layer. The folded prismatic layer grades into a dark, homogenous nacreous layer which is *c.* 0.6 mm in thickness (Text-fig. 5B). This nacreous layer continues uninterrupted with more or less the same thickness across nearly the whole posteroventral section (Text-fig. 7B), before the layer becomes thicker towards the dorsal margin. A clear separation of the nacre lobes is apparently not present in *S. plotii*, at least not in the position of the cross-section. The separation of lobes is well indicated on the internal moulds of *S. granulata* and *S. obliquata* (Text-fig. 7; Pl. 4, Figs A, D).

The dark aragonitic nacreous layer is in the central position of the longitudinal cross-section (Text-figs 5C, 9B), about 1.5 mm thick and underlain by a thin aragonitic prismatic shell layer of greyish colour. The thin, calcitic outer SP-shell layer is not preserved



Text-fig. 5. *Stegoconcha plotii* (Arkell, 1933). FPJ 21621, Lower Callovian (Ifenthal Formation, Châtillon Member) of the "Tunnel de Choindez" (A 16), Switzerland, natural cross-sections. A – dorsal margin of articulated valves (LV up), 1, calcitic, regular simple prismatic outer shell layer, 2, internal aragonitic nacreous shell layer (recrystallised), B – anteroventral margin of RV, 1, folded calcitic, regular simple prismatic shell layer (SP), 2, nacreous internal shell layer, C – longitudinal cut, middle of shell, 1, continuous aragonitic nacreous shell layer (not divided into lobes), 2, thin aragonitic prismatic shell layer, D – longitudinal cut, posterior end, 1, calcitic, regular simple prismatic outer shell layer, 2, internal probably calcitic simple prismatic layer, 3, aragonitic nacreous layer (grading into 2 in posterior direction). Scale bars equal to 5 mm (A) and 3 mm (B-D)

here but can be observed towards the posterior end where the layer becomes thicker and varies between 2.5 and 3 mm. The underlying nacreous layer (1 mm thick) grades posteriorly into a probably originally calcitic SP-layer (Text-fig. 5D).

OCCURRENCE: Cosmopolitan (Europe, Asia, Africa); Middle Jurassic to Paleocene.

REMARKS: *Stegoconcha* is a long-ranging, cosmopolitan genus with a preference for shallow-marine environments, usually found in biodetritic horizons of carbonate and siliciclastic shelves. The genus has been regarded by Cox and Hertlein (1969) as restricted to the Jurassic. Yet, younger species are also known, for instance *S. gmuelleri* (Krenkel, 1910), which ranges from the Kimmeridigian to the Lower Cretaceous (Krenkel 1910, p. 203; Cox 1965, p. 47). Even younger is *Cardium neptuni* Goldfuss, 1837, a species included by Böhm 1907, together with *Pinna granulata* J. Sowerby, 1822, in his original definition of *Stegoconcha*. However, *S. neptuni* was usually assigned to genera such as *Mytilus* Linnaeus, 1758 and recently *Gervillaria* Cox, 1954 (for synonymy see: Niebuhr *et al*. 2014, p. 107). The species is known from the Upper Cretaceous (Cenomanian to Senonian) of Germany (Böhm 1907, p. 148; Wanderer 1909, p. 25). Overlooked by most authors is the occurrence of *Stegoconcha faxensis* (Ravn, 1902) in the Paleocene of Denmark, Scania and Greenland (Rosenkrantz 1970, p. 436).

Two major species groups can be distinguished within the genus *Stegoconcha*. The first group consists of taxa with a reticulate/pustulose shell sculpture and morphologically close to the type species. The following species can be assigned to the *granulata* group: *Stegoconcha granulata*, *S. obliquata*, *S. occidentalis* (Choffat, 1888), *S. plotii* (Arkell, 1933), *S. reticulata* (Rollier, 1914), and *S. thiessingi* (Rollier, 1914).

The *neptuni* group consists of radially ribbed species, which has its origin in the densely ribbed species of the Jurassic such as *S. ampla* and *S. gmuelleri*.

These early species have many narrow radial ribs covering the whole shell except for the area ventral of the umbonal carina. Cretaceous and Paleocene species have less numerous but broader and more distinctly developed radial ribs, some even ventral of the umbonal carina. Species of the *neptuni* group include: *S. ampla* (J. Sowerby, 1812), *S. faxensis* (Ravn, 1902), *S. gmuelleri* (Krenkel, 1910), *S. iburgenis* (Weerth, 1884), *S. neptuni* (Goldfuss, 1837), and probably also *S.*? *stoliczkai* (Cox, 1940).

It is noteworthy that some authors, e.g., Rollier (1914) and Arkell (1933), who were unaware of *Stegoconcha* Böhm, 1907, included species of *Stegoconcha* into the apparently similar genus *Trichites* Voltz in Thurmann, 1832. However, both taxa are not related and *Stegoconcha* can be distinguished by having equivalved and much thinner shells, which are usually covered with an ornament of fine radial ribs, rectangular pits and/or small granules. In turn, *Trichites* has several-centimetres-thick and strongly inequivalved shells, which are occasionally smooth or have thin radial threads, but usually carry some thick bifurcating radial ribs. Furthermore, shells of *Trichites* are often encrusted by oysters and serpulids, and are usually penetrated by *Gastrochaenolites*-borings of the bivalve *Lithophaga* Röding, 1798. This difference suggests a more exposed or even epibenthic growth position for *Trichites*. Additional criteria for distinguishing both taxa are the presence of a ventrally curved umbonal carina in *Stegoconcha*, a weakly developed and non-inserted posterior adductor muscle scar, and two diverging lobes of internal nacre, which are completely absent in *Trichites*.

Stegoconcha appears to be closely related to *Plesiopinna* Amano, 1956. The type species *Plesiopinna atriniformis* Amano, 1956 (Albian?−Cenomanian of the Gosyonoura group, Cretaceous, Shishijima, Japan) does not show the typical ornament of *Stegoconcha* but the nearly smooth species *S. obliquata* might represent a heterochronic evolutionary trend that leads to *Plesiopinna* (see also this work under comparisons of *S. obliquata*). If this assumption turns out to be true, then *Plesiopinna* has to be regarded as a separate genus and not as a subgenus of *Pinna* as proposed by Cox and Hertlein (1969, p. *N*283) and Schultz and Huber (2013).

Atrina and *Stegoconcha* are seen here as close relatives. The occurrence of *Atrina* in the Middle Jurassic was already indicated by Cox and Hertlein (1969, p. *N*283) but subsequent authors seem to have avoided assignments of Jurassic pinnids to this genus. Recently, the Middle Triassic species *Atrina sinuata* Waller and Stanley, 2005 has been described from Nevada (USA). The authors suggest that ham-shaped pinnids with a wide umbilical angle and a missing median carina, indicating an undivided internal nacreous layer, belong to *Atrina* rather than one of the comparatively narrow Palaeozoic genera *Aviculopinna* Meek, 1864 and *Meekopinna* Yancey, 1978, which have subterminal rather than terminal beaks.

A possible transitional species between *Stegoconcha* and *Atrina* was described as *Pinna stoliczkai* by Cox (1940, p. 135, pl. 10, figs 9, 10) from the Callovian of Kachchh, India. Cox (1940) was unsure whether he should assign the species to *Stegoconcha* or *Atrina* and kept it as *Pinna*. He argued that the radial sculpture, the strong inflation and the absence of a median ridge would speak for an assignment to *Stegoconcha*, but the transversely elongated and less mytiliform shape are features unusual for the genus. He did not observe an internal median ridge (or groove on internal moulds), which divides the lobes of the internal nacre and suggested therefore a possible relation to *Atrina*. In this study the author prefers an assignment to *Stegoconcha*, even though its shape is not typical of the genus.

Clearly, more basic systematic work is needed on these poorly known species to clarify the phylogeny of the family. Heterochrony is a possible explanation of the shape change by maintaining juvenile features as seen on the densely ribbed and narrow umbo of species such as *S. gmuelleri* of the *neptuni* group.

Stegoconcha granulata (J. Sowerby, 1822)

(Text-figs 6A–D, 7A; Pl. 2, Figs A–F; Pl. 3, Figs A–D)

* 1822. *Pinna granulata* n. sp.; J. Sowerby, p. 65, pl. 347.
v 1859. *Pinna granulata* Sow.; Contejean, p. 297.
1860. *Pinna granulata* Sow.; Damon, p. 41.
v 1862. *Pinna ampla*, Goldf.; Thurmann and Etallon, p. 217, pl. 28, fig. 2.
1866. *Pinna granulata* Sow.; Contejean, p. 552.
1868. *Pinna granulata* Sowerby; de Loriol and Cotteau, p. 199.
non 1872. *Pinna granulata* Sowerby; de Loriol *et al*., p. 354, pl. 20, figs 2, 3.
1874. *Pinna granulata* Sowerby; Brauns, p. 305.
1875. *Pinna granulata* Sowerby; de Loriol and Pellat, p. 162.
1877. *Pinna granulata* Sow.; Blake and Hudleston, p. 267.
? 1888. *Pinna granulata,* Sowerby.; Choffat, p. 66.
? 1897. *Pinna granulata*, Sowerby; de Loriol, p. 121.
1901. *Pinna granulata* Sowerby; de Loriol, p. 91 (see for synonymy).

1927. *Trichites granulatus* (Sowerby); Arkell, p. 168.
1933–34. *Trichites granulatus* (J. Sowerby); Arkell, p. 228, pl. 29, fig. 5 (1934).
1940. *Stegoconcha granulata* (J. Sowerby, 1822); Cox, p. 133.
non 1971. *Stegoconcha* sp. aff. *granulata* (Sowerby, 1824); Vörös, p. 175, pl. 1, fig. 3 (= *Stegoconcha ampla*)
1988. *Stegoconcha granulata* (J. Sowerby, 1822); Fürsich and Werner, p. 137.
non 1996. *Pinna granulata* Sowerby; Colleté, p. 22, fig. 28.
v 2006. *Stegoconcha ampla*; Hicks, p. 36.
v 2006. *Stegoconcha ampla* (J. Sowerby 1812); Richardt, pp. 9, 18.
non 2009. *Pinna* (*Plesiopinna*) cf. *granulata* J. Sowerby, 1822; Diedrich, p. 337, fig. 4.1a–c.

HOLOTYPE: *Pinna granulata* J. Sowerby, 1822 (Sowerby 1822, p. 65, pl. 347), by monotypy, "Kimmeridge Clay" of Weymouth in Dorset, England, UK. A Kimmeridgian age of the type is doubtful; according to Arkell (1933, p. 228) it was most likely found in the Upper Oxfordian "*Trigonia clavellata* Beds". The type is from the collection of Sir Henry de La Beche, but its whereabouts remain unknown; acording to Arkell (1933) it is probably lost.

MATERIAL: Nine more or less complete specimens from the Kimmeridgian of the Porrentruy region. Some are partially exfoliated and/or deformed. The oldest specimens are from Bressaucourt-Chalembert (BRE-CLB) and Creugnat (CTD-CRE) near Courtedoux, discovered in the "Nautilid beds" (basal *R. cymodoce* Biozone, Lower Kimmeridgian). Most specimens are from the Banné Marls (top of the *R. cymodoce* Biozone, Lower Kimmeridgian) of Vâ Tche Tchâ (CTD-VTT), Tunel le Banné (POR-TLB; TLB001-210, Pl. 2, Figs A–C) and Vendlincourt (VEN-ECO; ECO009-29, Pl. 2, Figs D–F). The material was found in the lower third of the Banné Marls, where higher energetic, coarse-grained sediments occur. The youngest specimens are from the upper *A. mutabilis* Biozone (*O. lallierianum* Subzone) of Sur Combe Ronde (SCR), found in life position in layer 2300, which is topped by a firmground. Several specimens were discovered in life position with the posterodorsal margin as the most exposed part (e.g., VTT011-99, VTT 006-656, bed 300; Pl. 3, Figs A–D). An additional specimen (S. 393, A.2.20.2.02) from the Thurmann collection (Jurassica Museum) is also from the Banné Marls of Porrentruy and was erroneously determined by Thurmann as *Pinna ampla* Sowerby.

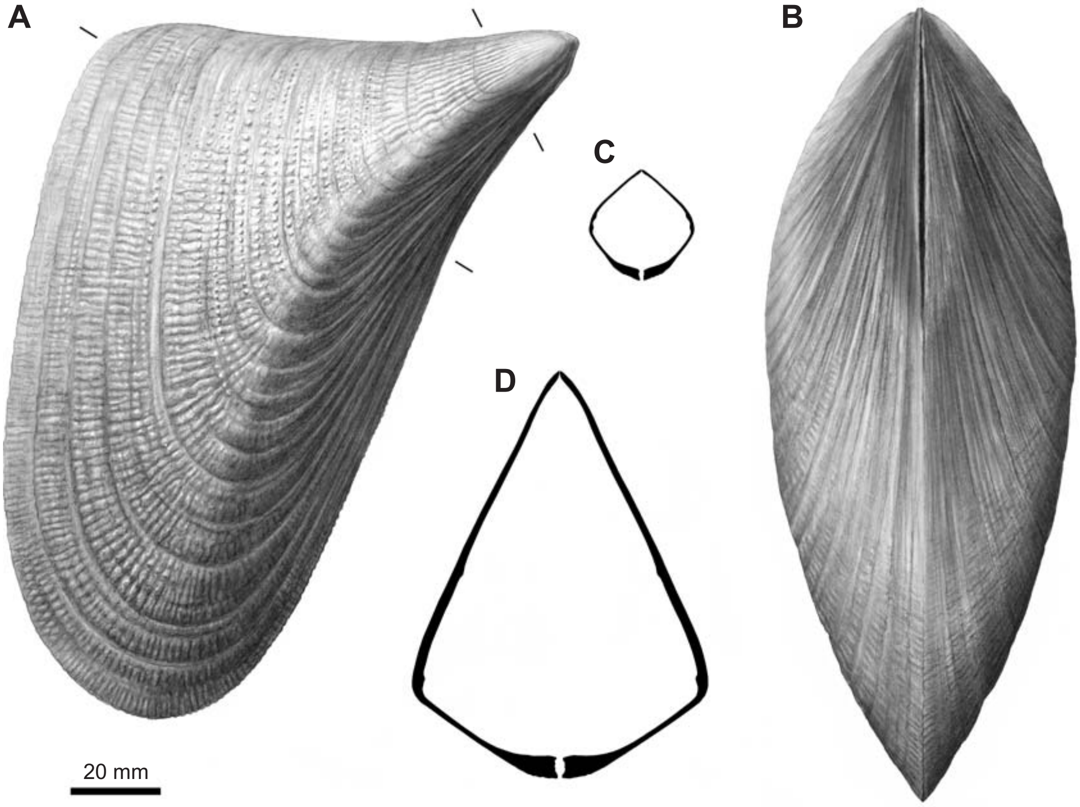
Measurements in brackets refer to partially incomplete specimens and denote estimated values based on reconstructed shapes.

Dimensions (in cm):

Specimen	H	L	I	H/L	α
TLB001-210	11.5	9.4	3.45	1.21	60°
ECO009-29	(8.0)	(7.5)	2.8	1.07	50°
VTT001-3978	(13.0)	(12.9)	3.2	1.01	55°
VTT006-250	(14.1)	(13.8)	3.95	1.02	63°
VTT011-99	(12.5)	(11.0)	3.73	1.14	62°
SCR002-52	13.8	(12.6)	3.8	1.1	61°
CLB007-7	13.5	12.5	4.06	1.08	57°
CRE000-337	10.5	(10.0)	3.25	1.05	58°

DESCRIPTION: **Shape, size** – Equivalve, large, mytiliform to ham-shaped, gibbose; slightly higher than long with terminal, pointed umbones and moderate inflation; greatest shell inflation midway of carina or slightly dorsal of it; anteroventral margin slightly gaping; shell thickness between 2 and 5 mm, caused by a byssal collar (*sensu* Carter *et al.* 2012) which supported the byssal attachment (Text-fig. 6B); dorsal margin short, weakly concave, meeting posterior margin in a blunt angle of about 100°; dorsal two-thirds of the posterior end straight to slightly convex and becoming rounded posteroventrally, forming a U-shaped and anteriorly inclined ventral margin; anteroventral margin nearly straight but slightly concave towards umbo; flank with pronounced umbonal carina, which is very prominent in anterior half, with rounded angle of around 90° to 120° between dorsal and ventral flank, carina becomes less pronounced towards the posteroventral angle; dorsal and anteroventral margins with an umbonal or apical angle of around 60°, but directly at the umbo (which is usually not preserved) more pointed with *c.* 45° (Text-fig. 6; Pl. 2, Figs A, D, E); anteroventral flank steep and often deformed by compaction, running nearly parallel to umbonal carina; shell generally thin, usually less than 1 mm thick, except in area along umbonal carina and anteroventral margin, shell becomes thinner towards umbo and towards dorsal and posteroventral margins; highest thickness of lateral shell 3 mm measured at mid-length of umbonal carina and along posterior margin.

Sculpture – Anterodorsal shell between umbonal carina and dorsal margin covered for about 3–5 cm with up to 18 radial threads or riblets (Text-fig. 6A), fading in ventral direction and changing posteriorly between 4 and 6 cm from the umbo into rows of small, irregularly spaced pustules or granules, which are gradually replaced towards the posterior margin by numerous radial, irregularly branching and



Text-fig. 6. Reconstruction of *Stegoconcha granulata* (J. Sowerby, 1822), based on several specimens (VTT011-99, TLB001-210, SCR002-52, CLB007-7), Lower Kimmeridgian; A – right valve; B – both valves, with narrow byssal gape, anterior view; C-D – schematic transverse cross-sections, after measurements of shell-thickness on various specimens (without internal aragonite); at umbo (C), between posterodorsal angle and anteroventral margin (D); lines mark the position of the virtual sections

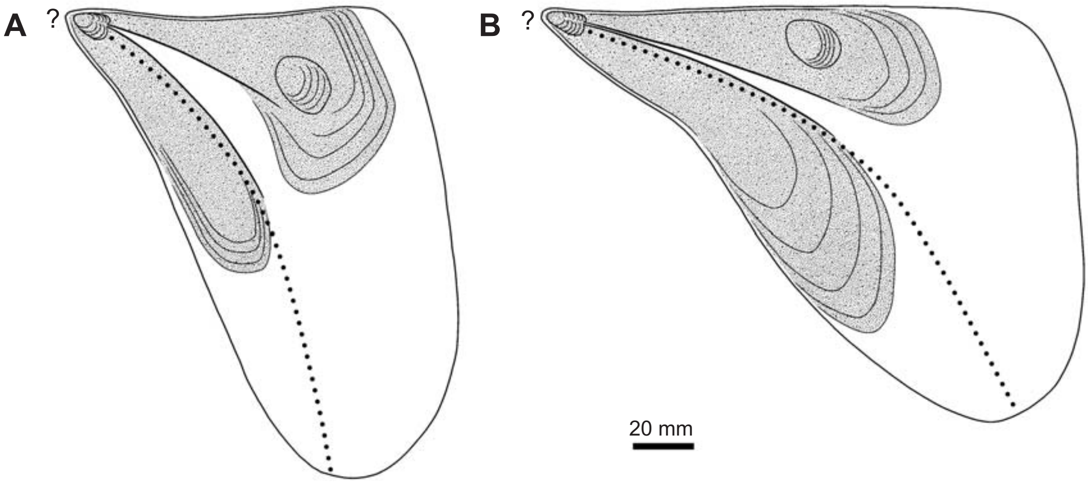
somewhat radiating grooves with few remnants of commarginally arranged granules; distance between branching furrows 1 or 2 mm, grooves deepening towards margins, passing the umbonal carina at its ventral third and covering only the most ventral, less strong inflated part of the anteroventral flank; towards umbo the shell bearing anteroventrally only commarginal growth lines with some plications close to the anterior end, which fade ventrally.

Internal shell characters – Internal moulds with two furrows between umbo and posterior adductor imprint (Text-fig. 7A), which form a chevron with an angle of 25°; these furrows correspond to keel-like narrow ridges on the inner side of the simple prismatic calcite shell; they are interpreted here as dorsal and ventral borders of two dissolved lobes of former nacre, occupying the anterior shell half up to the posteroventral angle; ventral furrow running along the centre of the umbonal carina and ventral lobe occupying the anteroventral shell; dorsal lobe of nacre somewhat larger and occupying half of the shell dorsal of the umbonal carina (Text-figs 6C, D; 7A).

The dorsal internal ridge ends close to the small, oval-shaped posterior adductor imprint, field of nacre bends down ventrally and runs more or less parallel with ventral nacre-lobe and posterior margin; towards umbo with very thin prismatic shell (around 0.2 mm); shell probably originally stabilised by a layer of internal aragonite; because of dissolution and damage of the anterior end no trace of anterior adductor observable; the marked imprint in the reconstruction (Text-fig. 7A) is adopted from modern pinnids.

OCCURRENCE: Oxfordian of England; Lower to Upper Kimmeridgian of Switzerland; Kimmeridgian of France, Germany and ?Portugal.

REMARKS: J. Sowerby (1822, p. 65, pl. 347) figured a large, somewhat distorted specimen with a length of 8½ inches (= 21.59 cm) and a height of 6 inches (= 15.24 cm). He noted that the anterior side is well inflated, especially along the carina. The species name refers to characteristic granules covering the shell, but details about the ornament were not given by him.



Text-fig. 7. Schematic reconstruction of internal features of right valves of *Stegoconcha*. **A** – *Stegoconcha granulata* (J. Sowerby, 1822), based on the specimens SCR002-52, CLB007-7; **B** – *Stegoconcha obliquata* (Deshayes, 1839); shaded fields dorsal and ventral of the umbonal carina (dotted line) mark imprints observed on internal moulds, which correspond to lobes of internal nacre; anterior adductor scar at the umbo was not preserved (shape adopted from a Recent *Pinna*)

However, deep furrows separating squares with some small pustules are visible on the original figure, on shell fragments close to the shattered posterior margin. The shape of the type somewhat differs from that of the studied material. Its dorsal margin is nearly as long as the ventral margin, but this difference might be explained by the much larger size of the English specimen. Large specimens appear to have grown preferably in a posterodorsal direction, which would lead to a more triangular shape with a greater length compared to smaller specimens, e.g., similar to the specimen of *Stegoconcha thiessingi* (Rollier, 1914) figured by Goldfuss (1837, p. 165, pl. 129, fig. 1) as *Pinna ampla* Sowerby from the Upper Jurassic (Portlandian) of Germany.

Arkell (1933, p. 228, pl. 29, fig. 5) redescribed *S. granulata*, but assigned it erroneously to *Trichites*. He stated that the type figure is barely recognisable, but noted that, after Sowerby's description and a comparison with material from Weymouth, his interpretation of the species is the most plausible one. According to Arkell (1933), *Stegoconcha granulata* occurs in Oxfordian and Kimmeridgian strata in some localities in Britain, including the Weymouth district. There the species occurs in the "*Trigonia clavellata* Beds" (Upper Oxfordian) several metres below the Kimmeridge Clay. He figured a specimen from the "Berkshire Oolite Series" (now Kingston Formation) found in the "Shell-cum-Pebble Bed" of Headington in Oxford, which corresponds well with the investigated material from the Reuchenette Formation in Switzerland. Small differences exist, the average outline of the Swiss specimens is more ham-shaped and the characteristic change of the ornamentation style (radial threads towards granules, followed by branching grooves) appears closer to the umbo in the Swiss material. Such differences are regarded here as being within the range of intraspecific variation.

COMPARISON: *Stegoconcha* is a rare genus with only a few species described. They are often defined on the basis of single specimens by using shape, length/height ratios, inflation and ornament patterns as distinctive characters. Because of the rarity of the taxon, little is known about the intraspecific variability of *Stegoconcha*. Due to their relatively thin and brittle prismatic outer shell, the shells are fragile and tend to shatter when found. Specimens are usually deformed, fragmentarily preserved and difficult to extract from the surrounding matrix. It is therefore not surprising that modern revisions of the majority of *Stegoconcha* species are still lacking. In the following, some of the better known species are briefly introduced in alphabetic order, including some taxonomic remarks.

Mytilus amplus J. Sowerby, 1812 (J. Sowerby 1812, p. 27, pl. 7) – This is so far the oldest known species of the genus. It was originally described from Mitford near Bath (Somerset, England, UK), where according to Cox and Arkell (1948, p. 11) it occurs in the Upper Inferior Oolite (Upper Bajocian). According to these authors the holotype no longer exists. A neotype should be designated from the type locality. However, *Stegoconcha ampla* was misinterpreted by some authors (e.g., Goldfuss 1837, p. 165, pl. 129, fig. 1; Morris and Lycett 1853, p. 31, pl. 14, fig. 4; Thurmann and Etallon 1862, p. 217, pl. 28, fig. 2) and confused with *Stegoconcha granulata* (J. Sowerby, 1822) or *Stegoconcha reticulata* (Rollier, 1914).

Sowerby's figure of the holotype has a similar shape as *S. granulata*, but the ornament differs and consists of numerous radial ribs separated by furrows, covering the complete shell dorsal of the umbonal carina. No granules are present, the ribs undulate to some degree and extend from the umbo to the posterior end.

Pinna cadomensis Bayle, 1878 (Bayle 1878, pl. 117, fig. 1) – This is another Middle Jurassic species of *Stegoconcha*, known from the Bathonian ("Calcaire de Caen") of Caen (Calvados, France). It is similar in shape to *S. granulata*, but has a larger height and thicker shell. In contrast to *S. granulata* the shell surface is nearly smooth and only covered with commarginal growth laminae and a few weak radial furrows at the posterodorsal end of the umbonal carina.

Pinna G.-Mülleri Krenkel, 1910 (Krenkel 1910, p. 203, pl. 21, fig. 3; *Stegoconcha gmuelleri*, nom. corr. by Cox 1965, p. 47) – The species is closely related to *S. ampla* and was first described by Krenkel (1910) from the Lower Cretaceous of East Africa. It is also known from the Upper Oxfordian of Kenya, some Kimmeridgian localities in Tanganyika (see Cox 1965), the Oxfordian of Ethiopia (Kiesling *et al.* 2011) and India (Jaitly *et al.* 1995). Differences in comparison to *S. granulata* are the presence of numerous and strongly developed radial ribs, which cover the whole dorsal surface, and the absence of well-developed granules.

Pinna (*Trichites*) *reticulata* Rollier, 1914 [Rollier 1914, p. 386, pro *Pinna ampla* Sowerby *sensu* Morris and Lycett (1853, p. 31, pl. 4, fig. 14)] – This species is known from the English Great Oolite of Minchinhampton, the "Stonesfield Slate" of Gloucestershire and the Cornbrash of Wiltshire. Rollier (1914, p. 386) chose a new name for *Pinna ampla* of Morris and Lycett (1853). In his opinion, the reticulated shell and its larger size compared to the real *S. ampla* (see Text-fig. 3A for a modified drawing based on J. Sowerby's type figure) separate the two species. However, Cox and Arkell (1948, p. 11), who revised Morris and Lycett (1853), regarded that specimen as *S. ampla* and treated Rollier's name as a subjective junior synonym. Unfortunately, the figured specimen of Morris and Lycett (1853) appears to be lost and the type locality and horizon are uncertain (see revised plate explanations of Cox and Arkell 1948). Herein, the different shape and ornament of *S. reticulata* are regarded as distinct features, which justify a separate species. However, the lectotypes of both species from the Inferior Oolite and Great Oolite need to be revised or neotypes need to be designated. *Stegoconcha reticulata* differs from *S. granulata* by a less stronger inflation, a triangular shape with a rounded posterior end, and by being slightly longer than high. The ornament is not granulated and consists of depressed radial ribs, which are interrupted by growth laminae and flanked by square-shaped pits, giving a reticulated appearance. The sculpture is more regular and the furrows do not bifurcate or radiate along the weakly developed umbonal carina.

Pinna occidentalis Choffat, 1888 (Choffat 1888, p. 66, pl. 12, fig. 4a, b) – This species is known from the Oxfordian and Kimmeridgian (Lusitanian) of Portugal and is closely related to *S. granulata*. Choffat's type is lost and a neotype was designated by Fürsich and Werner (1988, p. 136, pl. 9, fig. 1a, b). The species differs from *Stegoconcha granulata* by having a more strongly inflated and much thicker shell (up to 8 mm). The umbo is blunt and less pointed and the ornament is less strongly developed, consisting of branching grooves including remnants of granules, which are restricted to the posterior end. Fürsich and Werner (1988) included the strong ornamented "*Trichites*" *praealtus* Arkell, 1934 into *S. occidentalis*, but Arkell's type appears to be much more similar to the investigated material of *S. granulata* than to the figured neotype of *S. occidentalis*. It cannot be decided here whether this synonymization was justified or not, but the English specimen is remarkably strongly inflated and has a more blunt apical angle (around 90°) in comparison to *S. granulata*. Fürsich and Werner (1988) suggest a rather strong degree of variation for *S. occidentalis*, whereas the Swiss material appears to be less strongly variable.

Pinna (*Trichites*) *thiessingi* Rollier, 1914 (Rollier 1914, p. 376, pl. 23, fig. 2a, b) – This rare species has been described from the Upper Oxfordian of Montfaucon (Franche-Montagnes, Switzerland) and includes most likely also "*Pinna ampla*" Sowerby as described and figured by Goldfuss (1837, p. 165, pl. 129, fig. 1) from the "Portlandian" of Groß Einsingen in Ulm (Baden-Württemberg, Germany). Goldfuss' specimen was chosen by Rollier (1914, p. 393) as the type for *Pinna* (*Trichites*) *danubiensis* Rollier, 1914. There are no significant differences recognizable between these two Upper Jurassic species and *P. danubiensis* should be treated as a subjective synonym of *S. thiessingi*. Whereas both *Stegoconcha granulata* and *S. thiessingi* share a similar ornamentation, the latter bears anterodorsally more numerous (up to 30) strongly pronounced radial threads. The granulated middle shell part extends over a larger area and the branching grooves are more closely spaced at the posterior end in comparison to *S. granulata*. The main differences include a longer shell (H/L ratio = 0.75), strongly concave, curved anteroventral and dorsal margins and a more elongated anterior end of *S. thiessingi*. The shell is not that strongly inflated (I/L = 0.23, according to the figured type of Rollier 1914, pl. 23, fig. 2a, b), especially anteriorly, and the umbonal carina is far less pronounced. Diedrich (2009, p. 337, fig. 4.1a–c) depicted an internal mould of a large *Stegoconcha* as *Pinna* (*Plesiopinna*) cf. *granulata* J. Sowerby, 1822 from the Upper Kimmeridgian of Bergkirchen (Germany). The specimen shows clearly the previously mentioned chevron-like furrows on the middle shell, which separated the internal nacre lobes. However, the outline of the specimen resembles *S. thiessingi* and it is better placed in the synonymy of that species.

Cardium neptuni Goldfuss, 1837 (Goldfuss 1837, p. 221, pl. 144, fig. 9a) – This Cretaceous species was first described from the Lower Cretaceous (Greensand, Albian?) of Wałbrzych (Waldenburg), Lower Silesia, Poland, and assigned to *Stegoconcha* by Böhm (1907). It is also known from the Cenomanian and Turonian (Wanderer 1909, p. 25, pl. 4, fig. 2) in the neighbourhood of Dresden (Saxony, Germany). *Stegoconcha neptuni* differs distinctly from *S. granulata* by having a greater length and strongly developed radial ribs ventrally of the umbonal carina.

ECOLOGY: All investigated specimens of *Stegoconcha granulata* are complete shells, commonly with a diagenetically deformed ventral margin and, with one exception (VTT001-3978), without traces of attached epifaunal organisms such as oysters, serpulids and bryozoans. Such epizoa commonly covered nearly all larger epibenthic bivalves or any exposed shells in the Reuchenette Formation and their absence indicates a semi-infaunal lifestyle (see Fürsich and Werner 1986, fig. 12). Species of *Stegoconcha* have been reported in life position by various authors with their posterior end exposed and therefore interpreted similarly to their modern equivalents as byssally attached, semi-infaunal suspension-feeding (Fürsich and Werner 1986, 1988) mud-stickers (Seilacher 1984).

Stegoconcha granulata was restricted to fully marine environments and is found in the studied sections commonly together with remains of the infaunal irregular echinoid *Pygurus* Agassiz, 1839. Nearly all specimens were found in mixed fine-/coarse-grained subtidal sediments, in a somewhat protected position close to a high-energy zone. These bioclastic marls and marly limestones, containing numerous small and strongly abraded bioclasts, appear to have been the preferred lithofacies. Layers with *S. granulata* occur usually directly above or below erosional surfaces such as firmgrounds (e.g., Vâ Tche Tcha, horizon 300, and Sur Combe Ronde, horizon 2300–2350) or hardgrounds (Vendlincourt, base of the section) (Text-fig. 2). The occurrence of *Stegoconcha granulata* in the "Shell-cum-Pebble Bed" ("Berkshire Oolite") of Headington near Oxford, England, UK (Arkell 1933) supports this palaeoecological interpretation.

Judging from the taphonomic context (deformation of the thin-shelled ventral area and dorsal margin), the life position of *Stegoconcha granulata* was most likely somewhat oblique in the sediment, with the posterior end exposed and the dorsal margin more or less perpendicular to the sediment surface. At least two-thirds of the shell length including the whole umbonal carina was probably covered by sediment. The presence of a byssal gape indicates that the specimens were anchored with byssus threads, probably to other shells or to an already consolidated sediment. Beds with *Stegoconcha granulata* are usually highly fossiliferous. In horizon 300 in Vâ tche Tchâ several specimens of *Stegoconcha* were discovered by the author during excavations in 2011. This layer is a soft, coarse-bioclastic marl, deposited above a firmground and containing numerous oyster species (Koppka 2015), e.g., *Nanogyra* (*N.*) *nana* (J. Sowerby, 1822) and *Nanogyra* (*Palaeogyra*) *virgula* (Deshayes, 1831), which often show imprints of the calcareous alga *Goniolina geometrica* (F.A. Roemer, 1839). In this layer the usually rare *Stegoconcha granulata* was common and remains of three deformed specimens were found in life position on an area of only 1 m^2.

Stegoconcha obliquata (Deshayes, 1839)

(Text-figs 7B, 8A–D; Pl. 4, Figs A–F)

* 1839. *Pinna obliquata* n. sp.; Deshayes, p. 24, pl. 38, fig. 3.
non 1846. *Pinna obliquata* Deshayes; Leymerie, p. 232, pl. 9, fig. 2 (= *Pinna suprajurensis* d'Orb. = *P. socialis*)
1850. *Pinna obliquata* Deshayes; d'Orbigny, tome 2, p. 19, no. 305.
1855. *Pinna obliquata* d'Orbigny; Cotteau, p. 89.
v 1859. *Pinna obliquata* Desh.; Contejean, pp. 61, 64.

v 1862. *Pinna intermedia*, Et.; Etallon in Thurmann and Etallon, p. 216, pl. 28, fig. 2a, b.
1863. *Pinna intermedia*, Et.; Etallon, p. 439.
1872. *Pinna granulata* Sowerby; de Loriol *et al*., p. 354, pl. 20, figs 2, 3.
1906. *Pinna obliquata* Deshayes, 1850; Péron, p. 144 (176), pl. 7, fig. 6.
1914. *Pinna* (*Trichites*) *pustulata* n. sp.; Rollier, p. 377, pl. 23, fig. 3, 3a.
? 1914. *Pinna* (*Trichites*) *intermedia* Etallon; Rollier, p. 393.
1941. *Trichites pustulata* Rollier; Dechaseaux, p. 47.
1988. *Pinna obliquata* Deshayes, 1839; Fürsich and Werner, p. 136. (species assigned to *Stegoconcha*).

HOLOTYPE: *Pinna obliquata* Deshayes, 1839, p. 24, pl. 38, fig. 3, by monotypy; La Rochelle (after d'Orbigny 1850, p. 19), Department Charente-Maritime, France; Middle Oxfordian, Upper Jurassic; type specimen probably stored in the collection of the "école des mines" in Paris (Péron 1906, p. 145).

MATERIAL: A large specimen from Bois de Sylleux (BSY009-664) near Courtedoux (Canton Jura), damaged on both ends (Pl. 4, Figs A–C). The loose specimen was found among dumped material excavated from the topmost layers during the construction of the A16 highway. The lithology refers to a horizon of dense white limestones (beds 6000–7000), which occur *c*. 2–3 m above the Lower *Virgula*-Marl, *Eudoxus* Biozone, Upper Kimmeridgian.

In the MJSN, two syntypes of *Pinna intermedia* Etallon in Thurmann and Etallon, 1862 have been traced by the author. One of them is labeled as the holotype (O 221, A.4.17.4.4) and was found in the Combe Franois near Porrentruy (exact position of the site unsure), in a pure and dense white limestone of the "Virgulien supérieur", Upper Kimmeridgian (*A. eudoxus* Biozone). Another specimen (S360, A.2.21.5.5) determined as *Trichites intermedia* Etallon was found in a dense grey limestone at Petite-Hollande (south of Montbéliard, France). The original label of Thurmann is preserved and refers to the "Astartien supérieur" (Upper Oxfordian). Additional material in the MJSN from the Scheurer collection includes a well preserved specimen (FS167, A.5.14.104; Pl. 4, Figs D–F) from La Baume near Montbéliard (Department Doubs), France. It was found in the "Calcaire à *Corbis*" (soft and porous white limestones) of the upper Lower Kimmeridgian (*R. cymodoce* or *A. mutabilis* Biozone). An additional, yet damaged specimen (FS532, A.5.14.2.02) with shell remains is from the Upper Kimmeridgian ("Virgulien inférieur", *A. eudoxus* Biozone) of Audincourt.

Measurements in brackets refer to incomplete specimens and indicate estimated values based on reconstructed shapes.

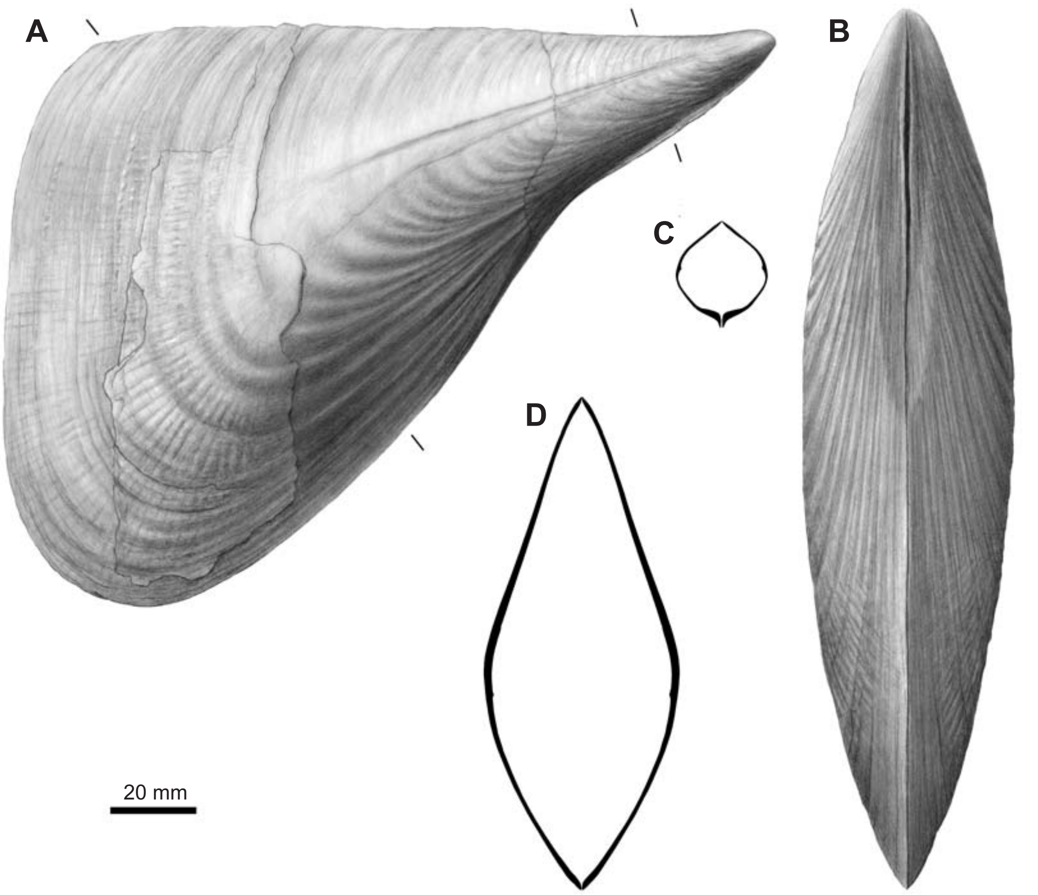
Dimensions (in cm):

Specimen	H	L	I	H/L	α
BSY009-664	(13.3)	(18.3)	2.25	0.73	43°
MJSN S 360	6.1	(11.5)	1.67	0.53	36°
MJSN O221	(8.3)	(13.5)	1.8	0.61	37°
MJSN FS167	11.8	14.5	2.13	0.81	38°
MJSN FS532	(11.0)	(13.0)	2.05	0.85	44°

DESCRIPTION: **Shape, size** – Equivalve, large, mytiliform to cuneate (wedge-shaped); length exceeding height; umbones terminal, remarkably elongated and pointed; apical angle between 36° and 44°; inflation weak to modest, most vaulted midway of shell length and slightly ventral of posteroventrally curved umbonal carina, running parallel to anteroventral margin and bending ventrally at 8 cm from umbo, becoming weaker and fading towards the posteroventral angle (Text-fig. 8); dorsal margin long and nearly perfectly straight, only slightly concave close to umbo; posterodorsal angle round and measuring between 90° and 110°; posterior margin mesially nearly straight but weakly convex towards dorsal and ventral margins; posteroventral angle of *c*. 70° broadly rounded; posteroventral margin slightly convex and grading into concave anteroventral margin, corresponding in length with well-defined lunule-like byssal collar (Text-fig. 8B), which reinforces a narrow byssal gape; ventral flank below umbonal carina relatively broad and gently curved towards ventral margin; most of shell very thin, usually < 1 mm (max. 2 mm), and particularly thin (0.5 mm or less) close to the umbo and towards the ventral and dorsal margins; thickest shell on lateral surface dorsal of umbonal carina and along thickened edge of concave anteroventral margin (Text-fig. 8D).

Sculpture – Flank of anterior half with prominent commarginal growth folds, which fade towards posterodorsal margin and disappear dorsally, grading into commarginal growth lines; with some irregularly spaced commarginal furrows towards the posterior end, partly accentuated by diagenetic compression; weak branching grooves separating *c*. 17 broad and low ribs, which are developed between the posteroventral margin and umbonal carina, fading in dorsal direction; commarginal aligned rows of poorly defined granules present but sparse on posterodorsal shell.

Internal shell characters – With straight internal median ridge (furrow on internal moulds) in the



Text-fig. 8. *Stegoconcha obliquata* (Deshayes, 1839). Reconstruction of internal mould with posterior shell remains, based on BSY009-664, MJSN FS167 (Kimmeridgian, Reuchenette Formation) and MJSN S360 (Upper Oxfordian, Vabenau Formation); A – lateral view of right valve; B – anteroventral view, with narrow byssal gape; C – virtual cross-section close to umbo; D – cross-section between posterodorsal angle and ventral margin

anterior third of shell, fading towards the umbo; median furrow branching after 5 cm into two narrow furrows (internal ridges) (Text-fig. 7B; Pl. 4, Figs A, D) divided by an angle of 8° and defining the dorsal and ventral limits of two lobes of former nacre; these lobes occupied half of shell length; dorsal lobe with ill-defined but relatively large posterior adductor imprint, situated at half length close to the dorsal margin (Text-fig. 7B); outer shell calcitic and of simple prismatic structure; internal nacre originally present but now dissolved; posterior parts of lobes with faint commarginal growth lines.

REMARKS: Deshayes (1839) figured a simple drawing of *Pinna obliquata* and gave no description or any further information about the age and the type locality of the figured type specimen. D'Orbigny (1850, p. 19) was the first who supplied additional information. According to him the species was found in the "Corallien" (= Rauracien, Middle Oxfordian) of La Rochelle (Department Charente-Maritime, France). Péron (1906) noted the presence of Deshayes' type specimen in the collection of the "écoles des mines" in Paris but did not provide a collection number. He further mentioned that the material of *Pinna obliquata* Deshayes, 1839 determined by d'Orbigny (1850) belongs to the same species. *Pinna obliquata* Deshayes, 1839 was assigned to *Stegoconcha* by Fürsich and Werner (1988, p. 136), a view shared herein. The outline of this species is somewhat unusual for the normally ham-shaped genus *Stegoconcha* and more similar to that of the Recent species of *Pinna* or *Atrina*. However, the ventrally curved umbonal carina, the ornamentation of branching grooves and the sparse granules as characteristic of *Stegoconcha* and two diverging lobes of internal nacre confirm the correct assignment to the genus. The species was probably ancestral to the Cretaceous genus *Plesiopinna* (type species *Plesiopinna atriniformis* Amano, 1956, p. 70), which was regarded by Cox and Hertlein (1969, *N*283) as a subgenus of *Pinna*. This point of view appears to be unlikely in a phylogenetic sense. Species of *Pinna* and *Atrina* were present in Jurassic times and exist until today with little morphological change. Therefore, using *Plesiopinna* as a subgenus of *Pinna* would make the latter paraphyletic.

Two species have been included by the author in the synonymy of *S. obliquata*. The first is *Pinna intermedia* Etallon in Thurmann and Etallon, 1862, which was erroneously assigned to *Trichites* by Arkell (1933). Syntypes of *P. intermedia* have been studied by the author in the Jurassica Museum, Porrentruy. They are very similar to the drawing of Deshayes' *Pinna obliquata* and agree well with the material described and figured by Péron (1906) from the Oxfordian and Kimmeridgian of France and the material used in this study. It has to be noted that the figure of Thurmann and Etallon (1862) in the "Lethaea bruntrutana" is misleading and obviously was based on an artificial combination of both syntypes, mixing details of the left and right valves in one figure.

Another species most likely synonymous with *S. obliquata* is *Pinna* (*Trichites*) *pustulata* Rollier, 1914 (Rollier 1914, p. 377, pl. 23, fig. 3, 3a) from the Middle Sequanien (Vellerat Formation, Middle Oxfordian) of Petites Crosette near La Chaux-de-Fonds (Canton Neuchâtel, Switzerland). The anteriorly strongly compressed type specimen when undeformed would be nearly identical in outline and inflation with the observed Kimmeridgian material of *S. obliquata*. Some differences are especially noteworthy. For instance, the ornamentation on the *pustulata* specimen is more elaborate, with well-developed branching grooves and granules on its posterior end. The anterodorsal flank above the carina is covered by numerous radial threads, which are completely missing on the observed material of *S. obliquata*. It is possible that Rollier's species is an early representative of *S. obliquata*, showing a probably neotenic morphological change that may have lead from *S. granulata* to *S. obliquata*.

COMPARISON: *Stegoconcha obliquata* is relatively isolated compared to other species of the genus. The elongated and rather *Pinna*-like appearance with a comparatively smooth shell, where weakly developed radial furrows, ribs and granules occur only toward the posterior end of adult specimens, are unique as for a *Stegoconcha*. The species is probably a grade taxon, which may have evolved during the Early Cretaceous into a species of *Plesiopinna*. Species of that genus are mesially inflated, have a posteroventrally curved umbonal carina (see Griffin *et al*. 2008, p. 146) and a concave anteroventral margin, which is characteristic also of *Stegoconcha*. The main difference appears to be the style of ornamentation in *Plesiopinna*, with rounded radial ribs separated by broad interspaces, which are only present dorsally on the umbonal carina. Granules, deeply incised and branching radial furrows or distinct commarginal growth folds, which are characteristic of *Stegoconcha*, are not present.

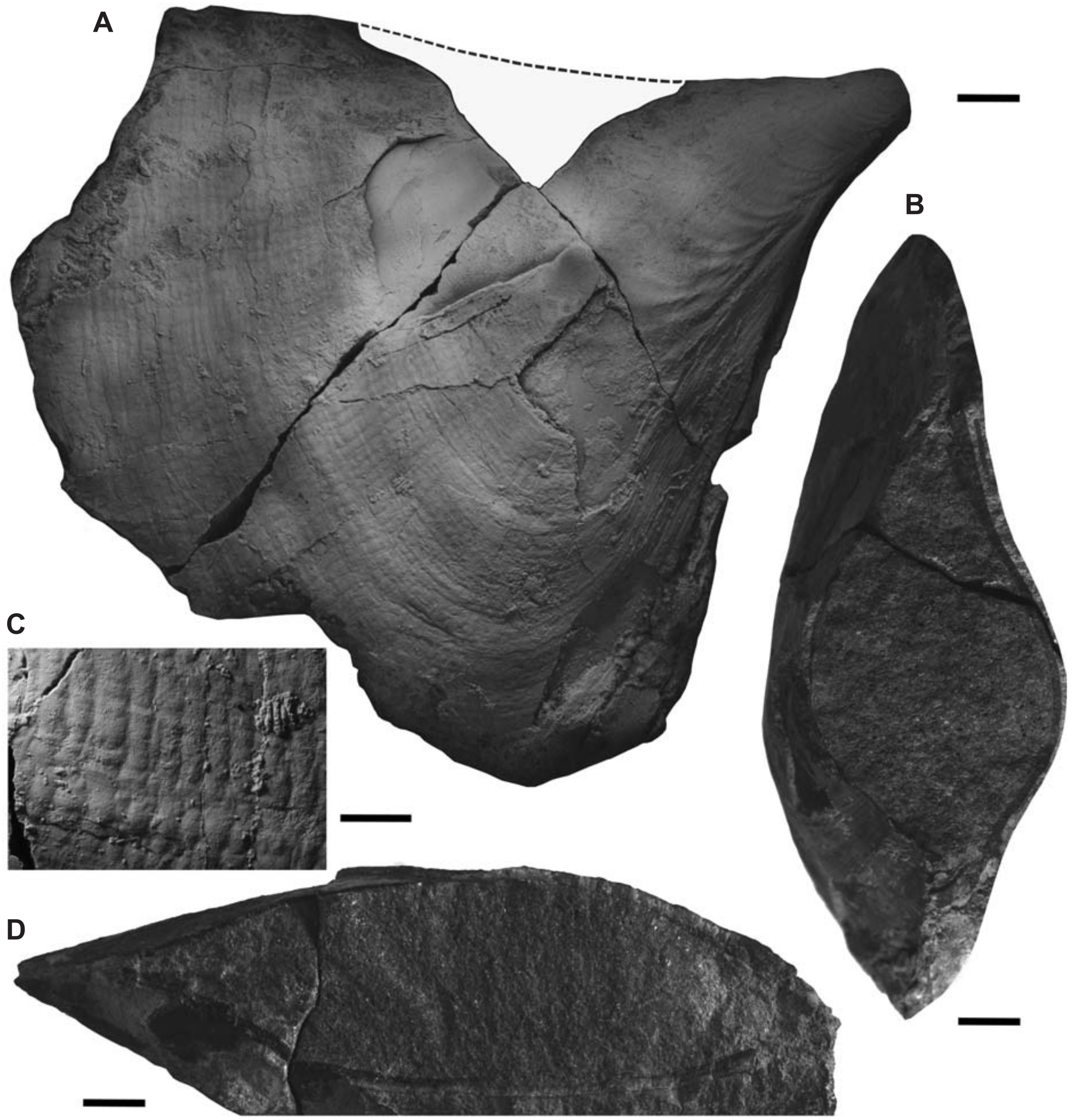
Because of the unique morphology of *S. obliquata*, this comparison includes also similar species of *Plesiopinna*, which are discussed below in alphabetic order.

Pinna (*Plesiopinna*) *atriniformis* Amano, 1956 (Amano 1956, p. 71, pl. 1, figs 1–5) – The type species of *Plesiopinna* from the Upper Cretaceous Gosyonoura Group (Albian?–Cenomanian) of Japan is known from Shishi-jima, one of the Amakusa islands in the Kumamoto Prefecture. Its shape, inflation and the position of its umbonal carina is nearly identical to *S. obliquata*. However, the dorsal margin of *P. atriniformis* is less straight in comparison, and the presence of broad, rounded radial ribs on its posterodorsal shell and the absence of granules and grooves are the main differences.

Pinna granulata J. Sowerby, 1822 (J. Sowerby 1822, p. 65, pl. 347) – The type species of *Stegoconcha* is much more gibbose and normally higher than long as compared to *S. obliquata*. It differs also by having a distinctly stronger ornamentation of radial threads, granules and branching grooves. Its pronounced umbonal carina is situated more ventrally, its apical angle is blunt and therefore the umbo is less pointed. The space between the two internal ridges is wider and the place of the posterior adductor imprint is closer to the carina than to the dorsal margin (Text-fig. 7A).

Plesiopinna pampeana Griffin, Parras and Casadio, 2008 (Griffin *et al*. 2008, p. 146, text-fig. 4: 3–6) – This species has been described from the Upper Maastrichtian Jagüel Formation of Barda Baya (La Pampa Province, Argentina). It differs from *S. obliquata* in having a wider apical angle, a stronger inflation and the presence of numerous anterordorsally rounded ribs. These are separated by broad intercostal spaces, become broader posteriorly, and vanish towards the posterior end. No branching furrows or granules are present.

Trichites plotii Arkell, 1933 (Arkell 1933, p. 225; 1934, pl. 30, figs 1, 2) – When Arkell (1933) revised *Trichites plotii* Lhyud, 1699, he was un-



Text-fig. 9. *Stegoconcha plotii* (Arkell, 1933). FPJ 21621, Lower Callovian (Ifenthal Formation, Châtillon Member) of the "Tunnel de Choindez" (A 16), Switzerland, A – RV lateral view, chevron-shaped furrow of middle part of shell covered by matrix and outer shell, B – dorsoventral cross-section, C – magnified portion of posterior shell surface, D – longitudinal cross-section, anterior on the left. Scale bars equal to 5 mm (C) and 10 mm (A, B, D)

aware of *Stegoconcha* Böhm, 1907 and erroneously based his concept of *T. plotii* on a large specimen of *Stegoconcha*. A thick fragment of a *Trichites* shell was originally figured by Plot (1677 p. 129, pl. 7, fig. 7) and thought to be conspecific by Arkell (1934, pl. 30, fig. 1). The species is based on that small fragment and was named without a description by Lhuyd (1699) as *Trichites plotii*. However, this pre-Linnaean species was never formally described, and was misinterpreted when treated by Arkell (1933). The several-cm-thick shell fragment is way too thick-shelled for any *Stegoconcha* and might belong to a species similar or identical with *Trichites giganteus* Quenstedt, 1857. The large mytiliform specimen, described and figured by Arkell (1933, p. 225; 1934, pl. 30, fig. 1) is from the Middle Oxfordian of the Coralline

Oolite Formation, Malton Oolite Member of Malton, Yorkshire (housed in the Yorkshire Museum) and is here chosen as the lectotype of *Stegoconcha plotii* (Arkell, 1933). *Trichites plotii* Lhyud remains an invalid pre-Linnaean species and a nomen dubium. The true nature of *S. plotii* was first observed by Kelly (1984) and is reasserted herein based on the new find of a single well-preserved specimen from the Swiss Callovian (FPJ 21621, Text-fig. 9). It was found in the debris that was removed during the construction of the "Tunnel de Choindez" at Courrendlin (A 16, Canton Jura, Switzerland) in Lower Callovian iron-oolitic, bioclastic mudstones ("*Macrocephalites* beds", Châtillon Member) and was later prepared by the author. It is smaller and somewhat older than the English specimen but shows the characteristic triangular shape and the radial ornament. Notable differences with *S. obliquata* are a shorter anterior end with a wider umbonal angle of 60° and a much more pronounced sculpture, consisting of weak anterior radial ribs that become broader posteriorly and grade into a more rectangular pattern when crossed by commarginal furrows (Text-fig. 9).

Stegoconcha aff. *plotii* (Lhyud) *sensu* Kelly, 1984 (Kelly 1984, p. 38, fig. 25; non *Trichites plotii* Lhyud, 1699, Oxfordian of Bullingdon near Shotover, England; see Arkell 1933, p. 225 and 1934, pl. 30, figs 1, 2) – This interesting specimen was briefly described by Kelly (1984) from the *Peregrinoceras albidum* Biozone (Ryazanian, Lower Cretaceous) of Hundon Manor near Caistor in Lincolnshire, England, UK. Kelly's specimen is not directly related to *S. plotii* (Arkell, 1933), but shows a strong similarity to *S. obliquata*. Unfortunately, Kelly (1984) depicted his specimen only as a simplified sketch, rendering a direct comparison difficult. However, compared to *S. obliquata*, the English specimen is somewhat larger, measuring 25 cm in length. It is ventrally more concave and has a broad, nearly blunt posteroventral margin. The main difference are *c.* 20 broad, low undulating radial ribs, which cover the dorsal flank.

ECOLOGY: Most of the Kimmeridgian material of *Stegoconcha obliquata* (including fragments) occurs in hard, dense, grey or white, micritic limestones and in horizons that contain relatively few macrofossils. Also, Péron (1906) reported finds of this species from a comparable facies, e.g., white limestones of the Sequanian (Upper Oxfordian). Somewhat different is the occurrence in relatively soft, fine-grained, bioclastic and porous white limestones of the "Calcaires à *Corbis*", known so far only from the Kimmeridgian of the Montbéliard region.

At Sur Combe Ronde, in 2011 the author had the chance to observe the white limestone sequence (horizons 6000–6500) above the "Lower Virgula Marls", which rarely yield remains of *S. obliquata*. Small associated bivalves representing *Nicaniella* Chavan, 1945, *Mesomiltha* Chavan, 1938, *Protocardia* Beyrich, 1845 and *Ceratomyopsis* Cossmann, 1915 are the most common endobenthic taxa. Among the epibentic components, numerous, mostly tiny specimens of *Nanogyra virgula* (Deshayes, 1839) and small specimens of *Gervillella* Waagen, 1907 prevail. Furthermore, few small-sized specimens of *Chlamys textoria* Schlotheim, 1820 have been found. Small fragments of *Stegoconcha* were discovered, together with the scarcity of articulated bivalves indicating reworking and transport of the material. Some layers with mass accumulations of small bivalve shells suggest an occasionally storm-influenced environment in the shallow subtidal zone of a large carbonate platform. Associated below and above are hard- and firmgrounds together with a stromatolite layer. Also the following "Coral limestone" facies agrees well with its interpretation as a shallow-marine environment.

In conclusion, the preferred environment appears to have been represented by sparsely populated white lime muds or bioclastic carbonate sands, deposited under a relatively high accumulation rate. The elongated shape of *S. obliquata* might be an adaptation to this environment. The umbo, including the byssus threads, would be deeper within the sediment compared with other species, allowing for the exposure of a relatively larger area of the posterior end before the shell became instable. Strong currents during storms could be expected in a shallow-marine environment. The lack of any clay particles in the white carbonates might speak for a central position on a relatively large carbonate platform, where siliciclastic input from the basin or terrestrial environments was absent.

CONCLUSIONS

The study provides a review of three Upper Jurassic species of the Pinnidae [*Pinna* (*Cyrtopinna*) *socialis*, *Stegoconcha granulata* and *S. obliquata*], all of which were found in the Reuchenette Formation (Kimmeridgian) of northwestern Switzerland and adjacent France.

One main result of the study is the exclusion of *Trichites* from the Pinnidae. The internal morphology of these thick-shelled bivalves differs dramatically, suggesting that the genus is not closely related to the Pinnidae.

Jurassic pinnids have been classified previously as either *Stegoconcha* or more commonly as *Pinna*, with all species belonging to the subgenus *Pinna* (*Pinna*). This study introduces *Pinna* (*Cyrtopinna*) *socialis* as the first Jurassic species assigned to *Cyrtopinna*. Several species (*Pinna banneiana, P. bannesiana*, *P. quadrata*, *P. sandfootensis*, and *P. romanikhae*) have been included by the author into the synonymy of *P.* (*C.*) *socialis*. These species are poorly known and require additional taxonomic work to show that the synonymization was justified or if a higher diversity may be present.

The majority of Jurassic *Pinna* species share a morphology that is rather different from Recent members of the genus. When preserved uncompacted, the Jurassic species usually have a rhomboidal or even quadrate transverse section and never any spines or long, arched scales. Most species are relatively narrow and therefore often lanceolate in shape. The median carina is usually prominent and developed over most of the adult shell length, dividing the shell into a dorsal and ventral flank, which differ in sculpture (radial threads dorsally, commarginal growth folds ventrally and there rarely crossed by radial elements). However, further investigation is required to establish whether Jurassic species of *Pinna* really belong to the subgenus *Pinna* (*Pinna*) and exactly when the first true *Pinna* evolved.

The poorly known genus *Stegoconcha* is revised and all of the so-far traced species (including Cretaceous and Paleogene taxa) are briefly introduced and discussed. The range of *Stegoconcha* is revised here to be from the Middle Jurassic (Bajocian) to the Paleogene. Two species groups are recognised within the genus, with one group close to the type species *Stegoconcha granulata* and with its species characterized by deep radial furrows with wide interspaces, crossed by concentric furrows and growth folds, and with rows of pustules covering particularly the posterodorsal shell. A second group comprises radially ribbed species related to the Cretaceous *S. neptuni*. The ribbing pattern changes over time. Early species, such as *S. ampla* and *S. gmuelleri*, bear dense radial ribs, which do not extend beyond the dorsal side of the umbonal carina. Younger species from the Cretaceous and Paleogene have fewer but more prominent radial ribs, which are also present on the ventral flank. The observed species of *Stegoconcha* show a clear facies dependence and occur therefore only in few horizons of the Reuchenette Formation, namely in bioclastic marls and pure white limestones deposited under shallow-marine conditions.

The present paper suggests a close relation between the Cretaceous *Plesiopinna* and *Stegoconcha*. The strongly elongated and relatively little inflated *S. obliquata* is seen here as an intermediate species, showing characteristic features of both genera. Heterochrony may be a likely explanation for the shape change, including the loss of the radial sculpture. A relatively smooth and rather elongated umbonal region is known from species of the *S. granulata* group and morphological changes due to neotenic development appear likely, leading to *Plesiopinna* during the Early Cretaceous. Further studies are necessary to prove this assumption, but if true, the current assignment of *Plesiopinna* as a subgenus of *Pinna* as recently suggested by Schulz and Huber (2013) would result in a paraphyletic status of the genus *Pinna*.

The observation of narrow, chevron-shaped furrows near to the centre on internal moulds of *S. granulata* and *S. obliquata* suggests the presence of divided nacre lobes (Text-fig. 7; Plate 2, Fig. D; Plate 4, Figs A, D). In contrast, an anteriorly situated transverse section of a specimen of *S. plotii* with preserved but recrystallised internal aragonite revealed a thick and continuous layer of former nacre (Text-fig. 9B), crossing the shell centre undivided. On this specimen, divided nacre lobes were present, but only in the posterior part of the shell. The dissolution of nacre in the Kimmeridgian material revealed a hidden median keel, restricted to the inner side of the simple prismatic calcite layer (causing the observed imprints on the internal moulds). However, better preserved material is needed to clarify the internal shell morphology. While the origin of *Stegoconcha* is still unknown, the oldest species *S. ampla* appears to have migrated into Europe during the Bajocian (Middle Jurassic). Even though older species have not been found in Europe, deposits elsewhere may eventually reveal additional information on the origin of this genus. The Middle Jurassic species *Stegoconcha*? *stoliczkai* from India was regarded by Cox (1940) as a possible early species of *Atrina*, but the sculpture of its densely ribbed and elongated shell appears also similar to *Stegoconcha* even though its outline differs from the usual ham-shape. An early species of *Atrina* is *Atrina sinuata*, described from the Middle Triassic of Nevada (USA). Waller and Stanley (2005) proposed that non-carinate, ham-shaped pinnids with a wide umbilical angle and no separation of the internal nacreous layer belong to *Atrina*. Comparable species in the Lower Jurassic should be present and would be highly interesting as possible ancestors of *Stegoconcha*.

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PLATE 1

Pinna (*Cyrtopinna*) *socialis* (d'Orbigny, 1850) from the Upper Jurassic of Switzerland and France. **A**, **B** – ECO009-25, Banné Marls, *R. cymodoce* Zone of Vendlincourt-Ecorchevez quarry (Canton Jura, Switzerland), A, LV lateral view, internal mould, B, both valves ventral view, with distinct byssal gape; **C** – lectotype (designated herein), MNHN-F-R09004, LV (bivalved specimen), Kimmeridgian of Châtelaillon-Plage (Department Charente-Maritime, France); **D** – MJSN S 412a, LV lateral view, Banné Marls of the Banné hill in Porrentruy (JU, CH), coll. Thurmann; **E** – MJSN S 412b, LV lateral view, locality same as for D; **F** – MJSN unnumbered, LV lateral view, Banné Marls (horizon 800) of Vâ Tche Tchâ near Courtedoux (JU, CH), coll. Hicks & Richardt/Erlangen (presently housed in MJSN); **G**, **H**, **M** – SCR011-1168, *A. mutabilis* Zone (*O. schilleri* horizon) of Sur Combe Ronde near Courtedoux (JU, CH), **G** – LV lateral view, **H** – both valves anterior view, **M** – shell detail of LV; **I** – VTT006-637, Banné Marls (horizon 800) of Vâ Tche Tchâ (JU, CH), RV lateral view; **J-K** – VTT001-7, Banné Marls of Vâ Tche Tchâ (JU, CH), **J** – RV lateral view; **K** – posterior view (LV up), **L** – shell detail of RV. Scale bar equals to 10 mm

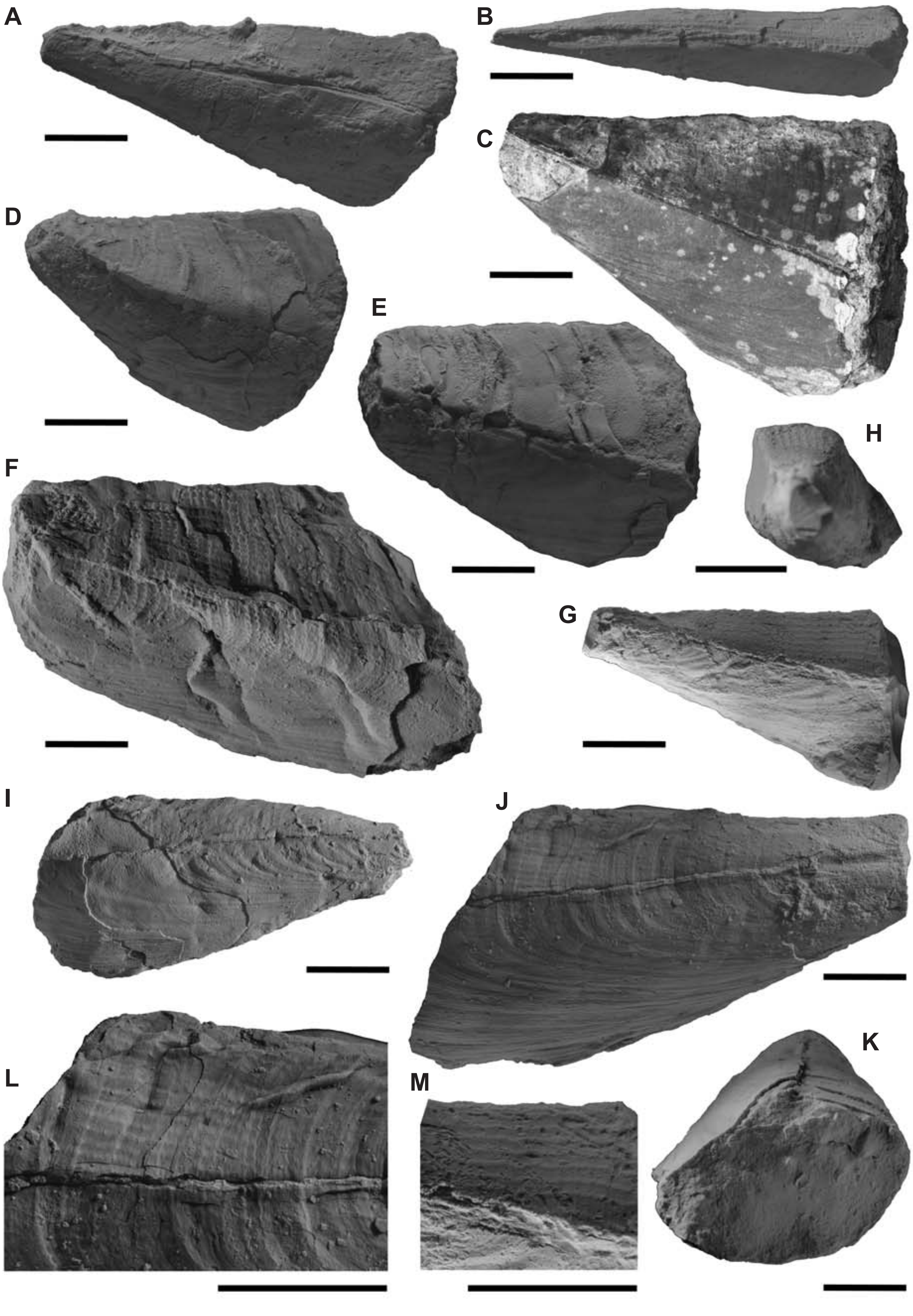
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PLATE 2

Stegoconcha granulata (J. Sowerby, 1822) from the Banné Marls of the Reuchenette Formation, *R. cymodoce* Zone, Lower Kimmeridgian, Switzerland. **A-C** – TLB001-210, Tunnel le Banné at Porrentruy (JU, CH), complete bivalved specimen, partially exfoliated, dorsal margin deformed, A – LV lateral view, B – anterior view (ventral side up), C – sculpture of LV; **D-F** – ECO009-29, Banné Marls (bed 170), Vendlincourt-Ecorchevez (JU, CH), semicomplete specimen, internal mould with few shell remains, D – RV lateral view, E – LV lateral view, F – anterior view (LV up). Scale bars equal to 10 mm

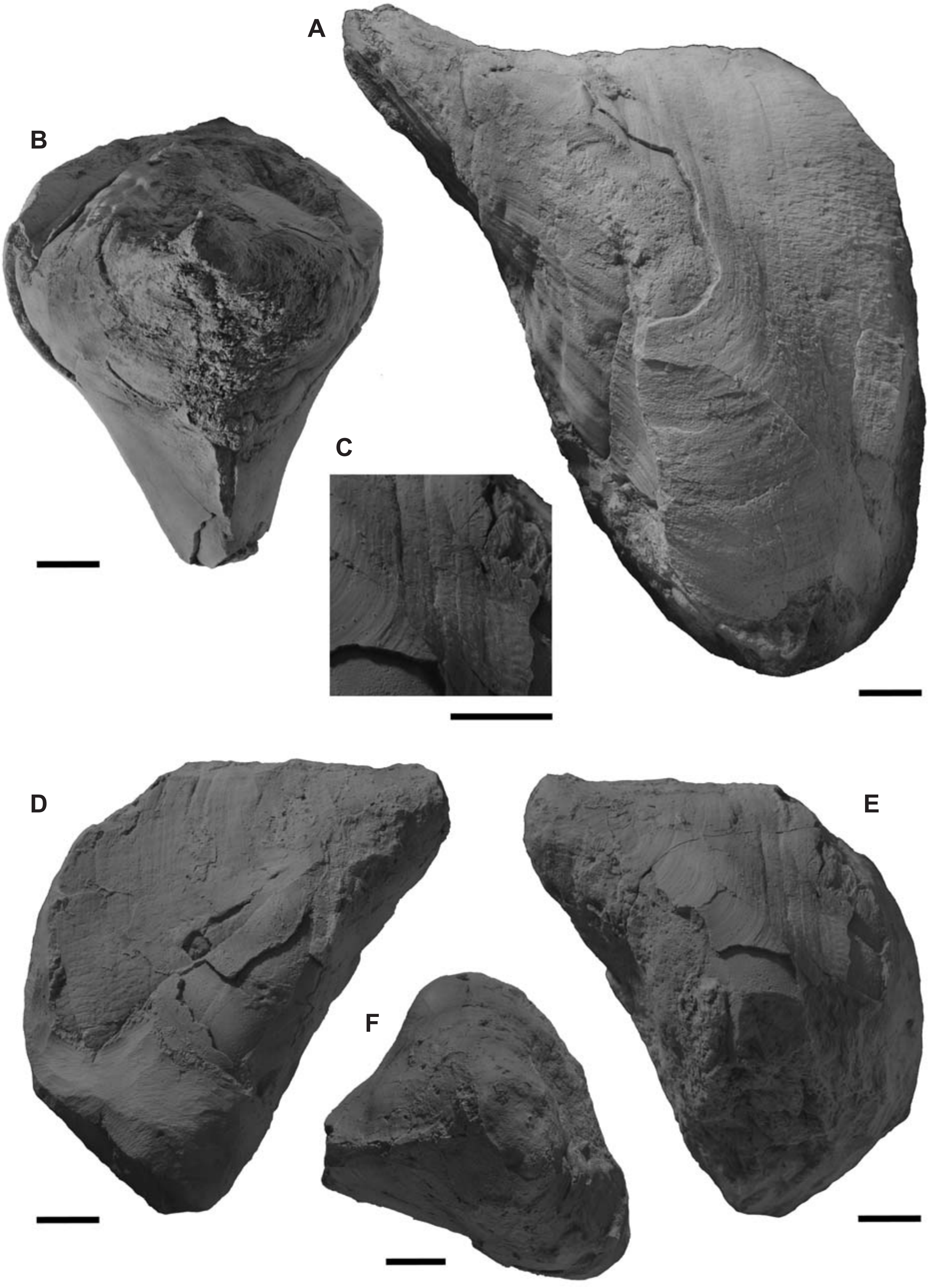

A
B
C
D
E
F

PLATE 3

Stegoconcha granulata (J. Sowerby, 1822), VTT011-99, bed 300, Banné Marls, *R. cymodoce* Zone of Vâ Tche Tchâ (CH), Lower Kimmeridgian, Reuchenette Formation. A – RV lateral view; B – magnified portion of RV, 2x; C – both valves anterior view; D – ventral view, shell strongly compressed. Scale bars equal to 10 mm

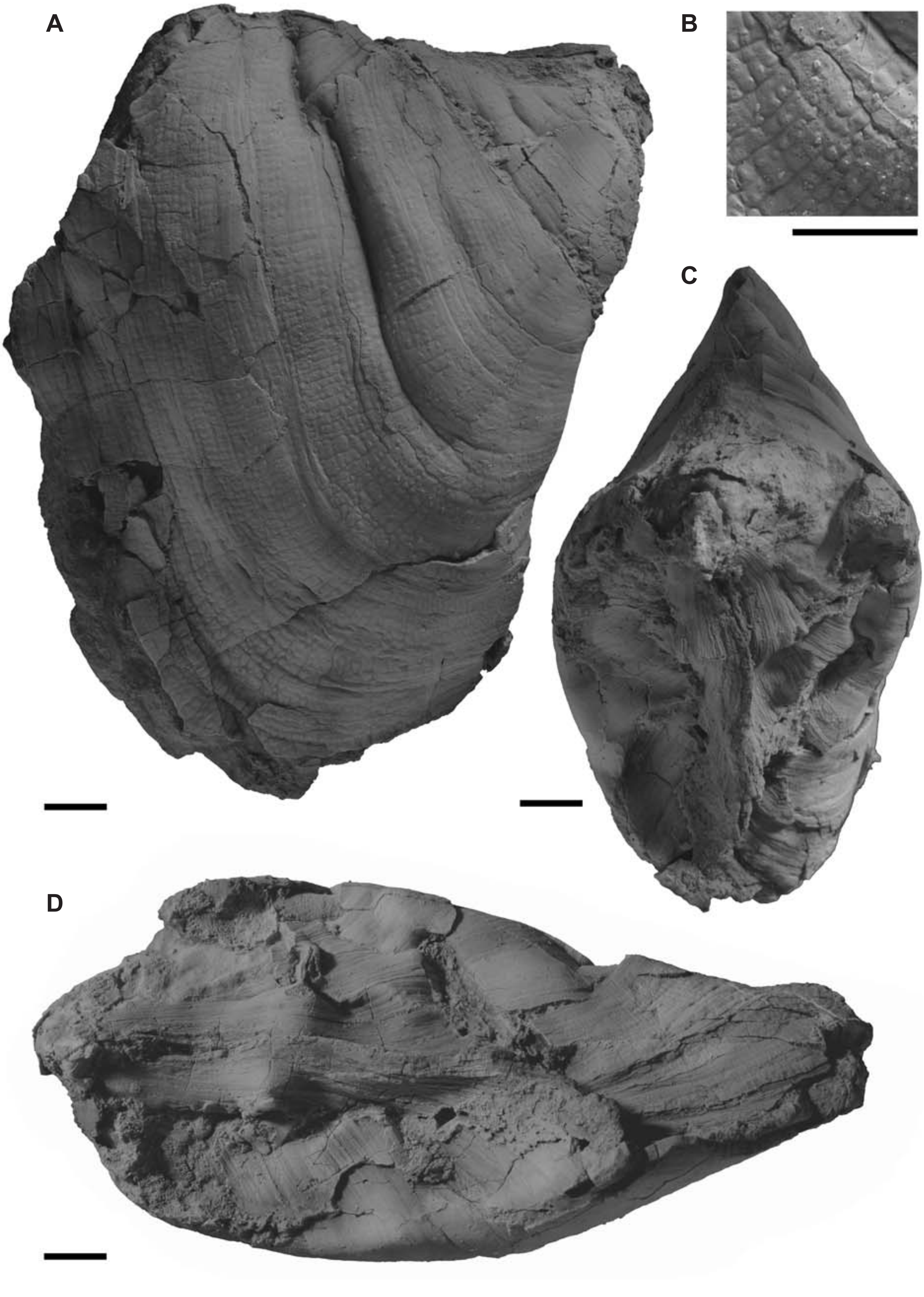
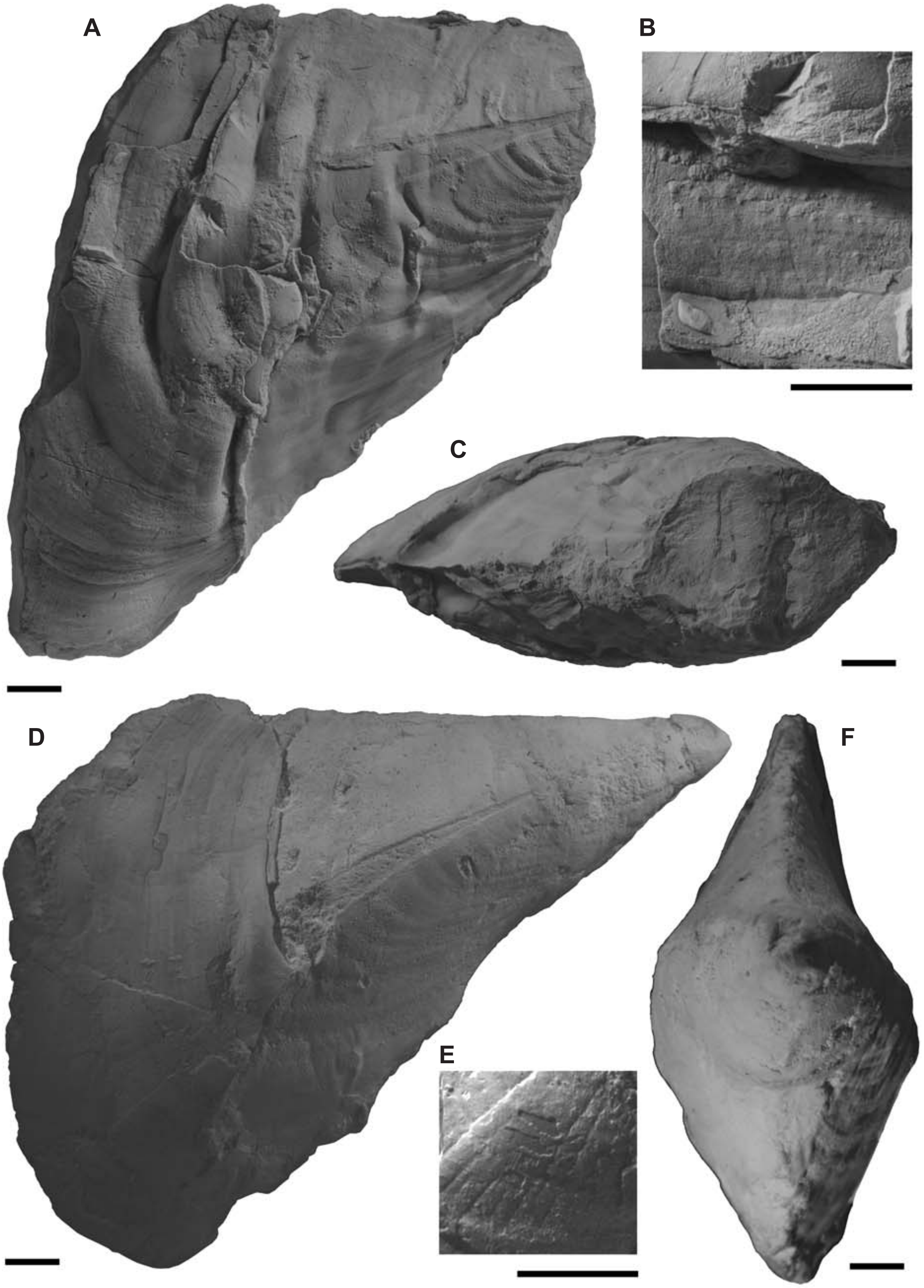

A
B
C
D

PLATE 4

Stegoconcha obliquata (Deshyes, 1839), Kimmeridgian of France and Switzerland. **A-C** − BSY009-664, bed 6500, Chevenez Member, *A. eudoxus* Zone, upper Kimmeridgian of Bois de Sylleux near Courtedoux (JU, CH); A − RV lateral view, B − magnified shell portion close to posterior end, C − anterior view (RV up, dorsal margin on the right); **D-F** – MJSN FS167, “Calcaire à *Corbis*”, *A. mutabilis* Zone of La Baume near Montbéliard (Department Doubs, France), D − RV lateral view; E − shell details close to posteroventral margin; F − anterior view. Scale bars equal to 10 mm


A
B
C
D
E
F