

AN INSIGHT INTO THE SYSTEMATICS OF PLICATOSTYLIDAE (BIVALVIA), WITH A DESCRIPTION OF *PACHYGERVILLIA ANGUILLAENSIS* N. GEN. N. SP. FROM THE LITHIOTIS FACIES (LOWER JURASSIC) OF ITALY

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Abstract. The *Lithiotis* facies represents an Early Jurassic global bioevent characterized by a remarkable spread of gregarious bivalves, which produced large sedimentary bodies in tropical shallow-water marine environments. The most peculiar and common genera *Lithiotis*, *Cochlearites* and *Lithioperna*, with aberrant and extremely elongated or strongly flattened shells, have been studied since the second half of the nineteenth century. Despite numerous systematic studies, their phylogenetic relationship with the other bivalve families is still uncertain. The *Lithiotis* facies yields other bivalve genera, among which a large multivincular mytiloid, provisionally determined as *Isognomon* (*Mytiloperna*) sp. ind. or *Mytiloperna* sp., is recorded in the literature. This taxon is here studied from a systematic point of view to clarify its taxonomic position and solve the open nomenclature adopted in the past. Here, we propose a new genus *Pachygervillia* and a new species *Pachygervillia anguillaensis*. The stratotype is located in the lower part of the Rotzo Formation (Calcarei Grigi Group, Lower Jurassic), while the type locality is in the Lessini Mountains (Verona Province, Trento Platform, Southern Alps). This new species is characterized by a thick aragonitic inner shell layer with a fibrous, irregular, spherulitic, prismatic microstructure combined with a nacreous middle layer, both also occurring in species of the genera *Lithiotis* and *Cochlearites* of the family Plicatostylidae. This microstructural layering is here proposed as the main taxonomic character of the family, which is here emended and divided into the following two subfamilies: Plicatostyliinae, yielding *Lithiotis* and *Cochlearites* with stick-like shells, and Pachygervilliinae nov. subfam., yielding *Ger-villeioperna*, *Lithioperna*, *Pachygervillia* n. gen., and *Pachyperna*, previously placed within the subfamily Isognomoninae.

INTRODUCTION

The Early Jurassic is characterized by a remarkable spread of gregarious bivalves with large and thick shells that proliferated in the tropical shallow-water marine environments of the Tethyan and Panthalassan coasts. This global bioevent is

recorded by thick shell accumulations which produced large sedimentary bodies of the *Lithiotis* facies (e.g., De Castro 1962; Bosellini 1972; Nauss & Smith 1988; Buser & Debeljak 1995; Leinfelder et al. 2002; Fraser et al. 2004; Posenato & Masetti 2012; Posenato et al. 2018; Brame et al. 2019). The most common and peculiar bivalves of this facies are three aberrant pterioid genera known as lithiotids: *Lithiotis*, *Cochlearites* and *Lithioperna*, which have

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been studied from systematic and paleobiological points of view by several authors (e.g., Accorsi Benini & Broglio Loriga 1977; Accorsi Benini 1979; Chinzei 1982; Posenato et al. 2022 with references therein). These genera are mostly restricted to the Pliensbachian and disappeared at the onset of the early Toarcian oceanic anoxic event (e.g., Fraser et al. 2004; Posenato et al. 2018).

The *Lithiotis* facies contains other gregarious and rock-forming bivalves such as the pteriods *Gervilleioperna* and *Mytiloperna*, the myalinid *Pseudopachymytilus*, the carditid *Opisoma*, and the megalodontids *Pachymegalodon* and *Protodicerus*. Among these genera, only *Opisoma* has been recently analyzed from systematic (Accorsi Benini 1981) and morpho-functional (Posenato et al. 2013) points of view, while only preliminary data have been published on the microstructures of the other taxa (Benini & Loriga 1974; Accorsi Benini 1980; Accorsi Benini & Broglio Loriga 1982). Among the above-cited genera, only specimens from the *Lithiotis* facies referred to *Mytiloperna* were not attributed to a species. Indeed, these specimens were determined by Benini & Loriga (1974) and Accorsi Benini & Broglio Loriga (1982) in open nomenclature as *Isognomon* (*Mytiloperna*) sp. ind. or by Broglio Loriga & Posenato (1996) as *Mytiloperna* sp. This taxon has been recovered from the Southern Apennines (Posenato et al. 2018) and Morocco (Fraser et al. 2004; Brame et al. 2019). Considering its wide geographical distribution and the lack of a specific assignment, a systematic revision of this taxon becomes necessary. This study, based on specimens from museum collections, analyzed both shell morphology and microstructural characters of *Isognomon* (*Mytiloperna*) sp. ind. or *Mytiloperna* sp. to better clarify its taxonomic position and to consider its relationships with the other pteriod bivalves of the *Lithiotis* facies.

STRATIGRAPHIC SETTING, PROVENANCE OF THE MATERIAL AND TERMINOLOGY

The studied material, stored in the Ferrara, Pavia and Camposilvano (Verona) museum collections, has been collected in the Rotzo Formation of the Calcarei Grigi Group in northern Italy (Lower Jurassic), which is characterized by remarkable lateral and vertical facies variability. The formation was deposited in a lagoonal environment which was

closed seawards by oolitic shoals and bars and bordered landwards by marshes (e.g., Bosellini & Broglio Loriga 1971; Clari 1975; Posenato & Masetti 2012; Fig. 1). Unlike in other areas, where the bivalves of the *Lithiotis* facies are contained in very hard limestone, the bivalves of the Rotzo Formation in some cases can be easily extracted from marlstone or claystone. Additionally, in some localities of the Trento Platform, the shells preserve their original mineralogical composition and microstructure (Posenato et al. 2022).

The studied specimens are known in the literature as *Isognomon* (*Mytiloperna*) sp. ind. (Benini & Loriga 1974; Accorsi Benini & Broglio Loriga 1982) or *Mytiloperna* sp. (Broglio Loriga & Posenato 1996). These specimens, hereinafter referred to as “*Mytiloperna* sp.”, have been mostly collected in the lower part of the Rotzo Formation, about 20 m above the base of the formation, from a road cut located on the right side of Vajo dell’Anguilla (Lessini Mountains; Fig. 1), ca. 100 m from the Anguillara bridge (Fig. 1). The specimens, arranged in clusters, occurred at the top of a *Lithioperna scutata* (Dubar, 1948) biostrome, about 2 m-thick, which is followed by marlstone and claystone with coal lenses and vertical roots and overlain by a further *L. scutata* biostrome. This fossiliferous horizon, about 5 m-thick, has been interpreted as a “complete marsh cyclothem” (Clari 1975; Figs 1, 2A). It is located within the *Orbitopsella* Zone, early Pliensbachian (Early Jurassic) in age (Posenato & Masetti 2012).

More than half of the “*Mytiloperna* sp.” specimens of the Benini & Loriga (1974) collection from Vajo dell’Anguilla consists of articulated shells, suggesting a biogenic shell accumulation *sensu* Kidwell & Jablonski (1983). However, the shells are strongly abraded. In some articulated specimens, the body chamber has been almost completely removed. The outer shell ornamentation is usually preserved only on the anterior surface, which was protected from erosion because resting in the substrate. Despite the strong abrasion, the shells maintained their autochthonous position because they were tightly packed and partially buried (Accorsi Benini & Broglio Loriga 1982).

“*Mytiloperna* sp.” has been also recognized in the Taramelli collection, stored in the Kosmos Museum of the Pavia University. The specimens are represented by an articulated and calcitized shell and by a small disarticulated right valve, both coming

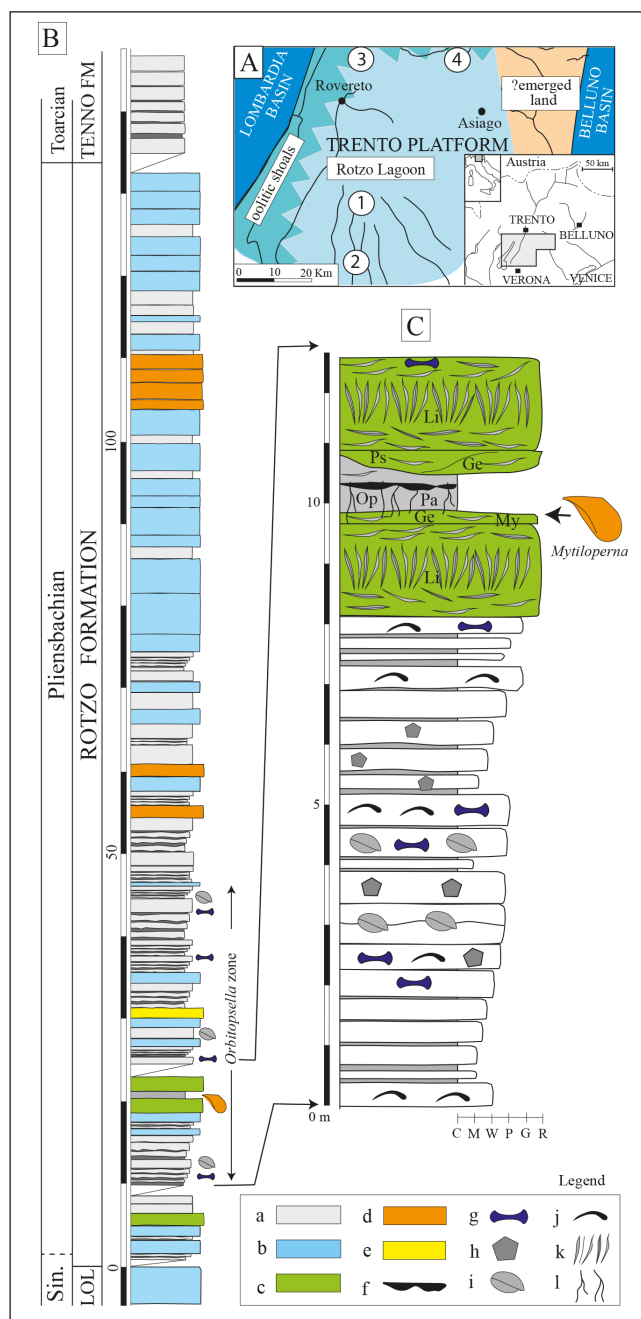


Fig. 1 - A) geographic position of the type locality (1, Vajo dell'Anguilla, Verona Province). B, C) the Lower Jurassic succession of the Rotzo Formation in Vajo dell'Anguilla (Verona Province) containing the stratotype of *Pachygerullia anguillensis* n. gen. n. sp. (B, from Posenato & Masetti 2012, mod.). Other cited localities: 2, Vajo del Paradiso; 3, Viote; 4, Val di Sella. Legend: a, mudstone/wackestone; b, packstone/grainstone; c, *Lithioperna* accumulation; d, *Cochlearites* accumulation; e, *Lithiotis* accumulation; f, coal lens; g, *Orbitopsella*; h, crinoids; i, *Lychnothyris rotzoana* (Schauth, 1865) (Brachiopoda); j, undetermined bivalves; k, *Lithioperna scutata* (Dubar, 1948); l, roots.

from the Premaloch Valley, near Asiago (Fig. 1). These specimens were assigned by Boehm (1884) to “*Perna* aff. *Taramellii*”. *Perna taramellii* Boehm, 1884,

was proposed for specimens housed in the Pavia and Verona museums, collected in the nineteenth century from Vajo del Paradiso (southern Lessini Mountains, Trento Platform), where the succession of the Rotzo Formation is about 60 m-thick. Based on the absence of *Orbitopsella* this succession is considered late Pliensbachian in age (Posenato & Masetti 2012). Most of the studied specimens are stored in the Museo “Piero Leonardi” of the University of Ferrara (MPL acronym). This material has been studied by Benini & Loriga (1974), Accorsi Benini & Broglio Loriga (1982), and Broglio Loriga & Posenato (1996). The other analyzed specimens are housed in the Kosmos Museum of the Pavia University (KM acronym) and in the Museo Geopaleontologico di Camposilvano (Verona; MC acronym; see the list of material in Tab. 1). We hereafter refer to these examined specimens of the *Lithiotis* facies, not assigned to a species, as belonging to “*Mytiloperna* sp.” or “*Mytiloperna*”, to distinguish them from the other species of the genus *Mytiloperna* von Ihering, 1903.

The bivalves of the *Lithiotis* facies are often characterized by aberrant shells and therefore different terminology has been used in the literature (Fig. 3). The morphological terminology of stick-like shells of *Lithiotis* and *Cochlearites* follows Posenato et al. (2022) who indicated as cardinal area the middle part of the elongated umbonal region where valves are in contact (Figs 3a1, b1). This area is anteriorly and posteriorly flanked by the feather-like or growth line areas. In the small body cavity, a myofringing crest connects the ventral extremity of the cardinal area to the muscle scar.

Since these bivalves have an unusual shell morphology, the morphological terminology adopted here (Fig. 3) needs some clarifications. The inner shell cavity has a wide median cardinal area which has been also indicated as contact or sub-ligamental area (Accorsi Benini 1979; Broglio Loriga & Posenato 1996). This surface may bear irregular, elongated and subparallel teeth. A broad and strong anterior radial carina delimits an anterior hearth-shaped flattened or concave surface representing the resting surface. This surface, here indicated as the anterior area, has been also named lunule (Broglio Loriga & Posenato 1996). However, it cannot be considered a true lunule, as the latter is defined as a depressed anterior area separated from the surrounding shell surface by an incised line or a change in sculpture and/or color (Carter et al. 2012).

SYSTEMATIC PALEONTOLOGY

The classification below follows that of Carter et al. (2011).

Class **BIVALVIA** Linnaeus, 1758 in 1758–1759

Subclass **AUTOLAMELLIBRANCHIATA**

Grobben, 1894

Infraclass **PTERIOMORPHIA** Beurlen, 1944

Superorder **Ostreiformii** Férussac, 1822 in 1821–1822

Order **Ostreida** Férussac, 1822 in 1821–1822

Suborder **Malleidina** J. Gray, 1854

Superfamily Pterioidea J. Gray, 1847b (Goldfuss, 1820)

Family Plicatostylidae Lupher & Packard, 1929

Emended diagnosis: Shape mytiloid to much elongated dorsoventrally, thick, subequivalve to strongly inequivalve; ligamental area with narrow and short median grooves to multivincular; monomyarian; shell internal surface with a variably developed cardinal area with or without teeth; body cavity small; outer shell layer made of prismatic calcite, middle layer nacreous, inner layer made of fibrous, irregular, spherulitic prismatic aragonite.

Type genus: *Plicatostylus* Lupher & Packard, 1929

Stratigraphic range: Early Jurassic - Eocene.

Remarks. Nomenclatural questions and the systematic position of the Plicatostylidae and other pteroid genera of the *Lithiotis* facies have been discussed by many authors. However, their taxonomic position and phyletic relationships with the other bivalve families are still uncertain. The genera *Lithiotis* Gümbel, 1871 and *Cochlearites* Reis, 1903 have been included by Cox (1971) in the family Lithiotidae Reis, 1903. However, Reis (1903) used the vernacular name “Lithiotiden”, which is an invalid name because published after 1900 (ICZN, Art. 11.7.2), therefore the author who erected the family Lithiotidae has to be considered Cox (1971) and not Reis (1903) (Bouquet & Rocroi 2010). Thus, Lithiotidae Cox, 1971 is a junior synonym of Plicatostylidae Lupher & Packard, 1929 (Bouchet & Rocroi 2010), a family included in the suborder Malleidina J. Gray, order Ostreida Férussac (Bieler et al. 2010; Carter et al. 2011). This family contains *Plicatostylus* Lupher & Packard, 1929, *Cochlearites* and *Lithiotis*, three monospecific genera characterized by aberrant, stick-like shells. The former genus is unanimously considered a junior synonym of *Lithiotis* (e.g., Accorsi Benini & Broglio Loriga 1974; Nauss & Smith 1988; Fraser et al. 2004; Ros-Franch et al. 2014). Previous

	shell	length	height	thickness	
MPL8660-M1	LV	135	100	42	
MPL8660-M2	RV+LV	112	90	55 (30, LV+25, RV)	
MPL8660-M3	RV+LV	115	110	38	
MPL8660-M3	RV	111	91	37	
MPL8660-M4	RV	71	70	37	
MPL8660-M5	RV+LV	115	97	35	
MPL8660-M6	RV+LV	112	68	65	
MPL8660-M7	RV+LV	60	70	50 (30, LV+20, RV)	
MPL8660-M8	RV+LV	111	87	30	
MPL8660-M9	RV+LV	135	71	28	
MPL8660-M10	RV	102	102	39	
MPL8660-M11	LV	125	100	35	
MPL8660-M12	RV+LV	fragment			
MPL8660-M13	RV+LV	65	75	70 (30, LV+40, RV)	
MPL8660-M14	RV+LV	fragment			
MPL8660-M15	RV+LV	67	53	80 (44, LV+36, RV)	
MPL8660-M16	RV+LV	70	76	53 (31, LV+22, RV)	
MPL8660-M17	LV	75	70	35	
MPL8660-M18	RV+LV	84	87	28	
MPL8660-M18		101	106	29	
MPL8660-M19	RV+LV	117	71	51 (30, LV+21, RV)	
MPL8660-M21	LV	100	75	30	
MPL8660-M22	RV	107	83	44	
MPL8660-M23	RV+LV	150	80	60 (35, LV+25, RV)	
MPL8660-M25	RV+LV	120	55	50 (LV, 15+35, RV)	
MPL8660-M26	RV+LV	105	60	25	
MPL8660-M28	RV	100	65	28	
MPL8660-M27	RV	93	106	35	
MPL8660-M29	LV	small			
MPL8660-M30	RV	95	80	28	
MPL8660-M31	RV	100	60	25	
MPL8660-M32	RV	90	55	30	
MPL8660-M33	RV+LV	110	70	75 (30, LV+45, RV)	
MPL8660-M34	LV	120	100	35	
MPL8660-M35	RV+LV	65	60	60	
MPL8660-M37	LV	90	50	35	
MPL8660-M38	LV	59	70	31	
MPL8660-M39a	LV	123	102	35	holotype
MPL8660-M39b	RV	112	130	36	
MPL8660-M40	RV	102	78	28	
MPL8660-M44	RV+LV	144	85	86	
MPL8660-M45	RV+LV	120	93	33	
MPL8660-M46		132	92	21	
KM16815a	RV+LV	105	85	55	
KM16815b	RV	75	55	20	
MC1208	RV	126	105	27	

RV, right valve; LV, left valve, RV+LV, articulated shell

Tab. 1 - Measurements of the studied specimens of *Pachygerwillia anguillaensis* n. gen. n. sp.

authors noted affinities of the taxa of this family with Ostreidae (e.g., Boehm 1892), Spondylidae (Reis 1903), Plicatulidae (Benini & Loriga 1977), and Bavevellidae (Seilacher 1984; Tëmkin & Pojeta 2010). Despite remarkable differences in the morphology of the cardinal area, *Lithiotis* and *Cochlearites* share a peculiar aragonitic microstructure of the inner shell layer consisting of fibrous, irregular, spherulitic prisms (FISphP, Posenato et al. 2022).

Carter (1990) noted affinities between Cassianellidae Ichikawa, 1958, a Triassic pteroid family with small-size shells, and Plicatostylidae. Similarities concern the occurrence of an internal “ridge or septum in the umbonal cavity” and of “a broad, flat, straight, nearly smooth, shelf-like cardinal area” (Carter 1990: 207-209) or ligamental area (Tëmkin & Pojeta 2010).

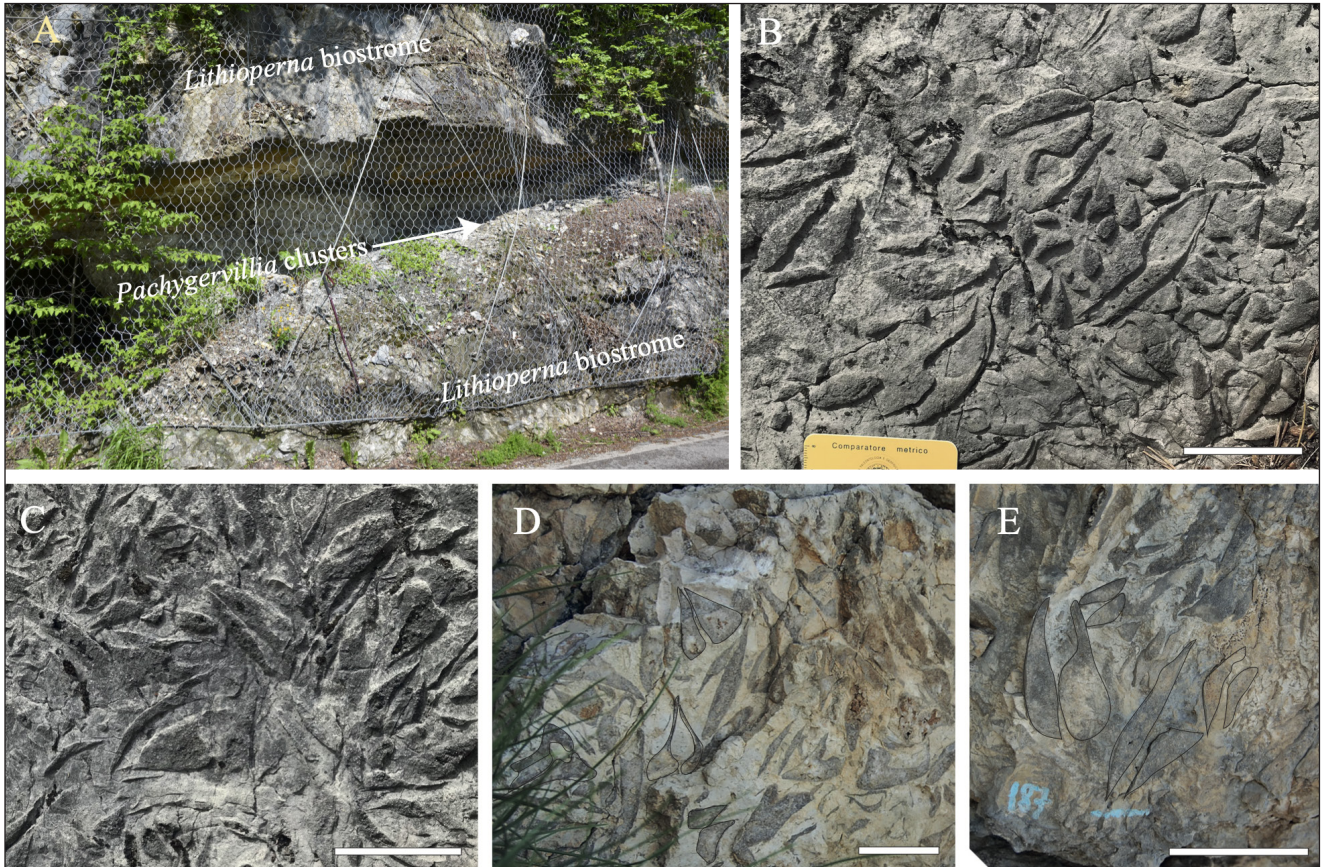


Fig. 2 - Outcrops of *Pachygerwillia anguillaensis* n. gen. n. sp. in some localities of the Trento Platform. A) the road outcrop with the stratotype of *Pachygerwillia anguillaensis* n. gen. n. sp., Vajo dell'Anguilla (Lessini Mountains, Verona Province); lower Rotzo Formation. B-E) *Pachygerwillia* beds from the lower Rotzo Formation, Trento Province; B, C: Val di Sella (Trento); D, E: Viote section (Trento). In these outcrops, the common occurrence of articulated and autochthonous shells suggests biogenic shell accumulations. Scale bar is 10 cm.

The internal septum of the Cassianellidae, placed posteriorly to the anterior muscle scar, corresponds to a myofringing ridge (Carter et al. 2012). The ridge in the monospecific genus *Cochlearites* is instead a myofringing crest because it is located on the posterior muscle scar. The anterior or posterior position of this crest with respect to the muscle scar depends on the shell orientation which is controversial because only very rare specimens preserve portions of the body cavity, therefore the systematic value of these ridges is questionable.

The most important character linking the Cassianellidae to Plicatostylidae seems to be the shell microstructure. The former family usually has an outer calcitic prismatic shell layer and middle and inner nacreous layers (Carter 1990). Unlike the other cassianellid species, Carter (1990) noted that *Cassianella decussata* (Goldfuss, 1836) has an outer shell layer with an aragonitic irregular fibrous prismatic microstructure. Prisms are 35 – 40 μm -thick and 0.5 – 2.0 μm -wide and show a gradual transition to the middle nacreous layer with the appearance of horizontal subdivisions

of prism, as thick as the underlying nacreous tablets. The nacre tablets decrease in thickness and increase in width towards the main part of the nacreous layer. The irregular fibrous prismatic microstructure and its gradual transition to the nacre microstructure could represent the ancestral stage from which the highly specialized FISphP microstructure (Posenato et al. 2022) of the family Plicatostylidae originated. This microstructural type, associated with a nacreous middle layer and an outer calcitic simple prismatic layer, is here proposed as the most important taxonomical character of the emended family Plicatostylidae which contains both the lithiotids (*Cochlearites* and *Lithiotis*) and the other pteroid bivalves of the *Lithiotis* facies (*Lithioperna*, “*Mytiloperna*” and *Gervilleoperna*). According to Bieler et al. (2014) bivalve taxa have different shell layers combined with different microstructures, whose differences are believed to be of phylogenetic and adaptive biomechanical significance. Indeed, microstructural information has been widely used as an important character in phylogenetic analyses, being also a feature that can be easily

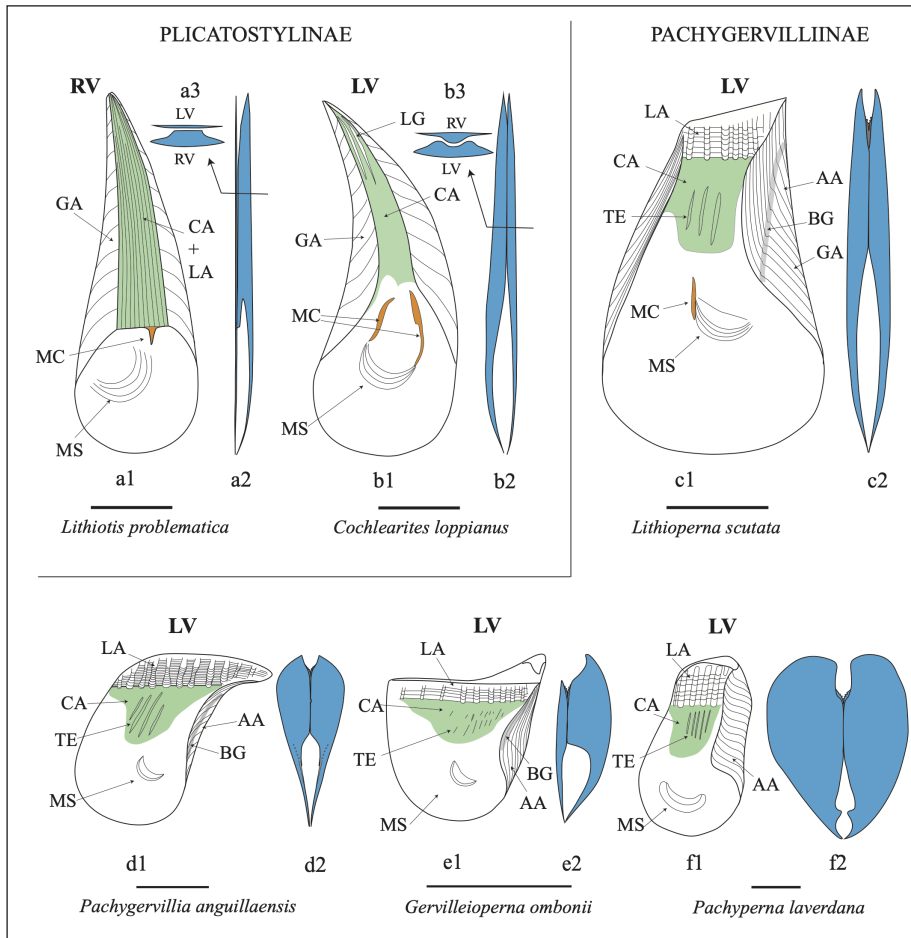


Fig. 3 - Internal morphology, orientation, and sections of the pteriod multivincular bivalves included in the emended fam. Plicatostylidae; a2, b2, c2, d2, e2, f2, dorsoventral sections; a3, b3, anteroposterior sections through the umbral region. Symbols: AA, anterior area; BG, byssal groove; CA, cardinal area (in green); GA, growth line area; LA, ligamental area; LG, ligamental groove; LV, left valve; MC, myofringing crest; MS, muscle scar; RV, right valve; TE, teeth. Position and inclination of the posterior muscle scar is based on specimens which have been schematically adapted from the following authors: a1, Accorsi Benini & Broglio Loriga 1977: pl. 5, fig. 2; b1, Accorsi Benini & Broglio Loriga 1977: pl. 1, fig. 1a; c1, Accorsi Benini 1979: pl. 1, fig. 2; d1, MPL8660-M39 holotype; e1, Seilacher, 1984: textfig. 5; f1, Posenato 1995: fig. 4a. Scale bar is 5 cm. In blue, shell sections.

inspected in fossil taxa for phylogenetic placement (e.g., Bieler et al. 2014).

The FISphP microstructure occurs in “*Mytiloperma* sp.” and *Gervilleioperna* (Accorsi Benini & Broglio Loriga 1982; Broglio Loriga & Posenato 1996). These two multivincular genera were included by Cox (1969) in the family Isognomonidae, which is now considered a subfamily (Isognomoninae) of Malleidae (superfamily Pterioidea) (Carter et al. 2011). “*Mytiloperma* sp.” and *Gervilleioperna ombonii* (Negri, 1891), two species occurring in the *Lithiotis* facies, have a thick inner shell layer with an aragonitic “fibrous prismatic” microstructure (Accorsi Benini & Broglio Loriga 1982). The microstructure of the first species has been here re-examined (see below) and corresponds to the FISphP microstructure, recently recognized in *Lithiotis* and *Cochlearites* (Posenato et al. 2022). The same microstructure is present in *G. ombonii* and, although with shorter prisms, in *Lithioperna* (Benini & Broglio Loriga 1982; Broglio Loriga & Posenato 1996). The FISphP microstructure can be therefore used as a taxonomic character at family level which links *Lithiotis* and *Cochlearites*, already

included in the fam. Plicatostylidae, to *Lithioperna*, *Gervilleioperna* and “*Mytiloperma*”. These pteriod taxa have quite different shell morphologies due to their gregarious and sessile (byssate or cemented) life habits. However, they share thick and large monomyarian shells with a small body cavity and a large median cardinal area.

Aragonitic prismatic microstructures also occur in other genera of the *Lithiotis* facies such as the myalinid *Pseudopachymytilus* (family Myalinidae, order Myalinida), the carditid *Opisoma* (family Astartidae, order Carditida), and the megalodontid *Pachymegalon* (family Pachyrismatidae, order Megalodontida). However, these prismatic microstructures are not associated with nacre but occur with the complex crossed-lamellar microstructure which is missing in the emended Plicatostylidae. Also, the prisms of the above-cited genera are shorter and thinner (myostracal type prisms of Accorsi Benini & Broglio Loriga 1982) than those of the FISphP microstructure and originate in *Opisoma* from a modification of the 2nd order lamellae which assume a columnar arrangement (Accorsi Benini 1980).

genus	author	type-species	Treatise on Invertebrate Paleontology 1969,1971		1)Benini & Loriga 1977; 2)Accorsi Benini 1979; 3)Accorsi Benini & Broglio Loriga 1982		This paper				
			order	superfam. / fam.	order/ suborder	superfam. / fam.	order / suborder	superfam.	family	subfamily	
<i>Plicatostylus</i>	Lupher & Packard, 1929	<i>P. gregarious</i> Lupher & Packard, 1929	incertae sedis	incertae sedis	Pterioida/ Lithiotina ¹	Lithiotacea ¹ / Lithiotidae	OSTREIDA / MALLEIDINA	PTERIOIDEA	PLICATOSTYLIDAE	PLICATOSTYLINAE	
<i>Lithiotis</i>	Gümbel, 1871	<i>L. problematica</i> Gümbel, 1871	incertae sedis	? Lithiotidae							Lithiotacea ¹ / Cochlearitidae ¹
<i>Cochlearites</i>	Reis, 1903	<i>Trichites loppianus</i> Tausch, 1890									
<i>Gervilleioerna</i>	Krumbeck, 1923	<i>G. timorensis</i> Krumbeck, 1923	Pterioida	Pteriacea / Isognomonidae	Pterioida/ Pteriina	Pteriacea / ? Isognomonidae ³				PACHYGERVILLIINAE	
<i>Lithioerna</i>	Accorsi Benini, 1979	<i>Perna scutata</i> Dubar, 1948	-	-	Pterioida/ Pteriina	Pteriacea / ? Isognomonidae ²					
<i>Pachygerwillia</i>	this paper	<i>P. anguillaensis</i> n. gen. n. sp.	-	-	-	-					
<i>Pachyperna</i>	Oppenheim, 1900	<i>P. laverdana</i> Oppenheim, 1900	Pterioida	Pteriacea / Isognomonidae	-	-					

Tab. 2 - Changes of classification at suprageneric level of the pteroid genera included in the emended fam. Plicatostylidae.

The inclusion of *Lithioerna*, *Gervilleioerna* and “*Mytiloerna*” into the emended family Plicatostylidae is also supported by their stratigraphic distribution. In the Trento Platform (Southern Alps), they occur earlier than *Lithiotis* and *Cochlearites* (e.g., Posenato & Masetti 2012). *Gervilleioerna buchii* (De Zigno, 1870) occurs in the upper part of the Monte Zugna Formation (Calcarei Grigi Group), middle Sinemurian in age, while *Lithioerna* and “*Mytiloerna*” appear in the lowermost portion of the Rotzo Formation (early Pliensbachian), just above the *Eomiodon* Horizon (Franceschi et al. 2014). Therefore, these pteroid groups could be closely related to the ancestral forms from which the stick-like lithiotid bivalves originated. The emended family Plicatostylidae Lupher & Packard, 1929, characterized by the FISphP microstructure combined with nacre, is here divided into two subfamilies: Plicatostylinae Lupher & Packard, 1929 and Pachygerwilliinae n. subfamily.

Genera included: *Plicatostylus* Lupher & Packard, 1929 (junior synonym of *Lithiotis* Gümbel, 1871); *Cochlearites* Reis, 1903; *Gervilleioerna* Krumbeck, 1923; *Lithioerna* Accorsi Benini, 1979; *Lithiotis* Gümbel, 1871; *Pachygerwillia* n. gen. (= “*Mytiloerna* sp.”); *Pachyperna* Oppenheim, 1900.

Subfamily Plicatostylinae Lupher & Packard, 1929

Emended diagnosis: Shells large, thick, very elongated dorsoventrally, compressed, slightly to strongly inequivalve, attached by the thicker valve; umbonal region very elongated, with a median cardinal area flanked by growth line areas; body cavity small with myofringing crest, hinge edentulous.

Type genus: *Plicatostylus* Lupher & Packard, 1929.

Stratigraphic range: Early Jurassic (Pliensbachian – early Toarcian).

Remarks. The emended diagnosis of the subfamily is based on the description of the family ?Lithiotidae by Cox (1971). The subfam. Plicatostylidae is composed of three monospecific genera: *Plicatostylus*, *Cochlearites*, and *Lithiotis*. Accorsi Benini & Broglio Loriga (1977) considered *Plicatostylus* as a junior synonym of *Lithiotis*. The morphological differences between *Plicatostylus gregarious* Lupher & Packard, 1929 and *Lithiotis problematica* Gümbel, 1871 could justify only a separation at species level. However, Accorsi Benini & Broglio Loriga (1977) left the specific question unresolved due to the scarcity of material at their disposal. *Cochlearites loppianus* (Tausch, 1890) and *Lithiotis problematica* Gümbel, 1871 have been carefully described by Accorsi Benini & Broglio Loriga (1977) and Chinzei (1982). These bivalves are characterized by very large and aberrant shells whose orientation is debated.

Reis (1903) interpreted both the attached valves of *Lithiotis* and *Cochlearites* as right valves. Accorsi Benini & Broglio Loriga (1977), orienting the shell on the base of the usually posterior setting of the muscle scar in monomyarian bivalves, considered both the larger and attached valves of *Cochlearites* and *Lithiotis* as the left ones, although they did not exclude that *Lithiotis* could also attach with the right valve. Chinzei (1982), based on the more expanded anterior space for gills accommodation in monomyarian bivalves, considered the attached val-

ve of *Lithiotis* as the right one but that of *Cochlearites* as the left. In the latter genus the myofringing crest is not as raised as figured by Reis (1903, figs 1, 2), but it is represented by weak undulations which may occur on both sides of the muscle scar (Reis 1923; Accorsi Benini & Broglio Loriga 1977; Chinzei 1982). In the living *Isognomon isognomum* (Linnaeus, 1758) and *I. ephippium* (Linnaeus, 1758) the muscle scar is reniform with the convex side oriented postero-ventrally (Yonge 1968: figs 7, 8). Following this criterion, the attached valves of *Lithiotis* with the preserved muscle scar (e.g., Accorsi Benini & Broglio Loriga 1977: pl. 1, fig. 1a) can be considered as the right valve (Fig. 3a1). The attached valves of *Cochlearites* (Reis 1923: fig. 1; Accorsi Benini & Broglio Loriga 1977: pl. 1, fig. 1a) have the muscle scar oriented in the opposite direction (Fig. 3b1); therefore, they represent left valves. This shell orientation, in agreement with that proposed by Chinzei (1982), is confirmed by the muscle scar orientation occurring in other allied genera (e.g., *Lithioperna* and *Pachygerwillia* n. gen., Figs 3c1, d1), the shell orientation of which follows the conventional criteria used for the bivalves (e.g., Carter et al. 2012).

The most significant difference between *Lithiotis* and *Cochlearites* is the morphology of the elongated cardinal area occurring in the middle umbonal region and the degree to which the valves are unequal (Figs 3a3, b3). The shell of *Lithiotis* is strongly inequivalve. It has a laminar, few mm-thick left valve, while the right valve is 1–3 cm-thick. *Cochlearites* is slightly inequivalve; the left valve is slightly thicker than the right one. In *Lithiotis*, the cardinal area is furrowed by narrow and parallel ligament grooves (cardinal area or furrowed plate) suggesting an origin from a multivincular bivalve (Savazzi 1996). In *Cochlearites*, the middle umbonal region is smooth and with an elongated groove in the left valve corresponding to a bulge in the right valve. It has only a few and irregular ligament grooves in the early stages of growth (Figs 3b1–b3). In the Rotzo Formation *Cochlearites* occurs stratigraphically above *Lithiotis* and the genus is very common in the upper part of the formation, in the *Lituosepta compressa* Zone (upper Pliensbachian; Posenato & Masetti 2012), while *L. problematica* is common in the upper *Orbitopsella* Zone (lower Pliensbachian). This latter species is also recorded in the lower Toarcian of South America (Peru and Chile; Hillebrandt 1982). Plicatostylinae, as well as most part of the large

bivalves of the *Lithiotis* facies, have been affected by the early Toarcian mass extinction (Fraser et al. 2004; Posenato et al. 2018).

Genera included: *Plicatostylus* Lupper & Packard, 1929 (junior synonym of *Lithiotis* Gümbel, 1871); *Cochlearites* Reis, 1903; *Lithiotis* Gümbel, 1871.

Subfamily Pachygerwilliinae nov.

Type genus: *Pachygerwillia* n. gen.

Derivation of name: From *Pachygerwillia* n. gen.

Diagnosis: Shell medium-sized to large, from subquadrate, mytiliform to ensiform, flattened to strongly inflated; subequivalve to highly inequivalve with left valve more convex than right valve; posterior wing undifferentiated to well-defined, anterior auricle small or missing; outer ornamentation concentrically lamellose; commissure plane flat or undulating; outer multivincular ligament area high and with numerous pits; with or without byssal gape affecting both valves; cardinal area large and smooth or with irregular and elongated teeth in adult stage.

Stratigraphic range: Early Jurassic - Eocene.

Remarks. This new subfamily contains *Gervilleioperna* Krumbeck, 1923, *Lithioperna* Accorsi Benini, 1979, and *Pachygerwillia* n. gen., whose specimens were previously known in the literature as *Isognomon* (*Mytiloperna*) sp. or *Mytiloperna* sp. (Benini & Loriga 1974; Accorsi Benini & Broglio Loriga 1982; Broglio Loriga & Posenato 1996). The former genus has been included in the family Isognomonidae by Cox (1969) (Crampton, 1988). However, the occurrence of teeth at the adult stage in *Gervilleioperna* prompted some authors (e.g., Damborenea 1987) to place it in the fam. Bakevellidae King, 1850, according to the Cox (1969) classification. According to Carter et al. (2011), Isognomoninae is now considered a subfamily of Malleidae which belongs, with

PLATE 1

Pachygerwillia anguillaensis n. gen. n. sp., Vajo dell'Anguilla (Lessini Mountains), Rotzo Formation, lower Pliensbachian. Figs 1–4) specimen MPL8660-M9, internal (1) and external (2) views of left valve, anterior (4) and ventral (3) views of the shell. Figs 5–9) specimen MPL8660-M3, external (5) and internal (6) views of left valve, external view (7) of right valve, dorsal (8) and anterior (9) views of the shell; Figs 10, 11) specimen MC 1208, external (10) and internal (11) views of a right valve collected from the marlstone located between the *Lithioperna* biostromes. Figs 12, 13) specimen MPL8660-M1, external view of left valve.

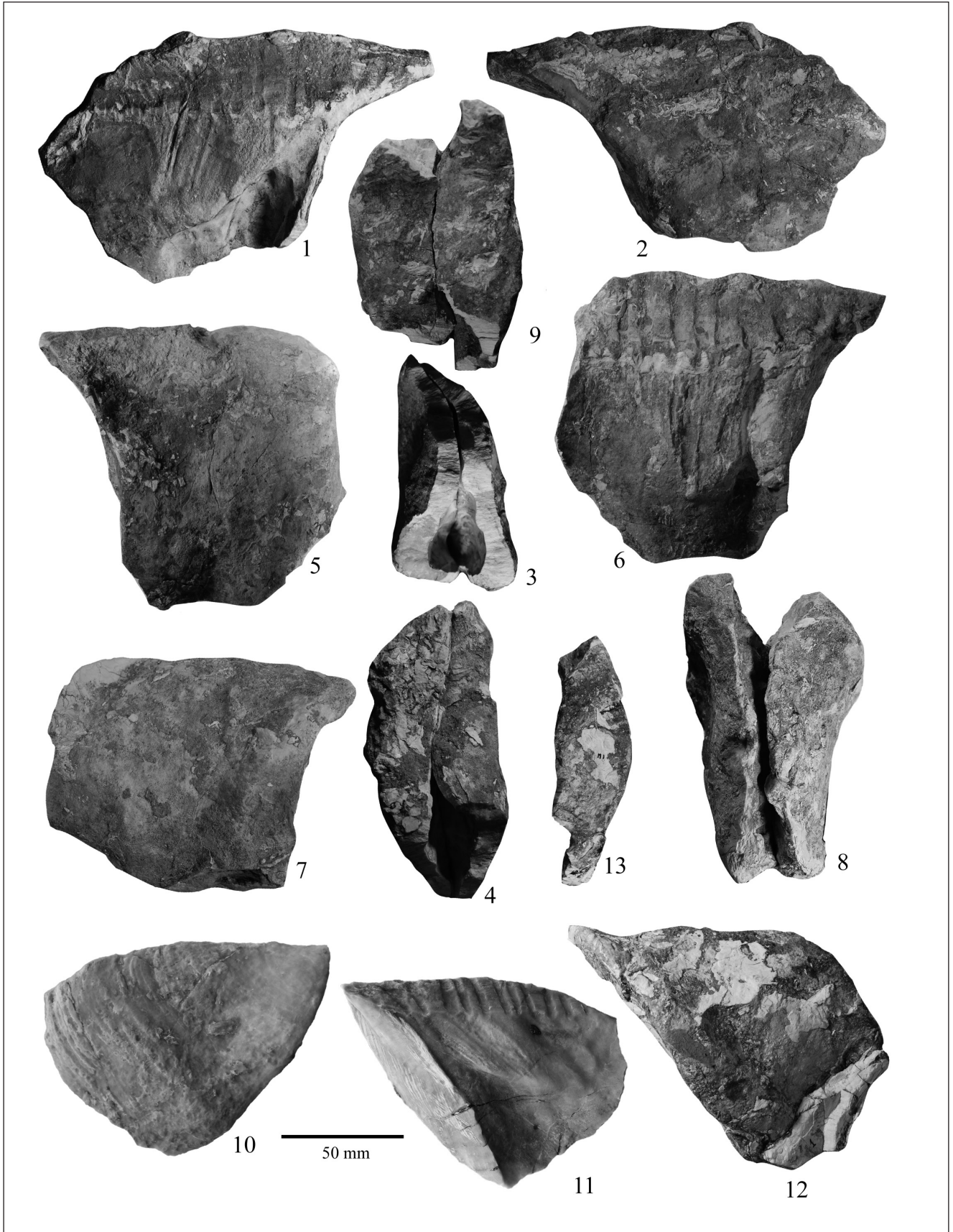


PLATE 1

Bakevellidae, to the superfamily Pterioidea Gray, 1847. Taxa of the latter superfamily are characterized in both valves by an outer shell layer composed of regular prismatic calcite and by nacreous middle and inner shell layers. The middle and inner layers are separated by a thin pallial myostracum (Taylor et al. 1969). According to Cox (1969) Isognomonidae (now subfam. Isognomoninae) probably evolved from the Bakevellidae (Cox 1969; Stanley 1972) losing the *Pteria*-like form. They have a similar shell microstructure, but they differ in the microstructure of the outer calcitic layer, which can be regular simple prismatic, irregular prismatic or homogeneous in the Bakevellidae, whereas in Isognomonidae (now Isognomoninae) it can be only regular simple prismatic (Carter 1990).

Gervilleioeperna and *Lithioeperna* are here moved to the subfamily Pachygerwilliinae nov., which comprises also *Pachygerwillia* n. gen., based on the occurrence in these genera of the peculiar combination of FISphP and nacre microstructures, which do not occur in other genera of the Bakevellidae and Isognomoninae. *Gervilleioeperna*, *Lithioeperna* and *Pachygerwillia* n. gen. are characterized by an inner large median cardinal area (area of contact of Accorsi Benini 1979), separated from the anterior margin by a conical appendix of the body cavity and, occasionally, from the posterior margin by a flattened appendix (Fig. 3). The dorsal apex of both the appendices reaches the ventral extremity of the ligamental area. A dorso-ventrally elongated cardinal platform acted as a fulcrum for shell opening and closing. This mechanism was based on the flexibility of the ventral margin predominantly composed of a thin outer calcitic prismatic layer rich of intercrystalline organic matrix as already described for the Plicatostyliinae (Posenato et al. 2022). The cardinal area may bear elongated and irregularly distributed teeth obliquely inclined with respect to the ventral margin of the ligamental area; they are more numerous in adult and large shells. The teeth are common in *Pachygerwillia* n. gen., less common in *Gervilleioeperna*, while they are rare in *Lithioeperna* (e.g., Broglio Loriga & Posenato 1996, pl. 4, fig. 1; Fig. 3). The occurrence or lack of teeth, their different length and number can be considered as intraspecific variability, therefore this character has little systematic value.

The middle Eocene *Pachyperna laverdana* Oppenheim, 1900 (type species of *Pachyperna* Oppenheim, 1900) is a large and multivincular bivalve (Figs

3f1, f2) having a shell morphology and microstructure closely related to the genera included into the new subfamily Pachygerwilliinae. This species has a boulder shape and an extremely thick shell. At the juvenile stage it had an epibyssate, pleurothetic lifestyle which became reclining orthothetic in the adult stage. The body cavity is very small, with a large cardinal plate occasionally carrying teeth in large shells (Posenato 1995). In addition to these morphological characters, *Pachyperna* shares with the above-described Jurassic bivalves also the same aragonitic FISphP microstructure of the inner shell layer, although the nacreous middle layer has not yet been documented. The FISphP microstructure consists of extremely elongated, fibrous and fusiform prisms with a highly variable outline in cross-section (Posenato 1995, fig. 11d-e). The prisms are several mm-long and about 30-40 μm in width. They are arranged in bundles with opposite orientations, as in *Pachygerwillia* n. gen. (see below). Therefore, we propose to move this genus to the Pachygerwilliinae nov. subfam. Further analyses are required to check the occurrence of the middle nacreous layer confirming or not the present attribution.

All the genera included in this new subfamily show a close correspondence in the morphological and microstructural characters of the shell, supporting the proposal to include them in the same systematic group and to reject the hypothesis that the proposed group is based on analogous characters and represents adaptive convergence.

In the Trento Platform, the appearance of Pachygerwilliinae is recorded by *Gervilleioeperna buchii* (De Zigno, 1870) which occurs in the Monte Zugna Formation, at the transition between the *turneri* and

PLATE 2

Pachygerwillia anguillaensis n. gen. n. sp., Vajo dell'Anguilla (Lessini Mountains), Rotzo Formation, lower Pliensbachian. Figs 1, 2) specimen MPL8660-M10, external (1) and internal (2) views of right valve; Fig. 3) specimen MPL8660-M31, external view of right valve; Fig. 4) specimen MPL8660-M21, external view of left valve; Figs 5-7) specimen MPL8660-M27, external (5), internal (6) and anterior (7) views of right valve; Figs 8, 9) specimen MPL8660-M37, internal (8) and external (9) views of right valve; Figs 10, 11) specimen MPL8660-M30, external (10) and anterior (11) views of right valve; Figs 12, 13) specimen MPL8660-M15, umbonal fragment of an articulated shell in posterior (12) and anterior (13) views.

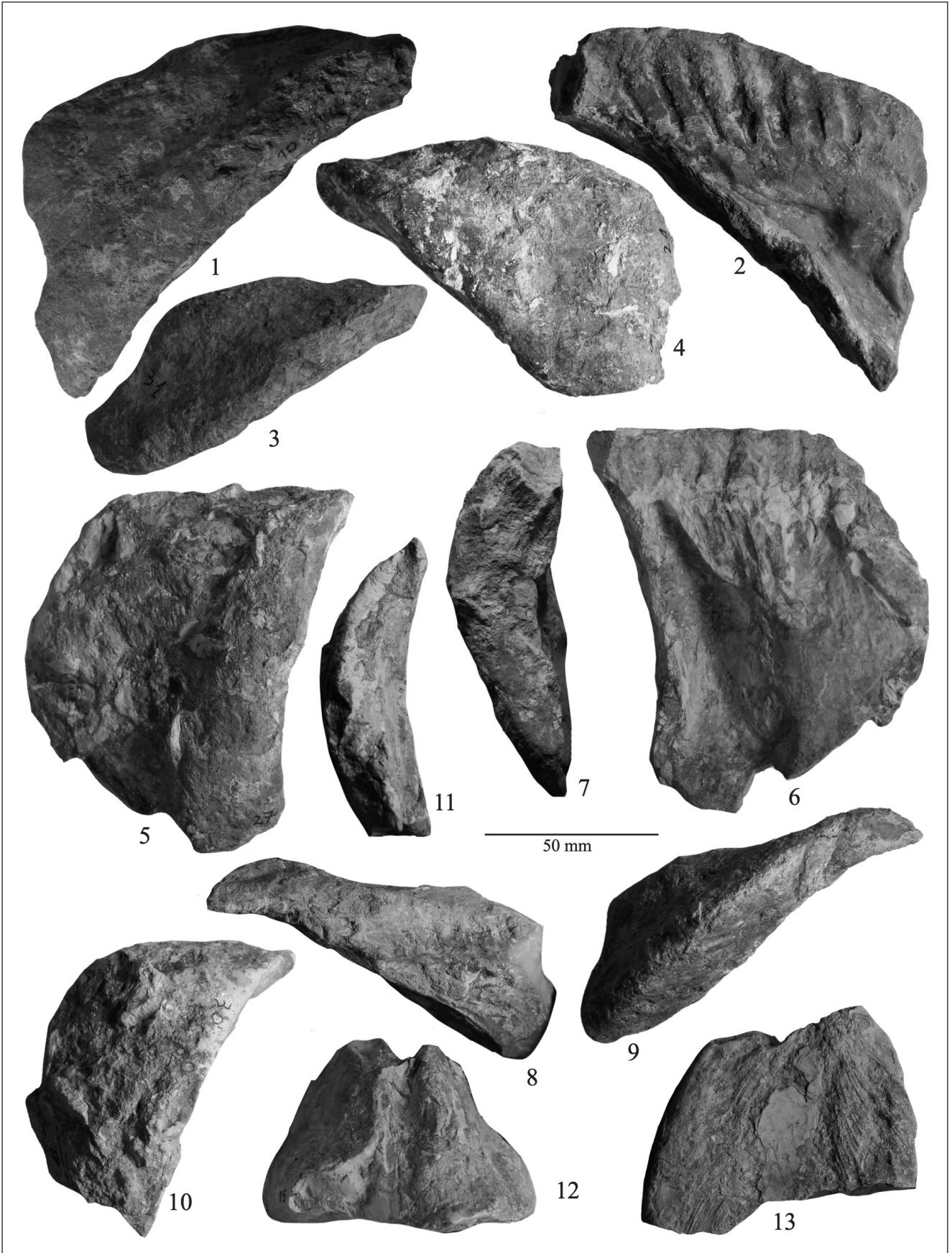


PLATE 2

obtusum zones (late early Sinemurian in age, Masetti et al. 2017). *Gervilleioperna* is also recorded in the upper Sinemurian - lower Toarcian of Morocco (Fraser et al. 2004), Argentina (Damborenea 1987) and northern Chile (Aberhan 1994). The type species of *Gervilleioperna* (*Gervilleioperna timorensis* Krumbeck, 1923) has been collected in the *Lithiotis* Facies of Timor, Sinemurian–Pliensbachian in age (Broglia Loriga & Neri 1976). This genus survived the early Toarcian extinction, and reached the Middle Jurassic (Aalenian; e.g., Aberhan & Hillebrandt 1996; Ros-Franch et al. 2014). *Lithioperna* and *Pachygervillia* n. gen. range from the latest Sinemurian-earliest Pliensbachian-aged formations (basal beds of the Rotzo Formation, Posenato & Masetti 2012) to the early Toarcian (e.g., Apennine Carbonate Platform, southern Italy), before the early Toarcian extinction (Posenato et al. 2018). *Pachygervillia* n. gen. and *Lithioperna* are very abundant in the *Lithiotis* Member of the Apennine Carbonate Platform. They occur in a thick succession deposited under very shallow marine conditions ranging from the late Pliensbachian to the early Toarcian (Posenato et al. 2018).

Genera included: *Gervilleioperna* Krumbeck, 1923; *Lithioperna* Accorsi Benini, 1979; *Pachygervillia* n. gen.; *Pachyperna* Oppenheim, 1900.

Pachygervillia n. gen.

Derivation of name: the name is a combination of two terms: *Pachys* (Greek) means thick and *Gervillia* is a genus of the fam. Bakevellidae.

Diagnosis: Shell subrectangular to mytiliform, subequivalve, large and thick with anterior carina running from beak to antero-ventral margin and separating a large anterior area from the rest of the shell; posterior wing undifferentiated; ligament area flat with numerous irregularly spaced ligament grooves; cardinal area large with elongated, usually oblique and irregular teeth.

Type species: *Pachygervillia anguillaensis* n. gen. n. sp.

Stratigraphic range: Latest Sinemurian – early Toarcian.

Remarks. In the past, the majority of the studied shells have been determined as *Isognomon* (*Mytiloperna*) sp. ind. (Benini & Loriga 1974; Accorsi Benini & Broglia Loriga 1982) or *Mytiloperna* sp. (Seilacher 1984; Broglia Loriga & Posenato 1996; Fraser et al. 2004). The genus *Mytiloperna* von Ihering, 1903 (type species *Perna americana* Forbes in Darwin 1841 from the Jurassic of Chile) is characterized by equivalve and mytiliform shells with undifferentiated wings, strong anterior carinas, few and widely spaced ligamental grooves and by lack-

ing a byssal notch and gape. As discussed above, the different microstructure of the inner shell layer of “*Mytiloperna*” (= *Pachygervillia* n. gen.) suggests a different position of these specimens at the family level than previously proposed in the literature. The occurrence of a large and toothed cardinal platform at the adult stage and the thick shell represent other remarkable differences to distinguish the specimens assigned to this new genus from those of *Mytiloperna*, which occasionally have only small and few teeth (e.g., *Mytiloperna patchamensis* Cox, 1940; Jaitly et al. 1995: text-fig. 19).

Pachygervillia and *Gervilleioperna* have both a swollen anterior radial carina separating the anterior flattened or concave surface from the posterior region. The most important characters to distinguish them are the occurrence in *Gervilleioperna* of a posterior wing and an inequivalve shell (Fig. 3e2). The posterior wing is lacking in *Lithioperna* and *Pachyperna*. *Lithioperna* has a strongly variable shell shape, ranging from dish- to cup shape. The dish-shaped morphotype is the most common, having flattened shells, attached with the commissure plane perpendicular to the substrate surface (orthothetic position). Cup-shaped individuals have concavo-convex shells that were byssally attached with the commissure plane parallel to the substrate surface (pleurothetic position) (Seilacher 1984; Broglia Loriga & Posenato 1996). *Pachyperna* differs from *Pachygervillia* by its extremely inflated, boulder-shaped shell (Figs 3f1, f2), a deeper anterior area and a lower number of resilifers.

Pachygervillia anguillaensis n. gen. n. sp.

Plate 1, figs 1–13; Plate 2, figs 1–13; Plate 3, figs 1–10; Plate 4, figs

7–11

PLATE 3

Pachygervillia anguillaensis n. gen. n. sp., Vajo dell’Anguilla (Lessini Mountains), Rotzo Formation, lower Pliensbachian. Figs 1-5 articulated specimen MPL8660-M45, internal (1), external (2) views of left valve, internal (4) and external (5) views of right valve, anterior (3) view of inequivalve shell; Figs 6-10 holotype, specimen MPL8660-M39a (6, 7, 10) and MPL8660-M39b (8, 9), external (6), internal (7) and anterior (10) views of left valve; internal (8) and external (9) views of right valve.

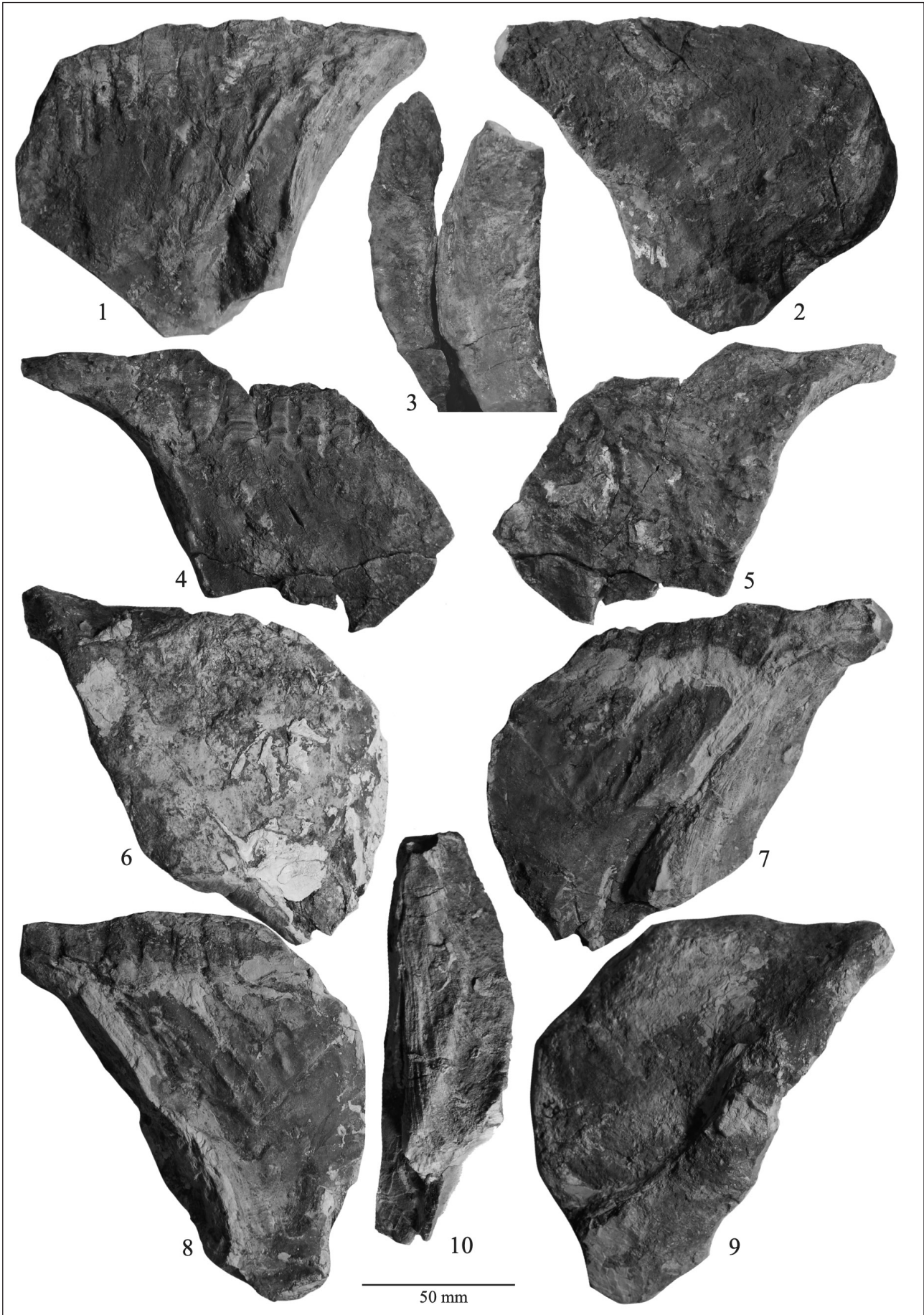


PLATE 3

- v 1884 *Perna* aff. *Taramellii* n. sp., Boehm, p. 766.
 v 1974 *Isognomon* (*Mytiloperna*) sp. ind., Benini & Loriga, p. 234-238, pl. 1, figs 1-3; pl. 2, figs 1-3; pl. 4, figs. 1-7.
 1976 *Isognomon* (*Mytiloperna*) sp. ind., Broglio Loriga & Neri, p. 655, fig. 1.
 v 1982 *Isognomon* (*Mytiloperna*) sp. ind., Accorsi Benini & Broglio Loriga, p. 801-803, textfigs 3-6, pl. 2, fig. 1.
 1984 *Mytiloperna* sp., Seilacher, p. 221, textfig. 5.
 v 1996 *Mytiloperna* sp., Broglio Loriga & Posenato, p. 54-56, pl. 5, figs 1-12.
 2004 *Mytiloperna* sp., Fraser et al., p. 53, figs 2, 10.

Derivation of name: The name derives from Anguilla, which is the name of the valley (Vajo) of the Lessini Mountains (Verona Province), which is the type locality.

Holotype: MPL8660-M39, an articulated shell with detached valves (MPL8660-M39a left valve and MPL8660-M39b right valve), Pl. 3, figs 6–10.

Paratypes: MPL8660-M1, MPL8660-M2, MPL8660-M3, MPL8660-M4, MPL8660-M5, MPL8660-M6, MPL8660-M7, MPL8660-M8, MPL8660-M9, MPL8660-M10, MPL8660-M11, MPL8660-M12, MPL8660-M13, MPL8660-M14, MPL8660-M15, MPL8660-M16, MPL8660-M17, MPL8660-M18, MPL8660-M19, MPL8660-M21, MPL8660-M22, MPL8660-M23, MPL8660-M25, MPL8660-M26, MPL8660-M27, MPL8660-M28, MPL8660-M29, MPL8660-M30, MPL8660-M31, MPL8660-M32, MPL8660-M33, MPL8660-M34, MPL8660-M35, MPL8660-M37, MPL8660-M38, MPL8660-M40, MPL8660-M44, MPL8660-M45, MPL8660-M46, KM1681a, KM1681b, MC1202.

Type locality and stratum: A road outcrop near Ponte dell'Anguillara (Fig. 2A), Vajo dell'Anguilla, 45.655° lat. N, 11.016° long. E., *Orbitopsella* Zone, lower Rotzo Formation, Calcarei Grigi Group.

Stratigraphic range: Latest Sinemurian–Pliensbachian.

Diagnosis: *Pachygerwillia* with subrectangular to ensiform outline; shell thick as inflated with strong anterior carina, umbo terminal and slightly twisted, occasionally with a short and blunt anterior wing; anterior area large with flattened or concave surface, byssal gape inconspicuous.

Description. Shell large, subequivalve and thick with a rather variable outline ranging from subrectangular to elongated mytiloid; beak terminal and slightly twisted; shell obliquity (angle between hinge margin and anterior carina) ranging from ca. 30° to 80°; occasionally with a short and blunt anterior wing. Anterior carina large and representing the maximum shell thickness, running from the umbo to the anteroventral margin and delimiting a broad and high anterior area ranging from flat to concave, inward inclined or perpendicular to commissural plane and furrowed by an oblique byssal groove; shell thickness gradually decreasing in ventral and posterior directions; anterior margin S-shaped, dorsal margin straight to gently convex, posterior margin straight to slightly convex, ventral margin not preserved; no distinct byssal gape. Ornamentation consisting of dense and irregularly

distributed growth scales usually better preserved in the anterior area. Ligamental area multivincular, high and extending ca. 1/5 or less of the preserved valve height; ligamental grooves large, usually about ten in adult individuals and, in most cases, as wide as crests or irregularly spaced. Cardinal platform large, irregular in outline, with subparallel and irregularly distributed teeth; their inclination corresponds to the shell obliquity; adductor scar reniform and located in the anterior-median part of the inner surface; anterior part of body cavity conical in shape with its apex directed anterior-dorsally, posterior part of body cavity, behind the cardinal platform, narrow and flattened.

Shell microstructure. The shell of *Pachygerwillia anguillaensis* n. gen. n. sp. consists of three layers (Pl. 5). The outer layer, not preserved in the studied specimens, is made up of calcitic simple prisms (Accorsi Benini & Broglio Loriga 1982). The middle layer is composed of nacre which, in specimen MPL8660-M2, is preserved on the growth scales occurring in the anterior and ligamental areas where it interdigitates with the prisms of the inner layer (Pl. 5, figs 9-13). The nacreous tablets of the ligamental area, about 20–30 µm wide and 2.5–5 µm thick, show a gradual transition to the aragonitic prisms of the inner layer. The prisms are very elongated, several mm-long and fusiform in shape with the long axis slightly inclined with respect to the inner shell surface (Pl. 5, figs 1–4). They are up to 200 µm wide and show a very irregular outline in horizontal section (Pl. 5, figs 5, 6), forming bundles of prisms with opposite orientations (Pl. 5, figs 1, 14, 15), as those occurring in *Pachyperna laverdana* Oppenheim (Posenato 1995: fig. 11). The lateral surface of each prism shows slightly incli-

PLATE 4

Pachygerwillia taramellii (Boehm, 1884), Vajo del Paradiso (Lessini Mountains), Rotzo Formation, upper Pliensbachian. Figs 1-4) articulated specimen KM17794a, lectotype, external (1) and internal (3) views of right valve, left external (4) and anterior (2) view of shell; Figs 5, 6) specimen KM17794b, external (5) and internal (6) views of an umbonal fragment of a small right valve.

Pachygerwillia anguillaensis n. gen. n. sp., Premaloch (Sette Comuni), Rotzo Formation, Pliensbachian. Figs. 7-11) 7-10: articulated specimen KM16815a, right external (7), anterior (8) and left internal (9) and exterior (10) views; 11: specimen KM16815b, exterior view of a small right valve.

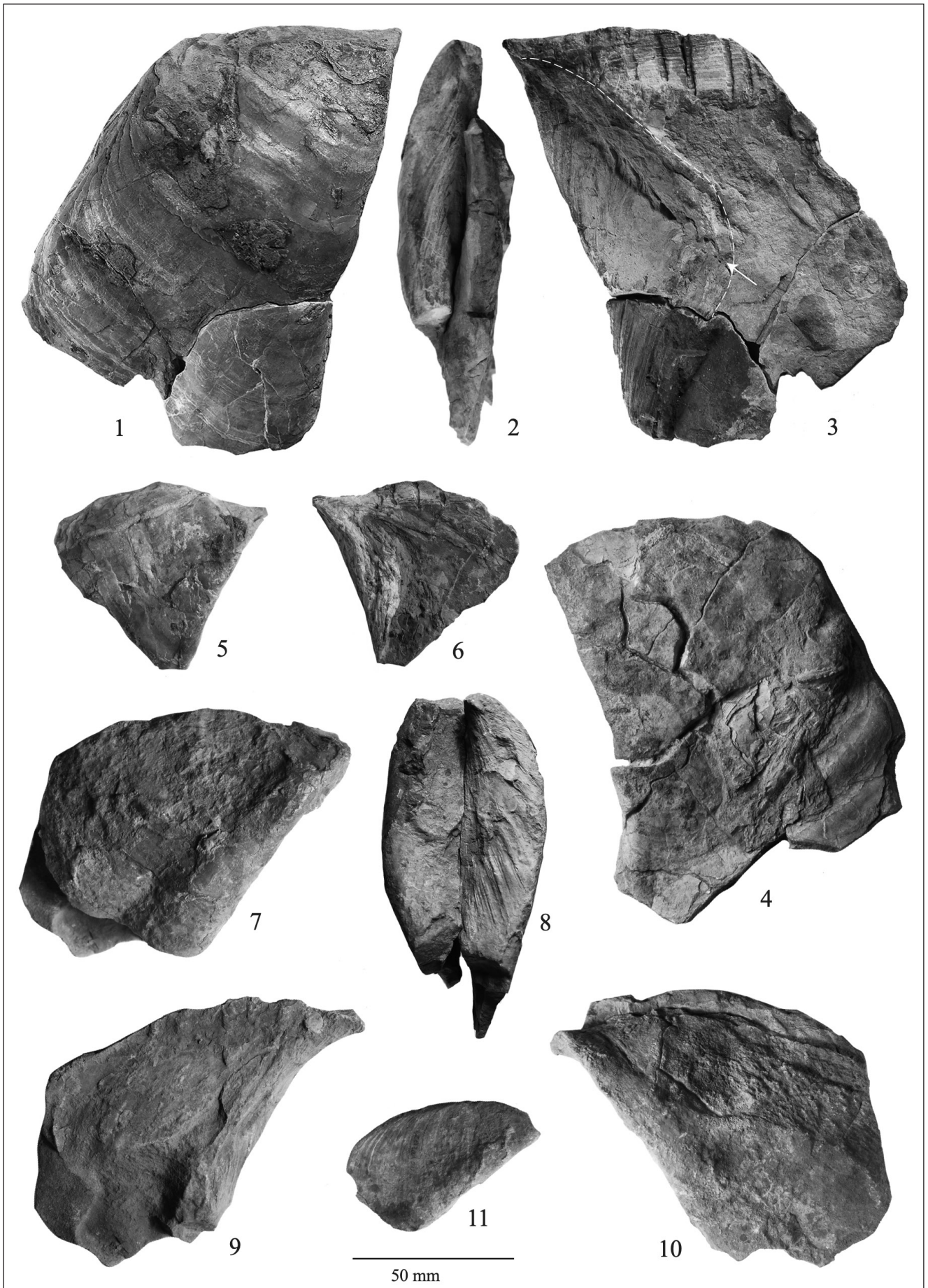


PLATE 4

ned ridges (Pl. 5, figs 3, 4) which interdigitate with adjacent prisms. These oblique ridges suggest a prism growth pattern like that of *Litbiotis problematica* and *Cochlearites loppianus* (FISphP microstructure) in which the large and elongated first-order prisms are built by lath-type second-order prisms, with helical development, raising from a nucleation site located at the apex of the first-order prisms (Posenato et al. 2022). This latter microstructure, which represents a very peculiar character of these bivalve taxa, has been extensively described, illustrated and discussed in Posenato et al. (2022), to which we refer. The myostracal prisms are very narrow and elongated, about 1 μm wide and more than 100 μm long (Pl. 5, figs 7, 8).

Remarks. Shells of the population of *Pachygerwillia anguillaensis* n. gen. n. sp. from Ponte dell'Anguillara are characterized by widely variable outlines mostly concerning the shell obliquity (angle between the hinge line and anterior carina) which range between ca. 30° and 80° (50° on average). In less oblique shells, with a subrectangular outline (e.g., MPL8660-M3, Pl. 1, figs 5-9; MPL8660-M27, Pl. 2, figs 5-7), the cardinal platform is large and elongated in a ventral direction. The teeth of these shells are almost perpendicular to the hinge margin and ventrally converging. In more inclined shells (e.g., MPL8660-M10, MPL8660-M31, MPL8660-M37; Pl. 2 figs 1-3, 8, 9), the cardinal platform is smaller; teeth decrease in number and their inclination follows the shell obliquity. The crest of the anterior carina ranges from sharp (e.g., MC1208, Pl. 1, figs 10, 11) to broadly rounded (e.g., MPL8660-M27, Pl. 2, fig. 5); it may be gradually merged to the middle-posterior part of the shell (e.g., MC1208, Pl. 1, figs 10, 11) or may be separated from it by a broad radial sulcus (e.g., MPL8660-M27, Pl. 2, Fig. 5). The anterior area is flattened and perpendicular (MPL8660-M3, Pl. 1, Fig. 9; MPL8660-M15, Pl. 2, fig. 13) to the commissural plane or concave and inwards inclined (MC1208, Pl. 1; fig. 11). The ventral margins are missing in all the specimens because they were made of calcitic simple prisms (outer layer) and nacre (middle layer) which are usually not preserved in the large bivalves of the *Litbiotis* facies (e.g., Posenato et al. 2022).

The muscle scar is seen in only two specimens (MPL8660-M27, Pl. 2, fig. 6 and MPL8660-M39, Pl. 3, fig. 8); it is located between the anterior part of the body cavity and the ventral extremity of the car-

dinal platform. The anterior auricle is variably developed. It can be absent (e.g., MC1208, Pl. 1, figs 10-11) or blunt and elongated (e.g., MPL8660-M21, MPL8660-M30; Pl. 2, figs 4, 10, 11). The byssal gape is not clearly seen. However, on the anterior area of some specimens (e.g., MPL8660-M15, Pl. 2, fig. 13) the occurrence of an oblique groove suggests its presence. It was probably a narrow and elongated slit along the anterior commissure, located where the byssal groove reaches the anterior margin.

The shell was covered by growth lines, but in most of the analyzed specimens, they are preserved only along the anterior region; on the rest of the shell surface, they are not visible as the outer calcitic layer is not preserved due to the high amount of organic matter occurring between the prisms which decomposed after the animal death causing prism disruption (e.g., Posenato et al. 2022). However, the scaly growth lines can be observed in the specimen MC1208 (Pl. 1, figs 10-11) where they indicate the shape of the ventral margin.

The two specimens from the Taramelli collection determined by Boehm (1884) as "*Perna* aff. *Taramelli*" are here attributed to *Pachygerwillia anguillaensis* n. gen. n. sp. They have been collected in the Premaloch Valley (Asiago, Vicenza Province) and consist of an articulated shell with an obliquity of ca. 50° and a twisted left beak (KM16815a; Pl. 4, figs 7-11), and of a small right valve with an obliquity angle of ca. 40° (KM16815b; Pl. 7, fig. 11). They display the most important morphological taxonomic characters of *P. anguillaensis* n. gen. n. sp. consisting of a very thick shell wall, large cardinal platform, and twisted beaks.

Paleoecology. The mode of life of *Pachygerwillia anguillaensis* n. gen. n. sp. has been discussed by several authors (Accorsi Benini & Broglio Loriga 1982; Seilacher 1984; Broglio Loriga & Posenato 1996; Fraser et al. 2004). It was a byssate and gregarious bivalve which formed clusters in shallow subtidal settings, transitional to swamps and emerged land (Accorsi Benini & Broglio Loriga 1982). The occurrence of a shallow byssal groove on the anterior surface, but of an inconspicuous byssal gape, suggests a weak byssal attachment. The bottom stabilization was therefore also guaranteed by a thick and heavy shell (edgewise recliner with a heavy-weight strategy of bottom stabilization *sensu* Seilacher 1984; Broglio Loriga & Posenato 1996; Fig. 4).

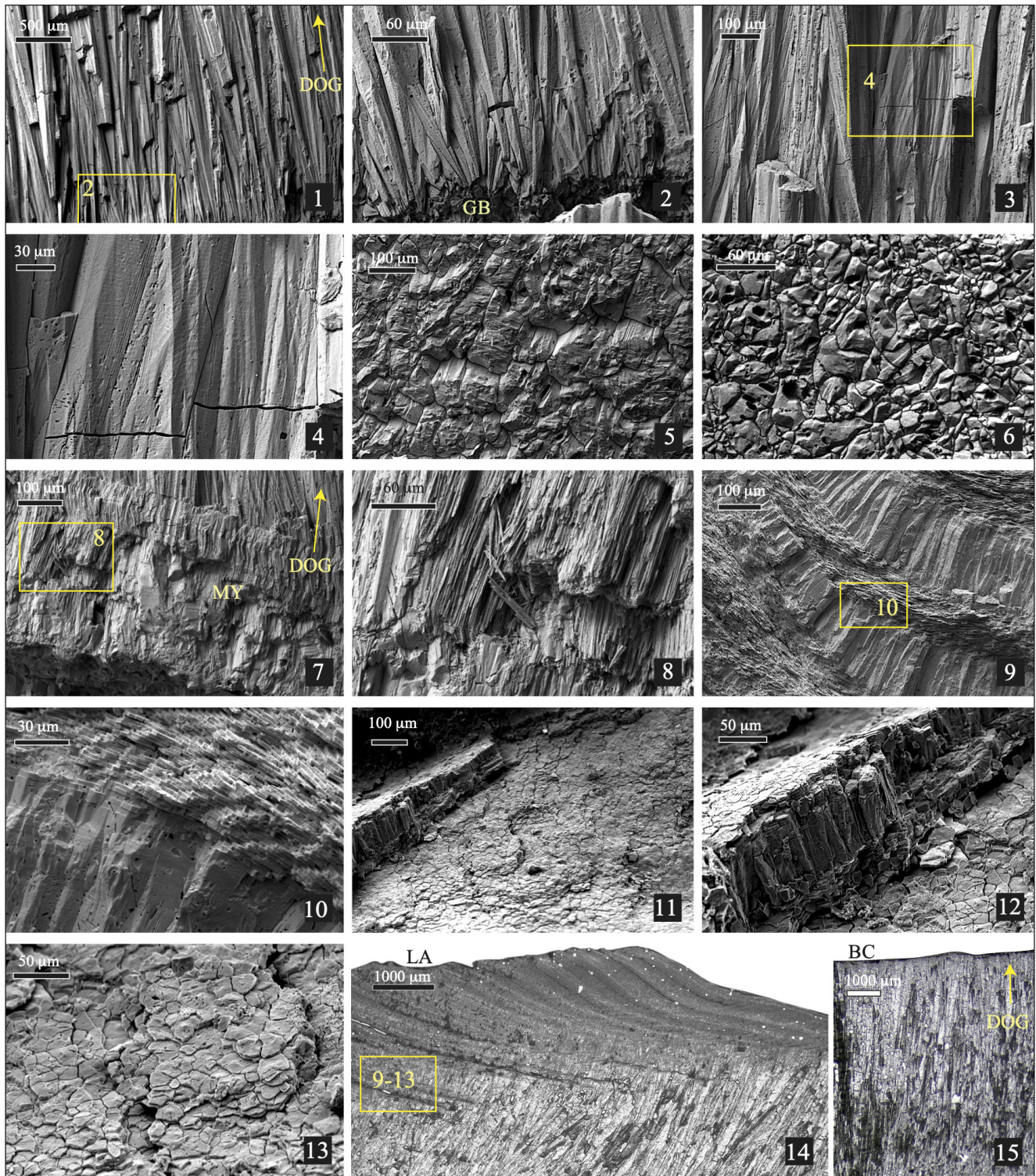


PLATE 5

Microstructures of *Pachygerwillia anguillaensis* n. gen. n. sp., Vajo dell'Anguilla (Lessini Mountains), Rotzo Formation, lower Pliensbachian, MPL8660-M2 (5, 6, 9-15) and MPL8660-M14 (1-4, 7, 8) specimens. Figs 1-4) first-order fibrous irregular spherulitic prisms (FISphP) on fractured tangential vertical sections in the inner part of the shell towards the cardinal area; prism rise from a marked growth break (GB; DOG, direction of growth). Figs 5, 6) horizontal sections of the inner shell layer with FISphP microstructure. Figs 7, 8) tangential radial vertical sections of the outer part of the shell with the myostracum (MY). Figs 9-13), fractured vertical sections, below the ligamental area, showing the interdigitation between nacre of the ligamental area and the underlain fibrous irregular spherulitic prismatic microstructure (the position of the photograph is indicated in Fig. 14). These samples have been etched with 1% HCl for 5 s, gold coated and observed at SEM. Figs 14 and 15, acetate peels of vertical radial sections below the ligamental area (LA, 14), where the prisms are fan-like arranged and slightly inclined with respect to the growth direction, and the body cavity (BC, 15) where the prisms are almost perpendicular to the inner shell surface.

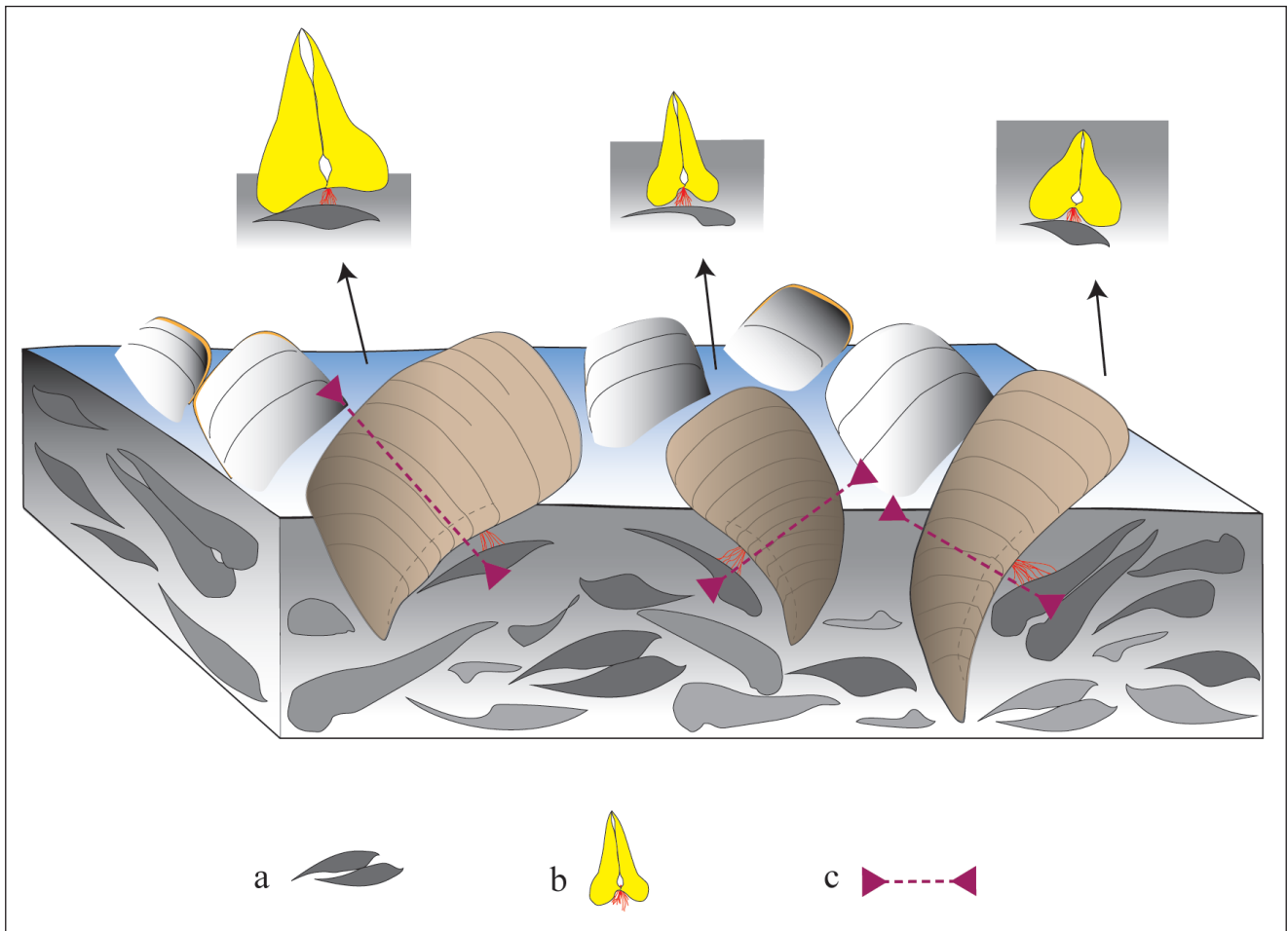


Fig. 4 - Reconstruction of the life habit of *Pachygerwillia anguillaensis* n. gen. n. sp. (from Broglio Loriga & Posenato 1996, mod.).

a) buried dead shells; b) living shell in life position; c) position of the antero-posterior sections sketched in the upper part of the figure.

The life style ranged from deep to shallow semi-infaunal, endobysate, respectively adopted by elongated mytiliform or stick-like shells and by subrectangular shells (Broglio Loriga & Posenato 1996: text-fig. 4; Fig. 4). The occurrence of a still functional ligament at the mature stage indicates that the shell maintained the ability to keep the valves articulated. However, a ventrally expanded cardinal area acted as a fulcrum for the muscle contraction on the thin and highly flexible ventral regions. Therefore, the margin flexibility reduced the angle of shell opening.

Pachygerwillia taramellii (Boehm, 1884)

Plate 4, figs 1-6

1884 *Perna taramellii* n. sp., Boehm, p. 766. pl. 17, figs. 1, 2; pl. 18, figs. 2-4.

1974 *Perna taramellii* Boehm 1884 - Benini & Loriga, p. 237.

Lectotype: KM17794a, an articulated shell with detached valves (Pl. 4, Figs 1–4), designated herein.

Description. Shell large, subequivalve, sub-rectangular to elongated mytiloid in outline, beak terminal and pointed; shell obliquity of about 60–75°; shell inflation about twice of wall thickness, anterior and posterior wings inconspicuous; anterior carina low, rounded and delimiting an anterior area with an oblique byssal groove emerging from a rounded gape along the mid anterior margin; anterior margin S-shaped, dorsal margin straight to gently convex, posterior margin straight, ventral margin weakly convex. Ornamentation consisting of irregularly distributed growth scales. Ligamental area flat with irregularly spaced and narrow pits, at least 8 in number in adult individuals; juveniles with elongated cardinal platform bearing transversally elongated teeth; adductor scar not preserved.

Stratigraphic range. Late Pliensbachian – early Toarcian.

Remarks. The description and discussion of this species are based on figured and non-figured

syntypes of “*Perna Taramellii*”, some of which belong to the Taramelli collection kept in the Kosmos Museum of the Pavia University. All the syntypes have been collected from the Rotzo Formation from Vajo del Paradiso (Lessini Mountains, Verona Province). In the Kosmos Museum, “*Perna Taramellii*” is recorded by two specimens: a juvenile right valve, and an articulated subequivalve mature shell with detached valves (Pl. 4, figs 1–4), proposed herein as lectotype. None of these specimens seems to be those figured by Boehm (1884). It cannot be excluded that the published drawings may not faithfully reproduce the studied specimens. The figured specimen of the Nicolis collection, Verona Museum of Natural History (Boehm 1884: pl. 18, fig. 4) consists of an umbonal fragment of a left valve in which the anterior area has a deep anterior byssal groove emerging from a rounded byssal gape.

“*Perna Taramellii*” is included in the new genus *Pachygervillia* because of a very large and toothed cardinal platform in adult individuals and subequivalve shells. It differs from *Pachygervillia anguillaensis* n. gen. n. sp. by a more pointed and non-twisted beak, a lesser shell thickness, and by the occurrence of a byssal groove and gape on both valves. It differs from *Gervilleioperna* because the latter genus has an inequivalve shell, an inconspicuous byssal gape, and a well-developed posterior wing. *Pachygervillia taramellii* occurs in younger layers than *P. anguillaensis* n. gen. n. sp. as the type-locality (Vajo del Paradiso succession, Lessini Mountains) and is late Pliensbachian in age (Posenato & Masetti 2012).

The syntypes of *P. taramellii* from the “Durga-horizonte” of Vajo del Paradiso are embedded in a marly rocky matrix and were deformed during diagenetic processes, thus the anterior area is usually folded inward (e.g., Pl. 4, figs 1–4). Therefore, the shell thickness is reduced, and the original morphology (e.g., shell inflation) is not completely detectable in the available fossil material. According to Dames (1891) *Perna taramellii* is characterized by a much higher intraspecific variability than according to Boehm’s description, but this variability could also be related to deformation, caused by sediment compaction. *Perna taramellii* is cited by Geyer (1977: 314) as *Isognomon taramellii* (Boehm). However, Geyer (1977) assigned to Boehm’s species the specimens figured by Berti Cavicchi et al. (1971: pl. 3, figs. 1–3) which were later classified by Accorsi Benini (1979) as *Lithioperna scutata* (Dubar, 1948).

The last occurrence of this species is probably recorded by “*Mytiloperna* sp.” specimens occurring in the upper part (early Toarcian) of the *Lithiotis* Member of the Apennine Carbonate Platform (Posenato et al. 2018, fig. 9). A precise specific determination of these specimens is impossible because they are embedded in hard limestone. However, the greater dimensions of the pallial cavity and the lower shell thickness make them close to *P. taramellii*.

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