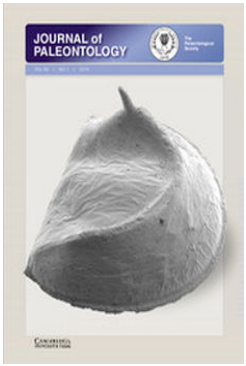

Parainoceramya n. gen. for *Parainoceramus* Cox, 1954 (*ex* Voronetz, 1936) *partim* (Bivalvia, Jurassic)

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Parainoceramya n. gen. for *Parainoceramus* Cox, 1954 (*ex* Voronetz, 1936) *partim* (Bivalvia, Jurassic)

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Abstract.—Several Jurassic pterioid bivalve species have been referred to *Parainoceramus* Cox by different authors, yet this has proved inadequate because the meaning of such genus has been compounded by nomenclatural and idiomatic problems, as well as misinterpretations. Hence, the new genus *Parainoceramya* is here proposed to accommodate several species previously referred to *Parainoceramus*, with *Crenatula ventricosa* J. de C. Sowerby as its type. Permian species originally assigned to *Parainoceramus*, including the type species, are referred to the genus *Kolymia* Likharev. All species attributed to *Parainoceramus* s.l. are reviewed and the new genus is compared with related genera. As here understood, the new genus is first recorded in the Hettangian and attained a cosmopolitan distribution; its last occurrence is probably Berriasian.

Introduction

Despite their abundance and diversity, the 'inoceramids' are a poorly understood set of bivalves, and especially Jurassic taxa allied to this group have been the subject of many controversies about their affinities (Crame, 1982; Crampton, 1996; Knight and Morris, 2009). In this context, several species of small pterioid bivalves known from Jurassic deposits worldwide, some of them formerly referred to "*Inoceramus*", were regarded by Cox (1954) as belonging to a separate genus, which he referred to *Parainoceramus* Cox, 1954 (*ex* Voronetz, 1936 [unavailable due to lack of type species designation]) instead of proposing a new taxon. This decision, which was followed by most subsequent authors, was later proved to be inadequate for several reasons discussed in this paper. Some of these Jurassic species were referred to the genus *Pseudomytiloides* Cox, 1969 (*ex* Koschelkina, 1963) or to *Parainoceramus* (e.g., *Parainoceramus lunaris* Hayami, 1960 and *Parainoceramus matsumotoi* Hayami, 1960 were referred to *Pseudomytiloides* by Hayami [1975]) but there are enough morphological characters to distinguish the two stocks (see Table 2). Ros (2009, p. 86), Ros et al. (2009) and Ros-Franch et al. (2014) noticed this situation and concluded that this group of Jurassic species can no longer be referred to *Parainoceramus* s.s.

We discuss here the Jurassic species referred to *Parainoceramus* s.l., and provide a solution to the taxonomic/nomenclatural problems by proposing a new genus to include some of them, while trying to maintain Cox's concept of Jurassic *Parainoceramus*.

Background

The generic name *Parainoceramus* was proposed by Voronetz (1936, p. 23–24) on the basis of 15 badly preserved specimens from sediments then dated as Carnian from northern Siberia. The author included four new species in this new genus: *P. bulkurensis*, *P. nikolaewi*, *P. lenaensis*, and *P.* (?) *gervillia*, but he did not designate a type species, and thus this generic name was not available. He described all species as being edentulous.

Years later Cox (1954) completed the requirements for the validity of the name by designating *P. bulkurensis* (Fig. 1.1) as the type (ICZN Art. 13B, 50). He did not see Voronetz' material, but nevertheless he included within *Parainoceramus* two other species, widely distributed in the European Early Jurassic: *Crenatula ventricosa* J. de C. Sowerby, 1823 (Fig. 1.7–9) and *Inoceramus substriatus* Münster in Goldfuss, 1835 (Fig. 1.2–4). On the basis of his knowledge of these Jurassic species, he added to Voronetz' original diagnosis the presence of an anterior auricle and anterior tooth-like ridges on some species. It is here necessary to point out that Voronetz' original diagnosis already mentioned the presence of an anterior auricle, but his Russian text was incorrectly translated into English in his paper (1936, p. 34), and the word "lunule" was used instead of the intended "auricle".

Cox's (1954) concept of the genus *Parainoceramus* was adopted by nearly all later authors dealing with Jurassic material (i.e., Hayami, 1960; Speden, 1970; Duff, 1978; Crame, 1982; Kelly, 1984; Damborenea, 1987, 1990; Chen, 1988; Conti and Monari, 1991; Monari, 1994; Knight and Morris, 2009), and

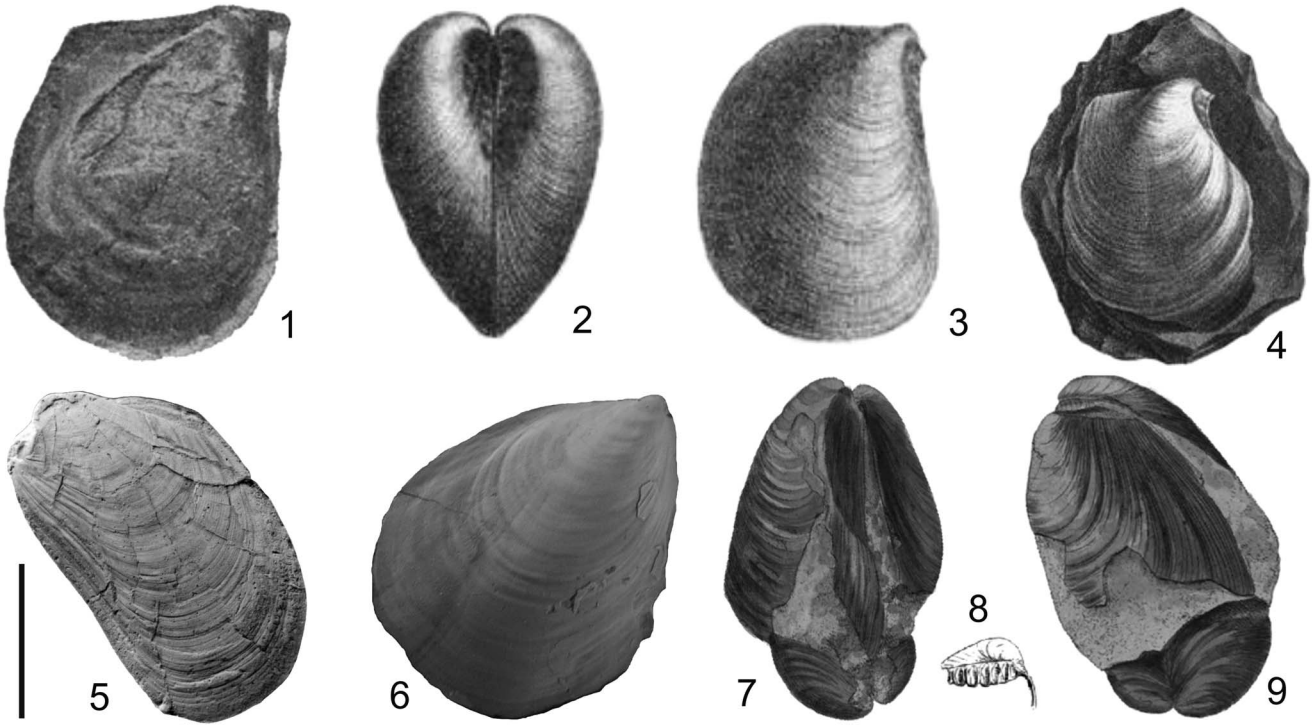

Figure 1. **(1)**, *Kolymia bulkurensis* (Voronetz), reproduction from Voronetz (1936), pl. 2, fig. 1; **(2–4)**, *Parainoceramya substriata* (Münster in Goldfuss, 1835), reproduction from Goldfuss (1835), pl. 115, fig. 1 and pl. 109, fig. 2; **(5)**, *Parainoceramya*? *apollo* (Leanza, 1942), lectotype, MLP 6252, composite mould of left valve, specimen figured in Leanza, 1942, pl. 2, fig. 1 and Damborenea, 1987, pl. 4, fig. 1; **(6)**, *Parainoceramya*? *dubia* (Sowerby, 1829), Dörnten, Harz, Germany, lower Toarcian, collected by G. Westermann, right valve, MLP 34455; **(7–9)**, *Parainoceramya ventricosa* (Sowerby, 1823), reproduction from J. de C. Sowerby (1823), pl. 443. Scale bar 1 cm for figures 1.5 and 1.6.

more Jurassic species from around the world were added (Table 1). Nevertheless, it is evident that this was often done in the absence of a better alternative; hence, almost all authors felt the need to provide their own diagnosis of the genus. These diagnoses differ from each other in important aspects of the hinge region such as the presence or absence of anterior and/or posterior teeth.

Along this line Hayami (1960) recognized the need to taxonomically group small Jurassic inoceramid species without regular ornamentation, which he referred to *Parainoceramus* following Cox (1954). Hayami (1960) described two Japanese species and reviewed previous literature, including in the genus *Parainoceramus* other Early Jurassic species from several parts of the world (Alps, Carpathians, Caucasus, Siberia, New Caledonia, and Argentina). He then extended the genus concept to include species with posterior teeth. Nevertheless, he later referred his Japanese species to *Pseudomytiloides* (Hayami, 1975).

A significant detail is that in the Treatise on Invertebrate Paleontology (Cox, 1969), the type species of *Parainoceramus* was not illustrated. Furthermore, although the figure legend states that fig. C48-4 corresponds to *P. substriatus* taken from Münster in Goldfuss (1835); in fact the reproduced figure does not correspond to any of Münster's illustrations of that species (pl. 109, fig. 2, and pl. 115, fig. 1, reproduced here on Fig. 1.2–4). Instead, the figure reproduced in the Treatise is Goldfuss (1835) figure 3 from plate 109, which corresponds to material referred to *P. ventricosus* (Sowerby, 1823) (=*Inoceramus pernoides* Goldfuss 1835), see Oppel (1856, p. 180) and Giebel (1866, p. 55). Significantly, the specimen figured in the Treatise lacks anterior auricles, which, together with the incorrect translation of Voronetz' diagnosis already mentioned, may have added confusion about recognition of *Parainoceramus* species and distinction between *Parainoceramus* and *Pseudomytiloides*, whose type species (*Mytiloides marchaensis* Petrova, 1947) lacks anterior auricles. The stratigraphical range of *Parainoceramus* was stated as Late Triassic-Jurassic by Cox (1969).

Another point overlooked in the Treatise and by later authors is that Emel'yantsev et al. (1960; see also Muromtseva, 1979 and Astafieva, 1986) had re-dated the beds where Voronetz' original material was found as late Permian (Wuchiapingian and Changhsingian), and thus the stratigraphical range of *Parainoceramus* sensu Cox (1954) should have been late Permian (Siberia), Hettangian to Tithonian (cosmopolitan), with no record during the Triassic.

Speden (1970) described a new species from the Ururoan (Early Jurassic) of New Zealand, and at the same time pointed out the differences between Voronetz' and later authors' concepts of the genus. He noticed that in Voronetz' original material no teeth were described, while either anterior or posterior (or both) teeth were mentioned in some Jurassic species. He stated the need to carefully re-examine the original species and those included in the genus by subsequent authors.

In his monographic work Duff (1978) described *Parainoceramus subtilis* (Lahusen, 1883), and included anterior and posterior teeth in his emended diagnosis of the genus.

A breakthrough was provided by Muromtseva (in Muromtseva and Guskov, 1984) who referred some of the species described by Voronetz (1936) to *Kolymia* Likharev, 1941 in Likharev and Einor, 1941 (type species *Kolymia inoceramiformis* Likharev, 1941), and by Astafieva (1986, 1993), who revised Voronetz' original material, and concluded that *P. bulkurensis* and *P. nikolaewi* are subjective synonyms, *P. lenaensis* probably does not belong to the same genus, and *P.* (?) *gervillia* was based on too poorly preserved material. She also compared the diagnosis and the species referred by their original authors to the nominal genera *Parainoceramus* and *Kolymia*, concluding that these two generic names should be regarded as synonyms, since they share the diagnostic characters and the stratigraphical distribution. She regarded *Parainoceramus* as the junior subjective synonym, as it was validated only in 1954. Astafieva (1986) thus placed the type species of *Parainoceramus* within the Paleozoic genus *Kolymia*, but did not include there any of the Jurassic species later referred to *Parainoceramus* by other authors.

Although *Kolymia* was regarded as a junior synonym of *Atomodesma* von Beyrich, 1864 by Newell (1969), Kauffman and Runnegar (1975, p. 43) later argued that they should be considered as different genera, since *Kolymia* "lacks any trace of an umbonal septum, has a well developed ear on each valve, and a prominent byssal gape." *Kolymia* and related genera were grouped in the separate Family Kolymiidae Kuznetsov, 1973 (see revision in Biakov, 2008, 2012).

More recently, Conti and Monari (1991) and Monari (1994) described new Early Jurassic species from Turkey and Italy, respectively, and referred them to *Parainoceramus*.

At the same time Polubotko (1992) described the new genus *Arctomytiloides* Polubotko, 1992 from Hettangian and Sinemurian beds of Far East Russia, with *Pseudomytiloides rassochaensis* Polubotko, 1968, as the type, and referred it to the Retroceramidae. This genus was only used again by Aberhan (1998) for Early Jurassic material from western Canada (*Arctomytiloides*? cf. *rassochaensis* and *Arctomytiloides*? cf. *turomtchensis* Polubotko, 1992).

Recently Knight and Morris (2009) thoroughly revised the morphology and ultrastructure of the hinge plate of Jurassic and Cretaceous 'inoceramids', including several of the species discussed here. They followed Cox's concept of *Parainoceramus* and thus referred several Jurassic species to that genus. Their descriptions and discussions of the hinge characters of these species are instrumental to understand their morphology and relationships.

Thus, if we follow Paleozoic specialists in restricting usage of *Parainoceramus* to late Paleozoic species, and including its type *Parainoceramus bulkurensis* within the genus *Kolymia*, several widely distributed and common Jurassic species which were referred to *Parainoceramus* remain without a genus to be allocated. Due to the differences between this group of species with related genera, as discussed further down, a new name is required, which is proposed below. The new genus is doubtfully referred to the Inoceramidae on account of its multivincular ligament, shell ultrastructure and general shell shape. To choose the type species we tried to preserve as far as possible the current usage of Jurassic '*Parainoceramus*', mostly based on Cox' (1954) concept. Suprageneric systematic arrangement follows Carter et al. (2011).

Systematic Paleontology

Class Bivalvia Linné, 1758
Order Myalinida Paul, 1939
?Superfamily Inoceramoidea Giebel, 1852
?Family Inoceramidae Giebel, 1852
(Placed on the Official List by Opinion 473 [1957, p. 281] but attributed erroneously to Zittel [1881])

Genus *Parainoceramya* new genus

Type species.—*Crenatula ventricosa* J. de C. Sowerby, 1823 (p. 64, pl. 443), from Pliensbachian (Lower Jurassic) beds of Great Britain. Original illustrations reproduced here in Figure 1.7–9; for illustrations of hinge details see Knight and Morris (2009, pl. 3, figs. 1–4).

Diagnosis.—Shell equivalve, convexity low to high, very inequilateral, obliquely elongated, with variable outline in lateral view (rectangular, mytiliform or rhomboidal), ortho- to proso-cline, with depressed posterior wing not clearly separated from body of shell, and usually with a small anterior auricle. Umbones terminal to subterminal, prosogyrate, only slightly protruding above hinge margin. Hinge plates diverging from each other. Multivincular ligament with numerous subtriangular resilifers separated by equally wide interspaces. Ventral margin of hinge plate undulate. Poorly developed anterior umbonal septa, larger on left valves. Some species with anterior denticles or crenulations. Ornament consisting of weak irregular concentric plicae, and sometimes regular growth lamellae. Few species with fine radial striae. Shell very thin, with outer prismatic calcite layer and inner nacreous layer. Hinge plate aragonitic in continuation with the inner nacreous shell layer and ligament attachment surfaces covered by a thin layer of aragonitic prisms.

Etymology.—After *Parainoceramus* plus *mya* (f., Latin), a sea-mussel.

Remarks.—All species of this genus show a great shell shape variability in lateral view. Despite their abundance and wide distribution, hinge plate and internal characters are unknown in many of them, thus hindering a comprehensive revision and a proper discussion of possible relationships. On the other hand, the hinge morphology of some of them (including the type species) was recently revised and superbly illustrated by Knight and Morris (2009).

A posterior tooth is mentioned in some of the species once referred to *Parainoceramus*, but this structure was not confirmed in any of the species included with certainty in *Parainoceramya*. Umbonal septa and clefts may have been interpreted as anterior teeth, and anterior "denticles" were illustrated by Knight and Morris (2009, pl. 4, figs. 4–6) for *P*?. *dubia* (J. de C. Sowerby).

Included species.—The nominal species once referred to this taxon are listed in Table 1, with indication of the species we regard now as belonging to *Parainoceramya* according to the diagnosis given here. For different reasons some species are

Table 1. List of species which have been referred to *Parainoceramus*, with indication of the original description and illustration of each of them, and their relationships according to the present paper.

Species name (Originally referred to)	Author, year; Description; Illustration	Referred to *Parainoceramus* by	Distribution; Age	Here referred to
altineri (*Parainoceramus*)	Conti & Monari, 1991; p. 250-251; t-fig. 4; pl. 2, figs. 11-17	Conti & Monari, 1991	W Pontides, Turkey; Sinemurian – Pliensbachian	*Parainoceramya*?
amygdaloides (*Inoceramus*)	Goldfuss, 1835; p. 110; pl. 115, fig. 4a-e	Hayami, 1960	Germany, Poland, Caucasus, Crimea, England, Spitsbergen, Siberia; Toarcian – Aalenian	*Mytiloides*?
apollo (Inoceramus)	Leanza, 1942; p. 157 (Damborenea, 1987, p. 143-144); pl. 2, fig. 1	Hayami, 1960	Neuquen & Chubut basins (Argentina), Chile; Sinemurian – Pliensbachian	*Parainoceramya*?
bileciki (*Parainoceramus*)	Conti & Monari, 1991; p. 251; t-fig. 5; pl. 3, figs. 5-10	Conti & Monari, 1991	W Pontides, Turkey; Sinemurian – Pliensbachian	*Parainoceramya*?
bulkurensis (Parainoceramus)	Voronetz, 1936; p. 24-25, 34; pl. 1, figs. 2, 8, 10	Voronetz, 1936	Siberia; late Permian	*Kolymia*
cantianensis (Parainoceramus)	Monari, 1994; p. 162-163; t-fig. 7; pl. 1, figs. 8-14	Monari, 1994	Italy, Hungary; middle Toarcian	*Parainoceramya*?
cinctus (Inoceramus)	Goldfuss, 1835; p. 110; pl. 115, fig. 5	Hayami, 1960	Germany, England, Caucasus; Toarcian	*Pseudomytiloides*
cramei (Parainoceramus)	Clausen & Wignall, 1990; p. 111-112; t-fig. 4; pl. 4, figs. A-D	Clausen & Wignall, 1990	England; Kimmeridgian	*Parainoceramya*
depressus (Inoceramus)	Münster in Goldfuss, 1835; p. 109; pl. 109, fig. 5	Hayami, 1960	Germany; Hettangian – Sinemurian	*Parainoceramya*
dubius (Inoceramus)	J. de C. Sowerby, 1829; p. 162; pl. 584, fig. 3 (Knight & Morris, 2009, pl. 4, figs. 1-6)	Hayami, 1960	Europe; Pliensbachian-Toarcian	*Parainoceramya*?
farinacciae (Parainoceramus)	Conti & Monari, 1991; p. 252; pl. 1, figs. 6-15	Conti & Monari, 1991	W Pontides, Turkey; Sinemurian – Pliensbachian	*Parainoceramya*?
fuscus (Inoceramus)	Quenstedt, 1858; p. 355-356; pl. 48, fig. 18	Monari, 1994	Europe; lower Bajoncian	*Parainoceramya*
gervillia (*Parainoceramus*?)	Voronetz, 1936; p. 25-26, 34; pl.1, fig. 11	Voronetz, 1936	Siberia; late Permian	*??*
golberti (Inoceramus)	Zakharov & Turbina, 1979; p. 30 (Kelly, 1984, p. 42); pl. 2, figs. 3-5, pl.3, figs. 1-5, pl. 4, fig. 1 (Kelly, 1984, pl. 6, fig. 11)	Kelly, 1984	N Siberia, E England; Volgian (=Tithonian), Ryazanian (=Berriasian)	*Parainoceramya*?
gryphaeoides (*Mytulites*)	Schlotheim, 1820; p. 296-297; Goldfuss, 1835, pl. 115, fig. 2	Hayami, 1960	Germany, Caucasus; Pliensbachian – Toarcian	*Parainoceramya*
jinjiensis (Parainoceramus)	Chen, 1988; p. 46-47 (Stiller, 2006, p. 21); pl. 4, figs. 7-14 (Stiller, 2006, pl. 1, fig. 12)	Chen, 1988	S China; Hettangian – Sinemurian	*Parainoceramya*?
lenaensis (Parainoceramus)	Voronetz, 1936; p. 25, 34; pl. 1, figs. 5, 7, 9	Voronetz, 1936	Siberia; late Permian	??
lunaris (Parainoceramus)	Hayami, 1960; p. 295-296; pl. 15, fig. 1	Hayami, 1960	Japan, China; Pliensbachian	*Bakevellia*?
martini (Parainoceramus)	Speden, 1970; p. 831; figs. 2-10	Speden, 1970	New Zealand; Ururoan (early Jurassic)	*Parainoceramya*
matsumotoi (Parainoceramus)	Hayami, 1960; p. 296-297; pl. 15, figs. 2-8	Hayami, 1960	Japan, China; Hettangian – Toarcian	*Parainoceramya*?
nicolaewi (Parainoceramus)	Voronetz, 1936; p. 24, 34; pl. 1, figs. 4, 6, 12, 13	Voronetz, 1936	Siberia; Late Permian	*Kolymia*
nicosiai (Parainoceramus)	Conti & Monari, 1991; p. 253; t-fig. 7; pl. 2, figs. 4-10	Conti & Monari, 1991	W Pontides, Turkey; Sinemurian – Pliensbachian	*Parainoceramya*?
nitescens (Inoceramus)	Arkell, 1933; p. 218–219; pl. 28, figs. 2-3	Jaitly *et al.*, 1995	England, India; Oxfordian, Callovian	*Parainoceramya*?
obliquus (*Inoceramus*?)	Morris & Lycett, 1853; p. 24; pl. 6, fig. 12	Hallam, 1976; Aberhan, 2002	England	*Retroceramus*?
pernoides (Inoceramus)	Goldfuss, 1835; p. 109; pl. 109, fig. 3	Hayami, 1960	Germany; Pliensbachian	*Parainoceramya*
pinnaeformis (*Gervillia*)	Dunker, 1851; p. 156; pl. 25, figs. 10-11	Hayami, 1960	Germany; Hettangian	*Parainoceramya*?
rasenensis (Inoceramus)	Blake, 1880, p. 235; Blake, 1875, p. 229 (as *I. expansus*); Blake, 1875, pl. 12, fig. 7 (Knight & Morris, 2009, pl. 4, figs. 9-13)	Hallam, 1976	England; Kimmeridgian	*Parainoceramya*?
substriatus (*Inoceramus*)	Münster in Goldfuss, 1835; p. 108; pl. 109, fig. 2, pl. 115, fig. 1 (Knight & Morris, 2009, pl. 3, figs. 5-9)	Cox, 1954; Hayami, 1960	Europe, Argentina; Liassic (early Jurassic)	*Parainoceramya*
subtilis (*Perna*)	Lahusen, 1883; Duff, 1978, p. 49-51; Duff, 1978, t-fig. 15-16, pl. 3-4	Duff, 1978	England, Russia; Callovian, Oxfordian	*Parainoceramya*
thermarum (Perna)	Moesch, 1867; p. 308-309; pl. 3, fig. 2	Hayami, 1960	Switzerland; Bathonian	??
ventricosa (*Crenatula*)	J.de C. Sowerby, 1823; p. 64; pl. 443 (Knight & Morris, 2009, pl. 3, figs. 1-4)	Cox, 1954; Hayami, 1960	England, France; Pliensbachian	*Parainoceramya*
westermanni (Parainoceramus?)	Damborenea, 1990; p. 742; figs. 6.3-6	Damborenea, 1990	Neuquen Basin (Argentina); Bajocian	*Parainoceramya*?

Table 2. Comparison of *Parainoceramya* with other related genera.

Genus	*Parainoceramus sensu* Cox, 1954 [=*Kolymia* + *Parainoceramya]*	*Parainoceramya* new genus	*Pseudomytiloides* Cox, 1969 [ex Koschelkina, 1963]	*Arctomytiloides* Polubotko, 1992	*Lenella* Koschelkina, 1962	*Arcticeramus* Koschelkina, 1962	*Lenoceramus* Polubotko, 1992
Type species	P*arainoceramus bulkurensis* Voronetz, 1936	*Crenatula ventricosa* J. de C. Sowerby, 1823	*Mytiloides marchaens*is Petrova, 1947	*Pseudomytiloides rassochaensis* Polubotko, 1968	*Lenella tiungensis* Koschelkina, 1962	I*noceramus arcticus* Koschelkina, 1962	*Mytiloceramus (Lenoceramus) vilujensis* Polubotko, 1992
Shell shape	Rectangular or rhomboidal	Rhomboidal, trapezoidal or obliquely elongated	Mytiliform, thin shell	Mytiliform	Mytiliform, thick shell	Rhomboidal	Mytiliform
Valves	Equivalve, of moderate convexity	Equivalve	Equivalve or slightly inequivalve	Slightly inequivalve, left valve more convex	Equivalve	Inequivalve, left valve more convex	Equivalve
Umbones	Not inflated, level with or not rising much above hinge-margin; beaks subterminal	Protruding only slightly above hinge margin, subterminal, prosogyrate	Prosogyrate, small	Left valve umbo more protruding	Low and narrow	Left valve umbo more protruding	Small, sligthly protruding, prosogyrate
Anterior auricle	Small	Usually small	No	Very small, different in left and right valves	Small, well defined, pointed	Unknown	Present in the left valve
Posterodorsal region	Sometimes posteriorly subalate	Flattened "wing" not clearly differentiated from body of shell	Not differentiated	Not differentiated	Obtuse, flattened	Small, blunt wing	Not differenciated
Hinge	Anterior teeth in some species	Some species with anterior denticles	Margin straight, short	Teeth absent	No teeth mentioned	Unknown	Teeth absent
Byssal gape	No	No	Unknown	Byssal notch below the umbo	Yes, below the anterior auricle	Unknown	Byssal notch below the umbo
Ligament area	Ligamental area flat, pits numerous (multivincular)	Multivincular, with pits and interspaces equally wide; aragonitic	Ligamental area narrow, 6- 8 ligamental pits	Moderately wide, up to 8 deep ligamental pits	Ligamental pits few and well separated	Short	Ligamental area narrow, at least 8 ligamental pits
Shell sculpture	Surface smooth or with weak concentric folds	Irregular commarginal plicae and sometimes regular growth lamellae	Regular closely spaced commarginal folds	Irregular commarginal folds, umbonal region smooth	Distant narrow commarginal folds	Strong commarginal folds	Almost smooth, with weak wrinkles
Shell microstructure	Prismatic layer thin except along hinge-line	Inner nacreous layer and outer pristatic calcite layer	Unknown	Prismatic layer thin	Unknown	Unknown	Nacreous shell layer moderately thin, prismatic layer allegedly not developed
Other internal characters	Unknown	Unknown	Unknown	Unknown	Small anterior adductor in early growth stages, later obsolete; pallial line discontinuous	Unknown	Unknown
Distribution	Permian – late Jurassic, cosmopolitan	Hettangian – Berriasian(?), cosmopolitan	Hettangian – Aalenian, Eurasia	Sinemurian – Toarcian?, NE Rusia and Canada?	early Jurassic, Siberia	Callovian – late Jurassic, N Russia	Toarcian – early Aaalenian, N Siberia and NE Russia

only doubtfully referred to this genus. For instance, *Inoceramus dubius* Sowerby was usually included into *Pseudomytiloides* (for instance Caswell et al., 2009), but it does not have the regular, closely spaced concentric folds mentioned in the original diagnosis of that genus. Instead, it bears a set of commarginal faint regular growth lamellae (which are not evident in all specimens), and thus it is most probably related to *Parainoceramya* (see Knight and Morris, 2009, pl. 4, figs. 1–6).

Geographical occurrence.—*Parainoceramya* had a cosmopolitan distribution during the Early Jurassic, especially during Pliensbachian times, but later it appears to have been mostly restricted to high latitudes (Damborenea, 1996; Ros, 2009).

Stratigraphical distribution.—The genus *Parainoceramya* as here understood ranges in age from Hettangian to Tithonian-Berriasian. The first appearance is *P. depressa* (Münster in Goldfuss, 1835, pl. 109, fig. 5) from the Hettangian-Sinemurian of Germany, and probably also *P.*? *jinjiensis* Chen (1988, pl. 4, figs. 7–14), from the same age in China, and *Inoceramus* sp. from Hettangian beds of Chile (Escobar, 1980, pl. 3, fig. 9). Late Jurassic species do show some differences with the Early Jurassic ones in the morphology of resilifer pits (e.g., Knight and Morris, 2009, appendix), and they may belong to another genus. With inclusion of these species in *Parainoceramya*, the last appearance of the genus would correspond to *Parainoceramus golberti* (Zakharov & Turbina, 1979) from upper Volgian (=Tithonian) of Eastern England (Kelly, 1984) and Ryazanian (=Berriasian) of northern Siberia. The genus was most diverse during the Early Jurassic times.

Systematic relationships.—The systematic affinities of this group of species have been subject of debate. Cox (1954) placed them within the Isognomonidae, but later several authors included them within the Inoceramidae (Hayami, 1960, 1975; Duff, 1978; Kelly, 1984; Damborenea, 1987, 1990; Clausen & Wignall, 1990; Conti & Monari, 1991; Monari, 1994; Aberhan, 1998). The new genus is here doubtfully referred to the Inoceramidae on account of the differential characters between both families listed by Crampton (1988). Recently Knight and Morris (2009) indicated important differences between the hinge plate of *P. ventricosa* and *P. substriata* and Cretaceous inoceramid species, involving both mineralogy and ultrastructure of the hinge plate. Even considering these differences, these authors propose that Jurassic 'inoceramids' with an aragonitic hinge plate could have been ancestors to the Upper Cretaceous inoceramids with calcitic hinge plate.

The comparison with similar genera with Jurassic occurrences is summarized in Table 2, mostly based on their type species. *Pseudomytiloides* differs from *Parainoceramya* by lack of anterior auricle and presence of more regular commarginal folds on the whole shell. *Arctomytiloides* and *Arcticeramus* Koschelkina, 1962 both have clearly inequivalve shells with left valves being more inflated. Species referred to *Lenella* Koschelkina, 1962 have thick shells, which are mytiliform in shape, and the anterior region is small and pointed. This genus may instead be related with the bakevellid *Aguilerella* Chavan, 1951, as indicated by Zakahrov (1965), who included it as its junior synonym (see also Damborenea, 1987, table 2 and Polutbotko, 1992, p. 61). *Lenoceramus* Polubotko, 1992 differs from *Parainoceramya* by having a conspicuous byssal notch and more developed anterior auricle; while the reported absence of prismatic layer may be a preservational artifact.

When the material is not well preserved and hinge characters are not clear, species of *Parainoceramya* can be particularly difficult to distinguish from species of *Pseudomytiloides* Cox, 1969 (Aberhan, 1998; Stiller, 2006).

Although the erection of *Parainoceramya* does solve the key nomenclatural problems associated to these Jurassic inoceramids, additional systematic work on them is necessary, which may eventually show the need to subdivide *Parainoceramya*, but that is clearly beyond the scope of this contribution.

Conclusions

Permian species originally included in *Parainoceramus* by Voronetz (1936) are referred to the genus *Kolymia*, while most of the Jurassic species later referred to *Parainoceramus* do not belong to this taxon and are assigned to the new genus *Parainoceramya* here proposed, with *Crenatula ventricosa* J. de C. Sowerby as type. As here understood, this was a cosmopolitan taxon ranging from Hettangian to (probably) Berriasian times.

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