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THE OCCURRENCE OF *NEOCOMICERAMUS CURACOENSIS* (WEAVER) IN THE AGRIO FORMATION, NEUQUÉN BASIN, ARGENTINA

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ABSTRACT—A number of Early Cretaceous inoceramids are widely known worldwide, but many are poorly understood. In particular the nature of ligaments and muscle scars are in need of major revision. The inoceramid genus *Neocomiceramus* Pokhialainen and the species *N. curacoensis* (Weaver) are revised based on newly collected materials in the Neuquén Basin, west-central Argentina. *Neocomiceramus curacoensis* is recorded in the Agua de la Mula Member of the Agrio Formation. A Late Hauterivian age is indicated by the associated ammonite fauna. *Neocomiceramus curacoensis* has a shell shape similar to *Inoceramus* J. Sowerby, but its ligament lies in a higher angle to the commissural plane and has a smaller number of pits. *Neocomiceramus curacoensis* probably lived reclined and byssally attached on muddy offshore substrates under restricted oxygen levels. The genus *Neocomiceramus* ranges from the Valanginian?, Hauterivian to Albian and probably is cosmopolitan. It differs from other well-recognized Early Cretaceous inoceramid genera, namely *Actinoceramus* Meek, *Anopaea* Eichwald, and *Coloniceramus* Pokhialainen by its shell shape, shell thickness, ornamentation, and ligament morphology.

INTRODUCTION

COMPARED WITH their Late Cretaceous counterparts, Early Cretaceous inoceramid bivalves have received little attention although they achieved a considerable diversity (Crame, 1985). They are best known from the study of Antarctic and North Pacific collections, and studies of Tethyan and South Pacific regions are incomplete. In particular, inoceramids from the Valanginian–Barremian interval are relatively poorly documented worldwide (see Dhondt, 1992). Studies of these inoceramids are needed to elucidate evolutionary pathways and to obtain correlation between Northern and Southern hemispheres. Inoceramids generally are referred to standard ammonite zonations that allow correlations with inoceramids from different parts of the world (e.g., Damborenea, 1990; Crampton, 1996b).

Extensive bed by bed collections in the Agrio Formation at four different localities in the Neuquén Province allowed the author to address the taxonomy and paleogeographic affinities of ''*Inoceramus*'' *curacoensis* Weaver, 1931 and discuss the genus *Neocomiceramus* Pokhialainen, 1972. In the Agrio Formation inoceramids are neither large (up to 15 cm in length) nor numerically dominant bivalves, but they are very abundant in several shale intervals cooccurring with other bivalves, small gastropods, crioceratid ammonites, and serpulids.

STRATIGRAPHY OF ARGENTINE CRETACEOUS INOCERAMIDS

Argentine Cretaceous inoceramids are not well understood. Most studies merely mention these bivalves and the lack of well-described and figured specimens. Inoceramids are known from two Mesozoic basins located in the Andes foothills in Patagonia (Fig. 1): the Neuquén Basin (36°–40°S) and the Austral Basin (44°–55°S). A brief review of the most relevant previous findings is presented in Table 1.

In the Neuquén Basin, inoceramids are mentioned in different Lower Cretaceous units, but they are only described and figured in the Agua de la Mula Member of the Agrio Formation by Weaver (1931). ''*Inoceramus*'' *mechanquilensis* Camacho, 1969 (fig. 1a) from the Late Cretaceous of Mechanquil Creek in Mendoza is based on the type specimen, CPBA8051. It shows a mytiliform outline and concentrically lamellose ornament that suggest close affinities to the Isognomonidae. This species should be placed within the genus *Isognomon* Lightfoot, 1786. Other records of Cretaceous inoceramids from the Neuquén Basin of questionable identity, age, and taxonomy can be found in Sokolov (1946).

In the Austral basin inoceramids are more abundant, ranging from Berriasian to Santonian, ?Maastrichtian. Berriasian, Hauterivian, and Albian records come from the Springhill, Río Mayer, and Yahgan Formations while Late Cretaceous inoceramids come mainly from the Cerro Toro Formation (Table 1). There are only two well-described and figured species: ''*Inoceramus*'' *andinus* Wilckens, 1907 and ''*Inoceramus*'' *steinmanni* Wilckens, 1907 (pl. 2, figs. 4, 5; pl. 3, fig. 1).

SYSTEMATIC PALEONTOLOGY

Annotations of synonymy entries follow recommendations of Matthews (1973) and Bengtson (1988). Only those citations with new and figured species of inoceramids are listed. Stratigraphic ranges of inoceramids from the Agrio Formation are based on the refined ammonite zonation proposed by Aguirre-Urreta and Rawson (1997, 2003) that correlates with the western Mediterranean (see Aguirre-Urreta et al., 1999). Descriptive terms and measurements are those described in Crampton (1996a) and Harries et al. (1996). Measurements were made on each specimen whenever possible using a digital caliper (accurate to 0.2 mm) and recorded in millimeters (Fig. 2): Length (L): total shell length measured parallel to the hinge axis; Height (H): total shell height perpendicular to length; Width (W): maximum width of articulated shell; L/H: elongation; W/H: inflation; Apical angle (AA): angle between the hinge line and tangent to the anterior margin; Length of ligament (L lig): maximum length measured parallel to hinge line; Height of ligament (H lig): maximum height measured perpendicular to hinge line; Pits: number of preserved ligament pits; Length of pits: maximum length measured parallel to hinge line; and Length of interspaces: maximum length measured parallel to hinge line. For measurements see Table 2. Shell size is said to be small, medium, or large as compared with other specimens of the same genus.

The holotype of ''*Inoceramus*'' *curacoensis* is deposited in the Burke Museum of Natural History and Culture, University of Washington (UWBM), Seattle, Washington, USA. The studied material of *Inoceramus cuvieri* J. Sowerby, 1814 is housed in the Natural History Museum (NHM), London, United Kingdom. All the specimens described in this article were collected from the Agua de la Mula Member of the Agrio Formation at four localities in the Neuquén Province (Fig. 1.2), and are housed in the Area de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (CPBA), Pabellón II, Ciudad Universitaria, 1428 Buenos Aires,

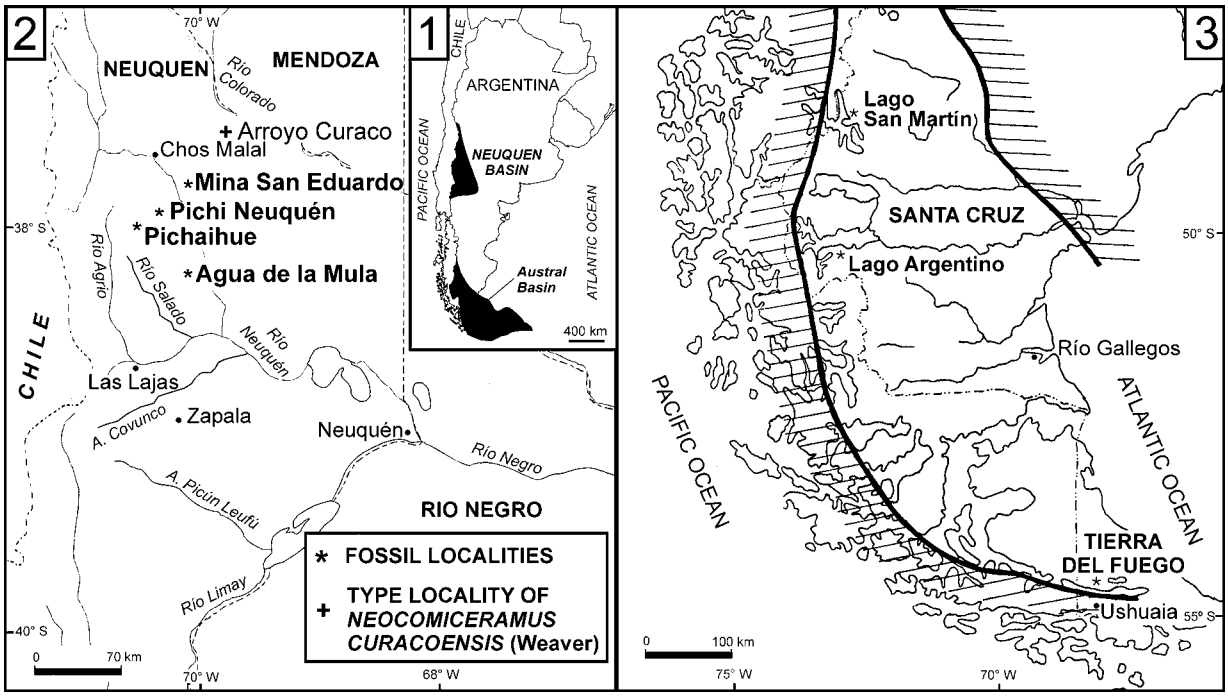


FIGURE *1—1,* Location of the Neuquén and Austral basins in the Andes foothills of Patagonia, Argentina; *2,* detailed map of the Neuquén Basin showing the studied localities; *3,* detailed map of the Austral Basin with location of fossil localities. In Mina San Eduardo, Pichaihue, and Agua de la Mula, a bed-by-bed analysis of the Agua de la Mula Member of the Agrio Formation was undertaken.

Argentina. Each catalogue number refers to a sample of specimens from a given section and stratigraphic position. Suffix number means the number of specimens discussed from a given catalogue number.

The systematic position of the family Inoceramidae within the bivalves has been changed from the traditional classification as pteriomorphians (see Cox, 1969) to place them next to Paleozoic praecardiodeans within the cryptodonts, based on morphological and paleoecological evidence (see Johnston and Collom, 1998). This conclusion should be regarded as provisional because the analysis was based on few Late Cretaceous inoceramid species and did not consider the highly variable morphology of other inoceramids.

Family INOCERAMIDAE Giebel, 1852

Diagnosis.—See Cox (1969) and Crampton (1988).

Occurrence.—Early Permian–Late Cretaceous (Harries and Crampton, 1998; Johnston and Collom, 1998).

Discussion.—In the Early Cretaceous there are at least three valid inoceramid genera: *Actinoceramus* Meek, 1864; *Anopaea* Eichwald, 1861; and *Coloniceramus* Pokhialainen, 1972. *Inoceramus* J. Sowerby, 1814 sensu lato (Harries and Crampton, 1998) encompasses a large number of Early Cretaceous *Inoceramus*-like species.

Actinoceramus (Albian to Cenomanian) is easily differentiated from *Anopaea* and *Coloniceramus* because it has a strongly to moderately inflated left valve with a terminal gibbous umbo, commarginal sculpture, and in many cases distinctive radial or oblique folds (Crampton, 1996b; see Fig. 3). *Anopaea* (Late Tithonian to Early Albian) has an elongated-pyriform equivalved shell, deep lunule, anteroventral sulcus, and anterior earlike buttress (Crame and Kelly, 1995; see Fig. 3). *Coloniceramus* (Early Hauterivian to Barremian) was originally described as a subgenus of *Inoceramus* (Pokhialainen, 1972) and later was considered as a new genus within the new family Coloniceramidae (Pokhialainen, 1985). This genus is characterized by a strongly gryphaeoid, very short, and almost smooth morphology and thick shell (see Fig. 3). The family Inoceramidae, as defined above, encompasses the morphology of *Coloniceramus* and, thus, this genus is considered here a member.

As suggested by Harries et al. (1996), *Inoceramus* sensu stricto, whose type species is *I. cuvieri* J. Sowerby, should only be used for those *Inoceramus*-like species ranging from the Cenomanian at least into the Middle Coniacian–?Early Maastrichtian. Early Cretaceous *Inoceramus*-like species, which are probably homeomorphic on *Inoceramus* s.s., should probably be excluded from *Inoceramus*. This group of *Inoceramus*-like species includes forms with different affinities and ages which are thus likely to be separated in new genera (e.g., "*Inoceramus*" *neocomiensis* d'Orbigny, 1845 and "*Inoceramus*" *heteropterus* Pokhialainen, 1969), including *Neocomiceramus*, discussed below.

Genus NEOCOMICERAMUS Pokhialainen, 1972

Type species.—*Inoceramus neocomiensis* d'Orbigny, 1845, p. 503, pl. 403, figs. 1, 2.

Other species.—Based on external characters and ligament morphology: *N. curacoensis* (Weaver, 1931). Based only on external characters and thus subject to some doubt: *N. anglicus* (Woods, 1911), *N. borealis* (Glazunova, 1973), *N. gusselkaensis* (Glazunova, 1973), *N. maedae* (Hayami, 1960), *N. obtusus* (Glazunova, 1973), *N. subneocomiensis* (Glazunova, 1973), and *N. volgensis* (Glazunova, 1973). At this time it is not possible to present an exhaustive list of component species until a revision of *Neocomiensis*-like species is made. Some authors have already attempted to make a synonymy list of *Neocomiceramus neocomiensis* (e.g., Woods, 1911; Dhondt and Dieni, 1988).

Emended diagnosis.—Subcircular to subquadrate outline, almost as long as high, subequivalve to inequivalve, with left valve more convex than right valve; commarginally folded; opisthodethic multivincular ligament occupying most of ligament area,

TABLE 1—Stratigraphic and geographic distributions of Argentine Cretaceous inoceramids. See locations in Figure 1.

Unit and locality	Species	Author	Ammonite zone	Age	References	Notes	Revision
Neuquen basin							
Agua de la Mula Mb, Agrio Fm, see fossil localities in Figure 1.2	*Inoceramus curacoensis*	Weaver, 1931	*Crioceratites schlagintweiti* and *C. diamantensis*	Late Hauterivian	Weaver, 1931	Newly collected materials revised here	*Neocomiceramus curacoensis*
Austral basin							
Sprighill Fm, Lago San Martín, Santa Cruz	*Inoceramus* aff. *I. anomiaeformis*	Feruglio, 1936–1938	*Jabronella*	Berriasian	Riccardi, 1977	Ligament not preserved. Uncertain affinities	"*Inoceramus*" aff. "*I.*" *anomiaeformis*
Rio Mayer Fm, Lago Argentino, Santa Cruz	*Inoceramus anomiaeformis*	Feruglio, 1936–1938	*Phyllopachyceras aureliae*	Hauterivian	Feruglio, 1936–1938; Aguirre-Urreta, 2002	Feruglio's collection needs reexamination	"*Inoceramus*" *anomiaeformis*
Rio Mayer Fm, Lago San Martín; Yahgan Fm, Tierra del Fuego	*Actinoceramus concentricus*	(Parkinson, 1819)	*Aioloceras argentinum*	Early-Late Albian	Bonarelli and Nágera, 1921; Camacho, 1949; Olivero and Martinioni, 1996; Aguirre-Urreta, 2002	Well-figured material, but no mention of ligament	*Actinoceramus*? *concentricus*
Yahgan Fm, Tierra del Fuego	*Inoceramus carsoni*	McCoy, 1865	?	Late Albian	Olivero and Martinioni, 1996	Well-figured material, but no mention of ligament	"*Inoceramus*" *carsoni*
Lower Mb, Cerro Toro Fm, Santa Cruz	*Actinoceramus*? cf. *A. concentricus*	(Parkinson, 1819)	*Pachydesmoceras*? sp.	Late Albian-? Early Cenomanian-? Early Coniacian	Kraemer and Riccardi, 1997	Based on undescribed material	"*Actinoceramus*" cf. *A. concentricus*
Upper Mb, Cerro Toro Fm, Santa Cruz	*Inoceramus andinus*	Wilckens, 1907	*Polyptychoceras*	Santonian	Wilckens, 1907; Feruglio, 1936–1938; Riccardi, 2002	Wilckens's collection needs reexamination	"*Inoceramus*" *andinus*
Upper Mb, Cerro Toro Fm, Santa Cruz	*Inoceramus steinmanni*	Wilckens, 1907	*Polyptychoceras*	Santonian	Wilckens, 1907; Feruglio, 1936–1938; Riccardi, 2002	Wilckens's and Feruglio's collections need reexamination	"*Inoceramus*" *steinmanni*
Upper Mb, Cerro Toro Fm, Santa Cruz	*Sphenoceramus* cf. *S. lingua*	(Goldfuss, 1826–1844)	*Polyptychoceras*	Santonian	Kraemer and Riccardi, 1997; Riccardi, 2002	Based on undescribed material	"*Sphenoceramus*" cf. *S. lingua*
Unknown unit, Santa Cruz	*Inoceramus lateris*	Rossi de Garcia and Camacho (1965)	*Eubaculites*? sp.	Turonian?, Maastrichtian?	Rossi de Garcia and Camacho, 1965; Riccardi, 2002	Holotype revised by the author. Ligament not preserved. Uncertain affinities	"*Inoceramus*" *lateris*

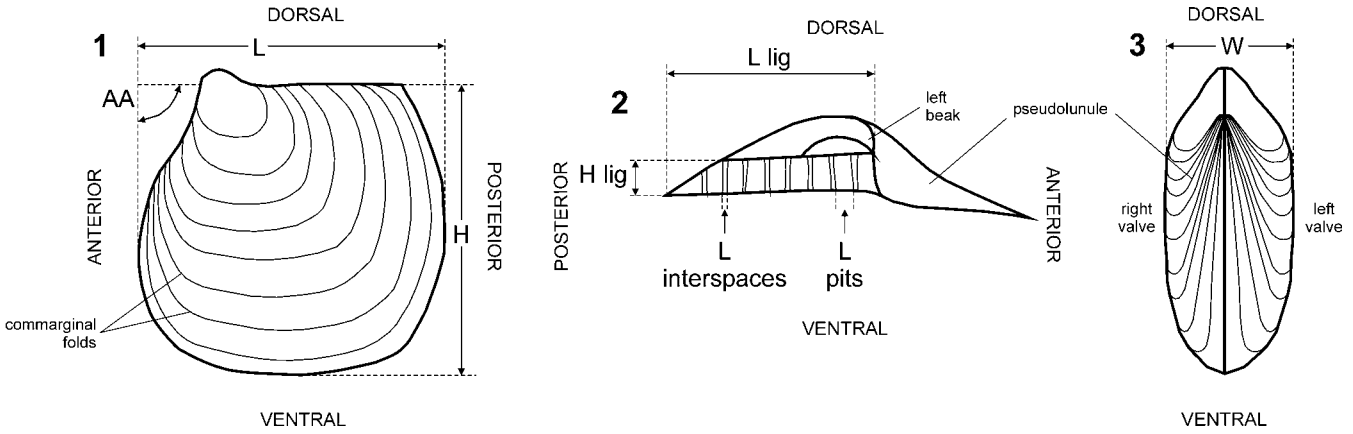


FIGURE 2—Measured morphologic variables of *Neocomiceramus curacoensis* (Weaver, 1931). *1,* Left lateral view; *2,* interior view of hinge line, left valve; *3,* anterior view. Abbreviations are as follows: AA, apical angle; L, length; H, height; W, width; L lig, length of ligament; L pits, length of ligament pits; L interspaces, length of interspaces. For the measurements see Table 1.

almost perpendicular to commissure, shorter than total shell length, rectangular pits few in number (<10?), wider than interspaces, narrow concave interspaces; musculature unknown (modified from Pokhialainen, 1972).

Occurrence.—Hauterivian to Albian, with a possible downward extension into the Valanginian (see Pokhialainen, 1969). Almost cosmopolitan.

Discussion.—In this work the subgenus *Neocomiceramus* is raised in rank to genus. This genus is easily differentiated from *Actinoceramus*, *Anopaea*, *Coloniceramus*, and *Inoceramus* s.s. by its shell shape, ornamentation, shell thickness, and ligament morphology (Fig. 3). *Neocomiceramus* is probably homeomorphic on *Inoceramus* s.s. regarding shell shape and ornamentation, but the two genera can be differentiated on the ligament morphology (Fig. 3). At present, musculature of *Neocomiceramus* is unknown. The lack of musculature is not necessarily a taphonomic bias, and might be of first-order taxonomic importance (see Crampton, 1996b). The musculature is a promising character to further differentiate it from other inoceramid genera as suggested by Kauffman (1977, p. 173), and to separate the Albian ''*Inoceramus*''

TABLE 2—Measurements (in mm) of *Neocomiceramus curacoensis* (Weaver, 1931). Abbreviations are as follows: MU, Agua de la Mula; PI, Pichaihue; PN, Pichi Neuquén; SE, Mina San Eduardo; ~, approximate measurement; >, underestimated measurement. For other abbreviations see Systematic Paleontology.

Specimen		Shell						Ligament			
CPBA	Fossil locality	Length	Height	Width	L/H	W/H	Apical angle	Length	# Pits	Length pit	Length intersp.
15879.1	PN	>59.0	62.7	25.3	—	0.40	117°	—	—	—	—
15884.1	PN	~52.0	~55.7	—	0.93	—	109°	—	—	—	—
15888.1	PN	65.4	61.5	—	1.06	—	~137°	3.5	—	1.0	0.4
20096.1	SE	>102.0	>94.0	34.3	—	—	128°	—	—	—	—
20096.24	SE	59.9	51.7	—	1.16	—	111°	—	—	—	—
20096.30	SE	~37.7	~35.5	—	1.06	—	113°	—	—	—	—
20101.2	PI	>88.7	>77.9	—	—	—	125°	—	—	—	—
20101.4	PI	82.8	>68.3	—	—	—	115°	—	—	—	—
20101.5	PI	—	—	—	—	—	115°	3.8	5	1.4	0.8
20101.6	PI	>51.9	>54.2	26.9	—	—	117°	—	—	—	—
20101.7	PI	>58.6	65.4	37.5	—	0.57	130°	—	—	—	—
20101.8	PI	>77.9	>69.8	—	—	—	116°	—	—	—	—
20101.10	PI	—	75.7	34.6	—	0.46	119°	—	—	—	—
20101.11	PI	>49.3	>56.1	26.0	—	—	115°	4.5	6	1.2	0.6
20101.12	PI	~48.1	49.6	—	0.97	—	111°	—	—	—	—
20101.14	PI	52.9	51.9	—	1.0	—	111°	—	—	—	—
20101.15	PI	>54.2	—	—	—	—	120°	3.5	—	1	0.6
20101.16	PI	27.1	30.8	—	0.88	—	135°	4.3	4	1.4	0.4
20101.17	PI	—	—	—	—	—	131°	4.9	5	1.4	0.5
20101.19	PI	50.6	>32.6	—	—	—	125°	3.3	7	1.3	0.5
20101.20	PI	30.8	29.4	—	1.05	—	106°	—	—	—	—
20101.21	PI	—	—	—	—	—	123°	3.6	4	1.3	0.7
20101.22	PI	57.3	53.9	—	1.06	—	~139°	3.0	5	1.4	0.4
20101.25	PI	>61.5	74.6	32.6	—	0.44	128°	3.7	6	1.6	0.9
20101.27	PI	—	—	—	—	—	—	3.9	7	1.3	0.4
20101.35	PI	~43.2	41.3	—	1.05	—	119°	4.0	4	1.3	0.5
20103.1	PI	>40.8	>54.1	—	—	—	115°	—	—	—	—
20103.2	PI	>47.4	>39.5	—	—	—	130°	2.8	—	1.2	0.5
20104.1	MU	>69.7	>98.0	43.5	—	—	100°	—	—	—	—
Mean	—	—	—	32.59	1.02	0.47	120°	3.75	—	1.29	0.55
Standard deviation	—	—	—	6.31	0.08	0.07	9.68°	0.58	—	0.17	0.16
Coefficient variation	—	—	—	19.38	7.77	15.56	8.06	15.56	—	12.82	29.13

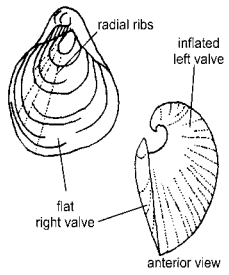
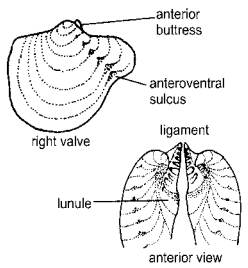
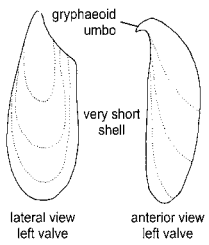
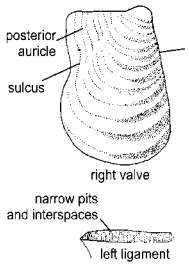
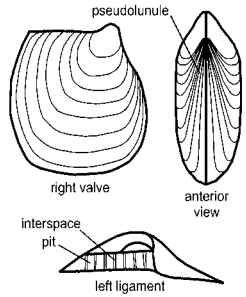
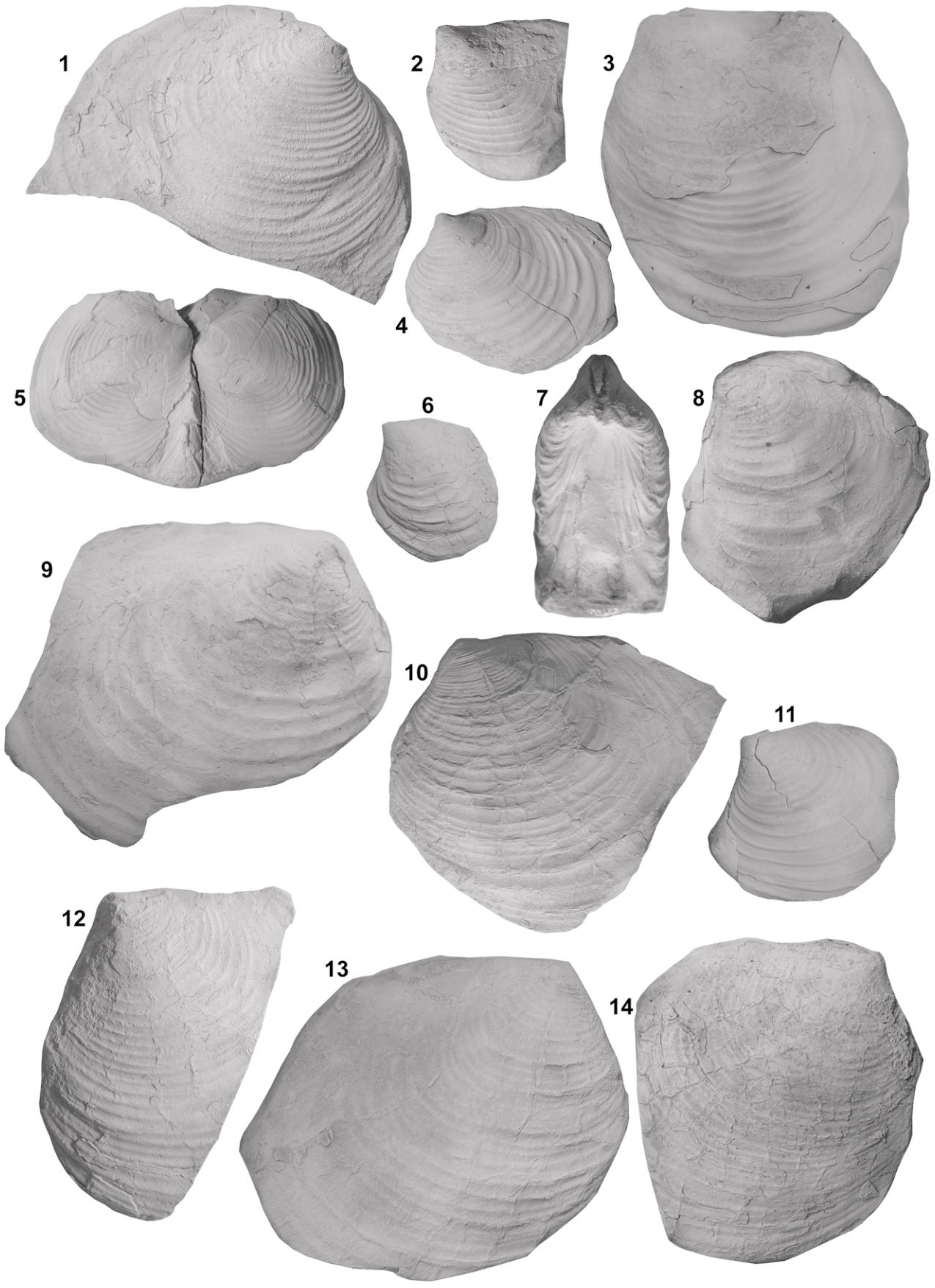
GENUS	*Actinoceramus*	*Anopaea*	*Coloniceramus*	*Inoceramus*	*Neocomiceramus*
AUTHOR	Meek, 1864	Eichwald, 1861	Pokhialainen, 1972	J. Sowerby, 1814	Pokhialainen, 1972
TYPE SPECIES	*Inoceramus sulcatus* Parkinson, 1819	*Inoceramus lobatus* Auerbach and Frears, 1846	*Inoceramus colonicus* Anderson, 1938	*Inoceramus cuvieri* J. Sowerby, 1814	*Inoceramus neocomiensis* d'Orbigny, 1845
SYNONYMY	*Birostrina* De Luc *in* J. Sowerby, 1821; *Inoceramus* (*Birostrina*) in Pokhialainen (1985)	*Inoceramus* (*Anopaea*) *in* Pokhialainen (1985)	*Inoceramus colonicus* informal group *in* Pokhialainen (1969) and Crame (1985)	*Inoceramus* (*Inoceramus*) in Pokhialainen (1972, 1985); *Inoceramus in* Harries et al. (1996); *Inoceramus* s.s. *in* Harries and Crampton (1998)	*Inoceramus* (*Neocomiceramus*) *in* Pokhialainen (1972, 1985); *Inoceramus neocomiensis* informal group *in* Crame (1985) and other authors
SHELL SHAPE	rhomboidal, parabolical, or elliptical outline; moderately to strongly inequivalve, with terminal, gibbous, prosogyrous umbo	elongated-pyriform outline; equivalved or subequivalved shell; deep cordiform lunule; anteroventral sulcus; anterior earlike buttress	extremely inequivalved and very short shell; left valve strongly gryphaeoid; right valve slightly convex or flat	erect-ovate, suquadrate, or subtrapezoidal outline; inequivalved shell; well-defined posterior auricle, auricular sulcus, postumbonal sulci; flattened anterior margin; byssal slit	subcircular to subquadrate outline, almost as long as high; subequivalved shell
ORNAMENTATION	regular commarginal ornament; large radial or oblique folds present or absent	regular commarginal ornament	almost smooth shells; faint irregular commarginal folds	regular commarginal ornament	regular commarginal ornament
SHELL THICKNESS	thin shell	thin shell	thick shell; umbonal region triple-layered with a prismatic portion under the inner shell layer	moderately thick shell	thin shell
LIGAMENT MORPHOLOGY	opisthodetic; multivincular; moderately concave area; rectangular pits; narrow ridges	opisthodetic; multivincular; rectangular area; on thickened prismatic layer (ligamentat); almost perpendicular to comissural plane; numerous rectangular uniserial pits; flat ridges	amphidetic?; multivincular; curved; short; on thickened prismatic layer (ligamentat); smaller than ligament area; almost parallel to commissural plane; small number of rectangular pits (< 5); additional area under the ligament variously sculptured	opisthodetic; multivincular; rectangular area; almost as long as total shell length; on thickened prismatic layer (ligamentat); almost parallel to commissural plane; high number of rectangular, very narrow, and shallow pits; narrow and rounded or angular interspaces	opisthodetic; multivincular; rectangular area; on thickened prismatic layer (ligamentat); occupying most of ligamentat; almost perpendicular to commissural plane; small number of rectangular pits (< 10?); narrow concave interspaces
UMBONAL SEPTUM	Absent or, at most, rudimentary	Absent?	Absent?	Present	Absent
MUSCULATURE	faint radial muscle tracks on the anterior and posterior parts of the disk	?	small radial muscle tracks below umbo	pallial line thin, continuous, or anteriorly pitted, at distal edge of small radial muscle tracks; posterior adductor boat-shaped, submarginal; large pedal-byssal retractor muscle below umbonal septum; 1-3 small, ovate, dorsoanterior pedal-byssal protractor just outside of pallial line	?
STRATIGRAPHIC RANGE	Albian - Cenomanian	Late Tithonian - Early Albian	Early Hauterivian - Barremian	Cenomanian - Middle Coniacian - ?Early Maastrichtian	Valanginian?, Hauterivian - Albian
DISTRIBUTION	Probably cosmopolitan	Mainly amphitropical: Antarctica, Australia, England, Indonesia, New Zealand, Russia, Tibet	California, USA; far eastern Russia	Cosmopolitan	Probably cosmopolitan
OTHER SPECIES	*A. concentricus* (Parkinson), *A. nipponicus* (Nagao and Matsumoto), *A. salomoni* (d'Orbigny), *A. tamurai* (Matsumoto and Noda), *A. tenuis* (Mantell)	*A. brachowi* (Rouillier), *A. sphenoidea* Gerasimov, *A. strambergensis* (Boehm), *A. callistoensis* Crame and Kelly, *A. gerasimovi* Kapitza, *A. pivanensis* Kapitza, *A. savrasovi* Kapitza, *A. stempeli* Kapitza, *A. amurensis* Kapitza, *A. trapezoidalis* (Thomson and Willey), *A. constricta* (Etheridge)	*C. subcolonicus* (Pokhialainen)	*I. pictus* Sowerby, *I. prefragilis* Stephenson, *I. scalprum* Woods, *I. virgatus* Schlüter	*N. anglicus* (Woods), *N. borealis* (Glazunova), *N. curacoensis* (Weaver), *N. gusselkaensis* (Glazunova), *N. maedae* (Hayami), *N. obtusus* (Glazunova), *N. subneocomiensis* (Glazunova), *N. volgensis* (Glazunova)
MAIN REFERENCES	Crampton, 1996b	Crame and Kelly, 1995	Pokhialainen, 1969, 1972, 1985, 1988; Crame, 1985	Harries et al., 1996	Pokhialainen, 1972, 1985
SCHEMES	 modified from Casey (1961)	 modified from Crame and Kelly (1995)	 modified from Pokhialainen (1969)	 modified from Cox (1969, pl. C46, fig.1)	

FIGURE *3*—Comparative scheme summarizing morphological features, stratigraphic ranges, geographical distributions, and component species of five Cretaceous inoceramid genera: *Actinoceramus* Meek, 1864; *Anopaea* Eichwald, 1861; *Coloniceramus* Pokhialainen, 1972; *Inoceramus* J. Sowerby, 1814; and *Neocomiceramus* Pokhialainen, 1972.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anglicus from *Inoceramus* s.s. Reexaminations of d'Orbigny's (1845) and Woods's (1911) type specimens are also necessary to improve the diagnosis, description, and knowledge of the distribution of *Neocomiceramus*.

NEOCOMICERAMUS CURACOENSIS (Weaver, 1931)
new combination

Figures 4.1–4.14, 5.1, 5.2, 6.1–6.3

v* *Inoceramus curacoensis* WEAVER, 1931, p. 213, pl. 16, fig. 71.
v. *Inoceramus* sp. Weaver, 1931, pl. 16, fig. 72.

Description.—Shell small to medium-sized (up to ~150 mm long), prosocline, inequilateral, subcircular in outline, almost as long as high (mean length/height = 1.02), subequivalve, left valve slightly more convex than right. Form of growth axis concave toward hinge line. Umbones small and prosogyrous. Variably defined pseudolunule and slit in front of beak. Posterodorsal area fairly wide but not clearly auriculated. Dorsal margin straight and shorter than total shell length. Posterior margin strongly convex. Ventral margin convex. Anterior margin meeting dorsal at obtuse angle (mean apical angle = 120°), concave dorsally and convex ventrally. No evidence of internal muscle scars, internal rib, or umbonal septum.

Hinge edentulous. Ligament area flat and rectangular, high-angled to commissural plane, shorter than total shell length, attached on thickened outer prismatic calcite shell layer (i.e., ligamentat, approximately 3 mm thick). Ligament multivincular just beneath umbonal sector. Resilifers rectangular, uniserial, wider than interspaces (1.29 mm vs. 0.55 mm, Fig. 6.1, Table 2), deep, concave anteroposteriorly, ventral margin slightly crenulated (Fig. 6.2, 6.3). Interspaces rectangular, narrow, shallow-concave anteroposteriorly, raised above resilifer floor.

Shell includes two shell layers, most shell sectors less than 1 mm thick, ornamented by narrow commarginal folds that affect entire thickness of shell, expressed on internal molds. Commarginal folds with rounded tops, separated by intervals that increase in width ventrally.

Material examined.—The holotype (UWBM 81) of *Inoceramus curacoensis* was collected by C. Weaver in the Agua de la Mula Member of the Agrio Formation, at the mouth of Arroyo Curaco east of Cerro Tromen in northern Neuquén (Fig. 1.2). The holotype is a poorly preserved internal mold of a left valve (Fig. 5.1). *Inoceramus* sp. (UWBM 44052) is a fragment of a left valve from the same locality figured by Weaver (1931, pl. 16, fig. 72). This specimen belongs to *N. curacoensis* (Fig. 5.2). The new material includes more than 100 valves and fragments collected by M. B. Aguirre-Urreta and the author in the Agua de la Mula Member of the Agrio Formation at four different localities of the Neuquén Province at west-central Argentina; these localities are described below.

Mina San Eduardo is an abandoned coal mine located 7 km west-southwest of the Curaco settlement (Fig. 1.2). Twelve bivalved specimens, 22 isolated right valves, and 21 left valves have been collected (CPBA 20093.1–6, 20094.1–2) from the *C. schlagintweiti* Zone, Late Hauterivian; and (CPBA 20095.1–4, 20096.1–35, 20097.1–8) *C. diamantensis* Zone, Late Hauterivian (Fig. 7.1). Agua de la Mula is located close to national road 40, 80 km south of Chos Malal on the western flank of Cordillera del Salado (Fig. 1.2). Three bivalved specimens, 13 isolated right valves, 10 left valves, and 13 incomplete left or right valves have been collected (CPBA 20098.1–11, 20099.1–19, 20100.1, 20104.1–8) from the *Crioceratites diamantensis* Zone, Late Hauterivian (Fig. 7.2). Pichaihue is situated 2 km southeast of Puesto Rivera, downstream along the Arroyo Pichaihue, at the northern end of Sierra Chorriaca (Fig. 1.2). Ten bivalved specimens, 19 isolated right valves, 20 left valves, and two undetermined valves have been collected (CPBA 20101.1–35, 20102.1–10, 20103.1–7) from the *C. diamantensis* Zone, Late Hauterivian (Fig. 7.3). Pichi Neuquén is situated 3 km northwest of the bridge on national road 40 over the Arroyo Pichi Neuquén (Fig. 1.2). Six bivalved specimens, five isolated right valves, and three left valves have been collected (CPBA 15877–15891) from the *C. diamantensis* Zone, Late Hauterivian.

Taphonomy and associated fauna.—Inoceramid bivalves from the Agrio Formation occur in dark gray to medium dark gray,

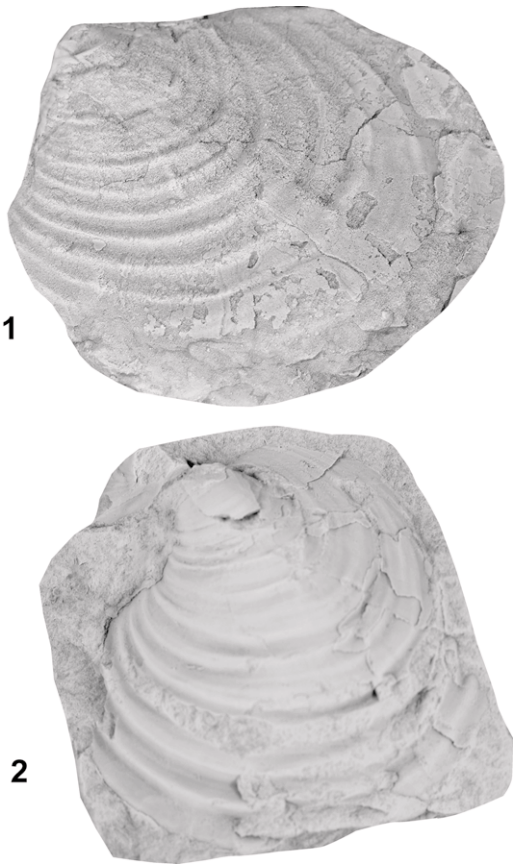

FIGURE 5—Type material of *Neocomiceramus curacoensis*. *1,* UWBM 81 holotype, internal mold in left lateral view; *2,* UWBM 44052 shell in left lateral view. From Arroyo Curaco, Neuquén, ×1, whitened with ammonium chloride. Photos are courtesy of the Burke Museum of Natural History and Culture, Seattle, USA.

←

FIGURE 4—*Neocomiceramus curacoensis* Weaver (1931). *1,* CPBA 20101.23 internal mold in right lateral view; *2,* CPBA 20101.20 internal mold in left lateral view; *3,* CPBA 15879 shell in left lateral view; *4,* CPBA 20103.2 shell in left lateral view; *5,* CPBA 20102.1 dorsal view of valves in ''butterfly'' position; *6,* CPBA 20101.16 shell in left lateral view; *7, 8,* CPBA 20101.6 internal mold in anterior and left lateral views; *9,* CPBA 20101.8 internal mold in right lateral view; *10,* CPBA 20101.9 internal mold in left lateral view; *11,* CPBA 20102.5 shell in left lateral view; *12,* CPBA 20101.10 internal mold in left lateral view; *13,* CPBA 20101.4 internal mold in right lateral view; *14,* CPBA 20101.7 internal mold in right lateral view. All from Pichaihue except *3* from Pichi Neuquén. All ×1. All whitened with ammonium chloride.

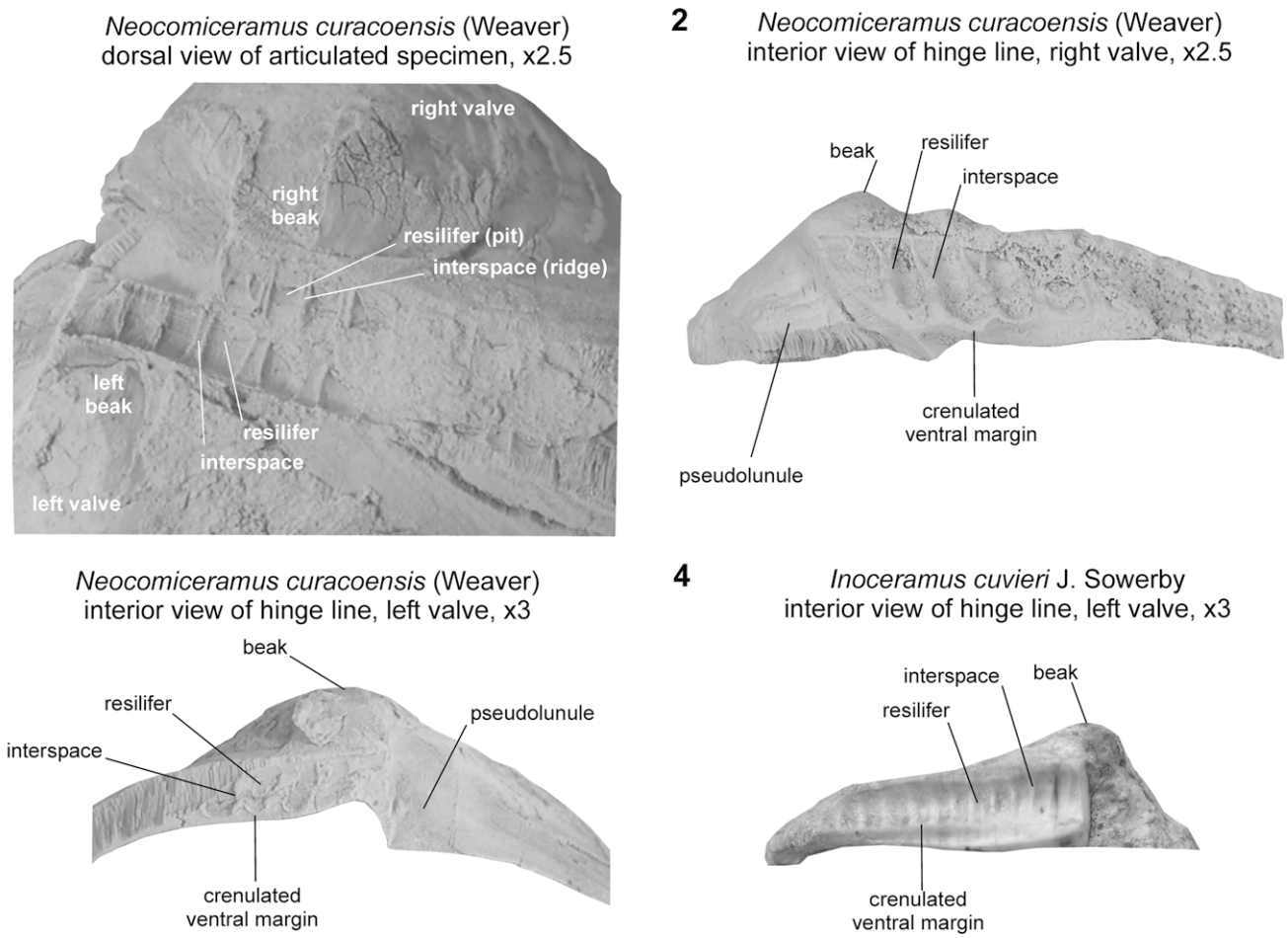

FIGURE 6—Detail of hinge line of *Neocomiceramus curacoensis* and *Inoceramus cuvieri* J. Sowerby, 1814. *1, N. curacoensis* CPBA 20101.25 articulated valves in dorsal view; *2, N. curacoensis* CPBA 20101.27 interior view of hinge line, right valve; *3, N. curacoensis* CPBA 20101.5 interior view of hinge line, left valve; *4, I. cuvieri* NHM 43264 interior view of hinge line, left valve. *1–3* from Pichaihue.

mainly massive shale (see Fig. 7), deposited in low-energy environments in the offshore zone below fairweather wave base (Lazo et al., 2005). Low degrees of abrasion and disarticulation also point to a quiet environment and indicate that lateral transport of shells was insignificant. The shale's fossil associations are regarded to represent autochthonous, time-averaged associations of ancient communities.

Macrofossils are generally sparse but locally abundant. They occur as thin shell beds (0.05–0.1 m thick) and pavements. The material is preserved either as shells or molds and most are fragmentary. Partially articulated and gaping (butterfly position) inoceramids are common. This mode of preservation characterizes regimes of high sedimentation rates (Brett and Baird, 1986). Preservation within precompaction carbonate concretions is common. Inoceramid shells are rarely encrusted by the small annelid *Parsimonia antiquata* (J. de C. Sowerby, 1829) and the bivalve *Ceratostreon* Bayle, 1878. Other than ammonites, inoceramids also are associated with a number of astartid bivalves and small gastropods. The sparse presence of benthic organisms (specially encrusters), abundant organic content (inferred from the dark color), relatively low diversity assemblages, and presence of *Chondrites* Sternberg, 1833 are likely to be related to low levels of oxygen (see Wignall, 1993).

Occurrence.—*N. curacoensis* occurs in the Agua de la Mula Member of the Agrio Formation in Neuquén Province, *Crioceratites schlagintweiti* and *C. diamantensis* zones, Late Hauterivian.

Discussion.—The ligament of *N. curacoensis* has a simple morphology with a low number of rectangular pits (<10) occupying most of the ligament area (Fig. 6.1–6.3). These characters resemble ligaments in other Early Cretaceous inoceramids (e.g., *Anopaea*), and contrast with ligaments that possess many biserial to multiserial pits and additional elements, as is typical within Late Cretaceous *Inoceramus*, e.g., *I. flavus* Sornay, 1965b (pl. a, fig. 2b) and *I. cuvieri* (Fig. 6.4).

Coloniceramus colonicus (Anderson, 1938) was originally described from the Barremian of northern California (Shasta and Tehama counties), USA (Anderson, 1938, p. 100, pl. 4, figs. 10–12; pl. 5, figs. 1, 2; pl. 6, fig. 3). This species also is found in the Hauterivian of far eastern Russia, in the northeast (e.g., northwestern Kamtchatka and Taigonos Peninsula) and the Sikhote-Alin Mountains (Pergament, 1965; Pokhialainen, 1969). *Coloniceramus colonicus* is easily differentiated from *N. curacoensis*. It has very unequal valves, a thick shell, a strongly incurved left umbo, and a very short and almost smooth shell. As described by Pokhialainen (1969, 1972, 1988), the ligament of *C. colonicus* seems very different from the ligament of *N. curacoensis*, although in the figured specimens by Pokhialainen (1988, pl. 4, figs. 1–3, 6, 7; pl. 5, fig. 5) the ligament pits and interspaces are not clearly visible. The ligament of *C. colonicus* has a curved shape, does not occupy the whole ligament area, and is almost parallel to the commissural plane. An additional area under the ligament may be smooth or have ridges and constrictions.

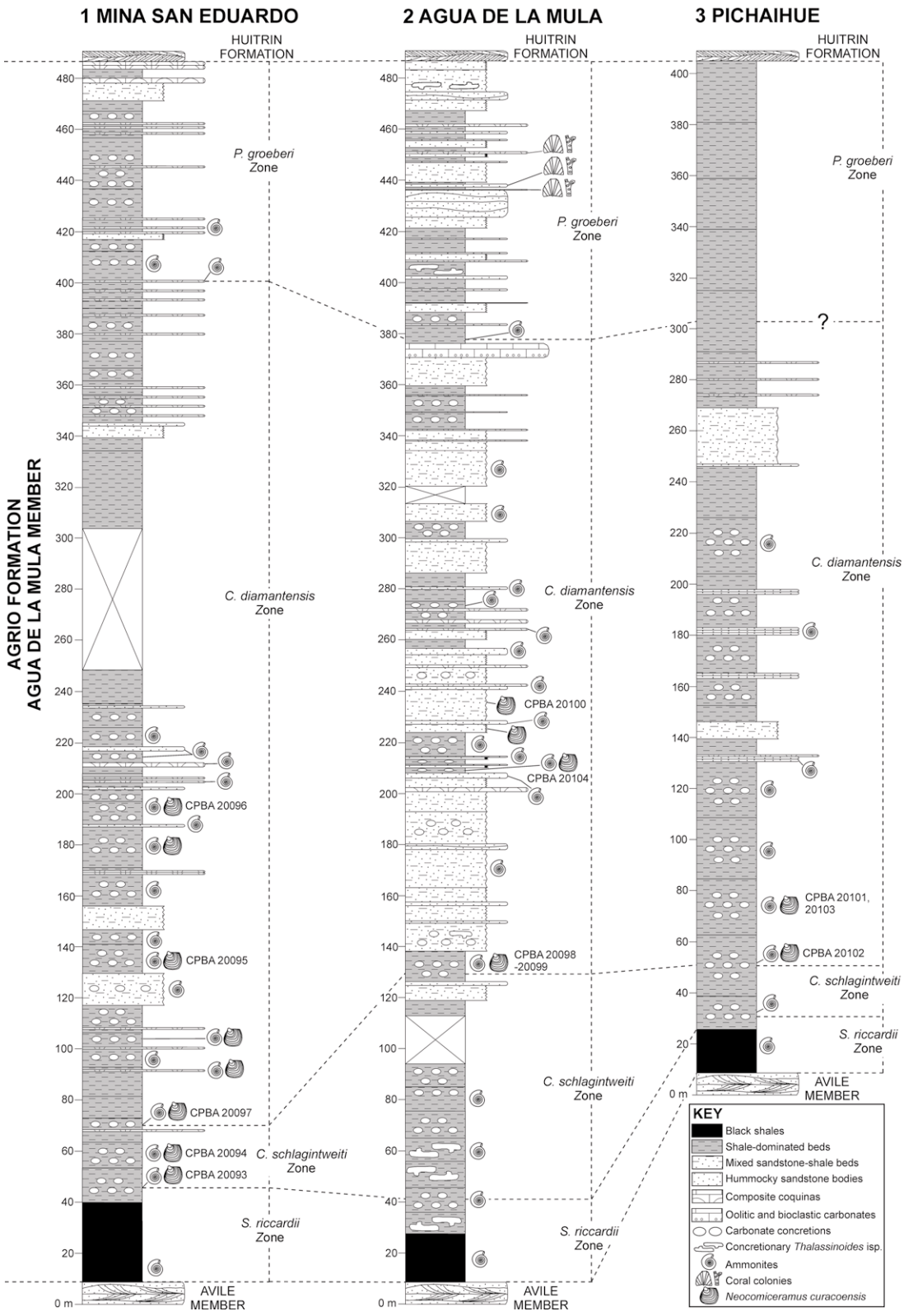

FIGURE 7—Lithological columns of the Agua de la Mula Member of the Agrio Formation, showing the stratigraphic distribution of *Neocomiceramus curacoensis* and ammonite zonation. *1,* Mina San Eduardo; *2,* Agua de la Mula; *3,* Pichaihue. See locations in Figure 1.2.

''*Inoceramus*'' *anomiaeformis* Feruglio, 1936–1938 from Hauterivian beds of Lake Argentino in Santa Cruz Province (South Argentina) is similar in outline to *N. curacoensis* but it has thin radial ribs that are absent in the latter (Feruglio, 1936–1938, p. 29–30, pl. 2, figs. 1, 2).

''*Inoceramus*'' *heteropterus* Pokhialainen, 1969 (p. 141–142, pl. 13, fig. 7; pl. 14, figs. 2–4; pl. 15, fig. 6; pl. 17, figs. 3, 4; pl. 21, fig. 4) from the Hauterivian of Russia (northwestern Kamchatka) has a very convex, often gryphaeoid left umbo. Unfortunately the figured specimens of ''*I.*'' *heteropterus* do not show clearly the ligament morphology. Pokhialainen (1972, 1985) and Crame (1985) proposed this species to typify a subgenus or subgroup within the genus *Inoceramus*, but its musculature and ligament morphology are still poorly known.

''*Inoceramus*'' *ovatus* Stanton, 1895 (p. 47, pl. 4, fig. 15) was originally described from a fragment of a right valve from the ''upper Knoxville beds'' in California, USA (Tehama County). These beds were subsequently assigned to the Paskenta Group of Berriasian?–Valanginian age (Anderson, 1938, p. 99). Although incomplete, the holotype is very different from *N. curacoensis* because it is elongate-ovate in outline and it has a lower apical angle (approx. 75°) and weaker commarginal folds. Crame (1985) proposed an informal species group based on ''*Inoceramus*'' *ovatus*, but its musculature and ligament are unknown, making diagnosis extremely tentative.

''*Inoceramus*'' *pseudopropinguus* Pergament, 1965 (p. 26–27, pl. 7, fig. 2 a–b) from the Early Cretaceous (Hauterivian?, see Pokhialainen, 1985) of Russia (northwestern Kamchatka) differs from *N. curacoensis* by being higher than long. ''*Inoceramus*'' *serotinus* Pergament, 1965 (p. 25–26, pl. 8, fig. 1) from the Albian of Russia (northwestern Kamchatka) is based on one specimen that is easily distinguished from *N. curacoensis* because it has a lower apical angle (approx. 104°) and a posterior winglike projection that is distinctly separate from the rest of the valve.

There are a number of ''*Inoceramus*'' species described by Glazunova (1973) from the Aptian of the Volga Region of Russia which are externally very similar to *N. curacoensis* and are referred here to the genus *Neocomiceramus*. It is apparent from the material figured by Glazunova that some of these species form a homogenous plexus and can probably be referred to a single species, although a thorough revision of the type material is needed. This plexus was mentioned by Pokhialainen (1985) and includes: *Neocomiceramus borealis* (Glazunova, 1973, p. 43–44, pl. 13, figs. 4, 5; pl. 14, figs. 1, 2; pl. 15, figs. 1–3; pl. 16, figs. 1, 2), *N. gusselkaensis* (Glazunova, 1973, p. 48, pl. 19, figs. 1, 2), *N. obtusus* (Glazunova, 1973, p. 46, pl. 13, figs. 1–3), *N. subneocomiensis* (Glazunova, 1973, p. 45–46, pl. 16, figs. 3–5; pl. 17, figs. 1–3), and *N. volgensis* (Glazunova, 1973, p. 43, pl. 12, figs. 1–5).

Neocomiceramus anglicus was originally described from the Middle and Late Albian (Gault, Red Chalk, and Upper Greensand) of England (southeast, southwest, and east Anglia regions; Woods, 1911, pl. 45, figs. 8–10; 1912, p. 5, figs. 28, 29, 56, 57). This species is widely distributed in the Albian of the North Temperate Realm. It has been found in northern Alaska, eastern Greenland, western Canada, the Western Interior of the USA (mainly in Montana, South Dakota, and Wyoming), Japan, and in the Volga and far eastern region of Russia (Imlay, 1961; Pergament, 1965; Glazunova, 1973; Kauffman, 1977; Zonova and Yazykova, 2001). Additionally it was recorded in the Albian of the northeast and southeast of France (Departments of Pas de Calais and Alpes Maritimes; Sornay, 1965a) and possibly in the Albian of the Antarctic Peninsula (Alexander and Dundee islands; Crame, 1985). *Neocomiceramus anglicus* is externally very similar to *N. curacoensis*. The ligament of *N. anglicus*, as figured by Woods (1911, pl. 45, fig. 8b), seems very similar to the ligament of *N. curacoensis*. It is high-angled to the commissural plane, occupies most of the ligament area, and has rectangular resilifers, although it has anteroposteriorly flat interspaces and a larger number of pits. Pokhialainen (1985) assigned ''*I.*'' *anglicus* as the type species of *Gnesioceramus* Heinz, 1932 but he did not include: 1) an emended diagnosis of the genus; 2) a list of component species; and 3) a discussion on the original designation by Heinz. Therefore this assignation should be regarded as provisional.

Neocomiceramus maedae from the Cretaceous? of Japan (Gifu Prefecture, Honshu) is very similar to *N. curacoensis*, in particular specimen 9076 shown in figure 3a, although a true synonymy cannot be made without revision of Hayami's material (Hayami, 1960, p. 308–311, pl. 17, figs. 1–3, text-fig. 2). As mentioned by Hayami, *N. maedae* is similar to *N. neocomiensis* (d'Orbigny, 1845) and *N. anglicus* and most probably is Early Cretaceous in age.

Neocomiceramus neocomiensis was originally described from the Neocomian of France: in the northeast (Departments of Haute Marne and Yonne), east (Department of Savoie), and southeast (Department of Vaucluse; d'Orbigny, 1845, p. 503, pl. 403, figs. 1, 2). It has been subsequently assigned to the Hauterivian with a possible upward extension into the Barremian and Aptian (see Sornay, 1965a). *Neocomiceramus neocomiensis* has also been found in the Lower Greensand (Aptian) of the southeast region of England (Woods, 1911, p. 262–263, pl. 45, figs. 1, 2; 1912, p. 5, fig. 27) and in the Early Cretaceous of Bulgaria, Caucasus, Crimea, and the Volga region of Russia (see Dhondt and Dieni, 1988). *Neocomiceramus neocomiensis* is similar to *N. curacoensis* but the former has a smaller apical angle (approximately 90° vs. 100°–139°) and a straight anterior margin. Sornay (1965a, p. 393) pointed out that the original figure by d'Orbigny is somewhat different from the actual fossil, and a redescription with photographic illustrations of the holotype is needed to aid proper identification.

DISCUSSION

Neocomiceramus curacoensis is a local marker of the Late Hauterivian in the Neuquén Basin, west-central Argentina. Apparently it is a facies-dependent species because it is recorded abundantly in shales in localities around the basin depocenter. The relatively expanded disk, subequivalved condition, thin shell, and anterior slit indicate an epibyssate life habit reclined on the left valve. This species periodically flourished on low-energy marine muddy bottoms in the offshore, possibly controlled by oxygen levels. At present, *N. curacoensis* is known exclusively from the Neuquén Basin, but it shows affinities to the Early Cretaceous cosmopolitan species *N. neocomiensis* and *N. anglicus*, and to *N. maedae* from Japan.

The genus *Neocomiceramus* is differentiated from other Early Cretaceous inoceramid genera by its ligament morphology. At present it is difficult to evaluate the stratigraphic range and biogeography of the genus, as most species are included only on the basis of their external morphology. However, a preliminary scheme would have *Neocomiceramus* in Argentina, the Tethyan region, and possibly far eastern Russia in the Valanginian?–Hauterivian to Barremian. *Neocomiceramus* and *Coloniceramus* likely had an overlapping distribution in the Hauterivian of Russia. In the Aptian–Albian, *Neocomiceramus* greatly extended its distribution, becoming cosmopolitan and thus coexisting with the genus *Actinoceramus*.

In the Early Cretaceous inoceramid diversity was considerable, although lower than in the Late Cretaceous. Four valid Early Cretaceous genera, which represent different combinations of characters, were present. *Actinoceramus* and *Anopaea* have diagnostic

shell shapes, although their ligaments are rather simple. *Actinoceramus* is usually strongly inequivalve and possibly had a reclined life habit, resting on its left valve. *Anopaea* is equivalve or subequivalve and has a rounded-elongated outline with a partially reduced anterior region. This general morphology resembles that of the genus *Modiolus* Lamarck, 1799, which in turn suggests an endobyssate life habit with the commissural plane in a vertical position (Crame, 1981). *Coloniceramus* has both a characteristic shell shape and ligament. Its shell morphology indicates a reclined life habit on its left valve. Finally, *Neocomiceramus* has a simple ligament and is externally *Inoceramus*-like with a broad and rather flat form, suggesting an epibyssate life habit reclined on its left valve.

CONCLUSIONS

1. *Neocomiceramus curacoensis* from the Agua de la Mula Member of the Agrio Formation in the Neuquén Basin, west-central Argentina, is a local marker for the Late Hauterivian. This species is facies-dependent with a reclined life habit.
2. *Neocomiceramus* is raised in rank to genus. It ranges from the Valanginian?, Hauterivian to Albian, with a near cosmopolitan distribution.
3. The genus *Neocomiceramus* is characterized by an *Inoceramus*-like shell shape and by a rather simple, and possibly primitive, ligament with a small number of rectangular pits and concave interspaces. This genus may include all Early Cretaceous *Inoceramus*-like species.
4. At least four valid Early Cretaceous inoceramid genera exist: *Actinoceramus*, *Anopaea*, *Coloniceramus*, and *Neocomiceramus*. The genus *Inoceramus* s.s. should be used only with Late Cretaceous *Inoceramus*-like species.

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