The bivalve *Pholadomya gigantea* in the Early Cretaceous of Argentina: Taxonomy, taphonomy, and paleogeographic implications

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Pholadomya gigantea is a widely distributed Early Cretaceous bivalve mollusc. It has been recorded in the North Temperate, Tethyan, and South Temperate Realms. Based on recent field work and newly collected material from the Neuquén Basin, the taxonomy, mode of occurrence and palaeobiogeography of this species is reviewed. In the Agrio Formation (Valanginian–Barremian) *P. gigantea* is neither abundant nor dominant, but occurs throughout the unit. It was facies-dependent being restricted to well-oxygenated waters and soft to firm, sandy and bioclastic substrates of shoreface to inner shelf environments. The life habit of *P. gigantea* was similar to that of Recent *Pholadomya candida*, deep burrowing and sedentary, but it has not a pedal gape and accessory muscle scars related to valve closure. Thus a suspension-feeding habit, not a pedal-feeding system, may be inferred as is commonly suggested in other Jurassic and Cretaceous *Pholadomya* species. *Pholadomya agrioensis* is a valid taxon that is recorded in the Berriasian–Valanginian of Neuquén. It is similar in outline to *P. gigantea* and had probably the same basic palaeoecology, even though it has a blunt anterior margin, deep umbonal-ventral sulcus and distinct anterior ornamentation. Once in life position this species was capable of further digging in the sediment. This species probably burrowed in muddy substrates in the offshore zone. *Pholadomya sanctaecrucis* from the Valanginian of Europe and also recorded in Argentina is ornamented only with commarginal lines and should be removed to the genus *Homomya*.

Key words: Bivalvia, Anomalodesmata, *Pholadomya*, palaeoecology, taxonomy, palaeogeography, Argentina, Cretaceous.

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Introduction

Pholadomya gigantea (J. de C. Sowerby, 1836) is an Early Cretaceous anomalodesmatan bivalve with a wide palaeobiogeographic distribution (Dhondt and Dieni 1988). It belongs to the Family Pholadomyidae (Early Carboniferous–Recent) which is a group of burrowing bivalves characterized by posteriorly elongated shells with strong radial ribbing, the presence of a pallial sinus and siphonal gape, a hinge with no functional teeth, and a ligament external and opisthodetic (Runnegar 1974).

Early Cretaceous pholadomyids from Argentina have not been fully described, figured, or dated properly, although they have been known since the beginning of the 20th century (e.g., Burckhardt 1900). Only three species of *Pholadomya* have been recorded from the Early Cretaceous of the Neuquén Basin, west-central Argentina. The best known taxon is *Pholadomya gigantea,* which occurs in the Agrio Formation and is discussed below. *Pholadomya agrioensis* Weaver, 1931 and *Pholadomya sanctaecrucis* Pictet and Campiche, 1864 have been described also from the Early Cretaceous of Neuquén, but their stratigraphic occurrence is restricted to the Quintuco Formation.

Based on detailed studies of the Agrio Formation at different localities in Neuquén the goals of the present paper are as follows: (1) describe newly collected specimens of *Pholadomya gigantea* from the Agrio Formation; (2) date accurately the study material based on a refined ammonite zonation; (3) analyze the mode of occurrence and facies relationships based on bed by bed study of the Agrio Formation in the locality of Agua de la Mula; (4) study the functional morphology of *P. gigantea* and *P. agrioensis*; and (5) reassess the palaeobiogeographic distribution of *P. gigantea* during the Early Cretaceous.

Institutional abbreviations.—CPBA, Area de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II, 1428, Buenos Aires, Argentina; NHM, Natural History Museum, London, UK; UWBM, Burke Museum of the University of Washington, Seattle, USA.

Stratigraphy and previous records in the Neuquén Basin

The Neuquén Basin is a backarc depocenter located in the Andes foothills of west-central Argentina, between 32° and 40° S (Fig. 1). Its fill comprises more than 7000 m of continental and marine siliciclastic, carbonate, and evaporitic deposits of latest Triassic to Oligocene age. From the Jurassic to the Early Cretaceous the basin formed a shallow embayment connected to the Pacific Ocean through an Andean volcanic arc at the western margin. The embayment covered the Neuquén and Mendoza and parts of La Pampa and Río Negro Provinces. During Barremian times there was a drop in the relative sea level and the Neuquén Basin was finally disconnected from the Pacific Ocean. The Early Cretaceous beds are grouped in the Andean sedimentary cycle that is composed of the Mendoza and Bajada del Agrio groups (Leanza et al. 2001). Pholadomyids have been found in three units of the Mendoza Group which are discussed below (see Fig. 2).

The Quintuco Formation (Tithonian–Valanginian) is a mixed carbonate-siliciclastic unit mostly developed in Neuquén where it overlies the Vaca Muerta Formation and underlies the Mulichinco Formation (Fig. 2; Weaver 1931). It reaches a maximum thickness of 750 m (Gulisano et al. 1984). It has been interpreted as a basinal to littoral marine environment (Rodriguez Schelotto et al. 1981). Two pholadomyid species have been recorded and figured: (1) *Pholadomya agrioensis* Weaver, 1931 (Weaver 1931: 316, pl. 36: 205, 206) collected 16 km northwest of Agua de la Mula in Berriasian–Valanginian beds (Figs. 1B, 2); and (2) *P. sanctaecrucis* Pictet and Campiche, 1864 (Weaver 1931: 317, pl. 36: 202, 203) collected in the Cerro Picún Leufú area from Tithonian?–Valanginian beds (Figs. 1B, 2). Weaver (1931) also mentioned the presence of *P. gigantea* in the Quintuco Formation, although he did not figure specimens. In addition, Leanza et al. (1997) mentioned the presence of *P. agrioensis*, *P. gigantea*, and *P. sanctaecrucis* in the Picún Leufú Formation at Cerro Picún Leufú, but they did not figure or describe any material. The Picún Leufú Formation is a time equivalent of the Quintuco Formation. The validity of these records will be examined during future field studies.

The Chachao Formation (Valanginian) is a calcareous unit developed in Mendoza (Uliana et al. 1977) where it overlies the Vaca Muerta Formation and conformably underlies the Agrio Formation (Fig. 2). It reaches a maximum thickness of 40 m, and towards the south becomes progressively thinner where it interfingers with clastic deposits of the Mulichinco Formation (Valanginian, Fig. 2). It has been interpreted as deposits of a low-energy sublitoral carbonate ramp (Damborenea et al. 1979). *Pholadomya* (*Pholadomya*) cf. *P. gigantea* was recorded but not figured (Fig. 2, Damborenea et al. 1979: 62).

The Agrio Formation crops out extensively from Mendoza to Neuquén with important variations in thickness, lithology, and fossil content (Marchese 1971). The stratotype has three

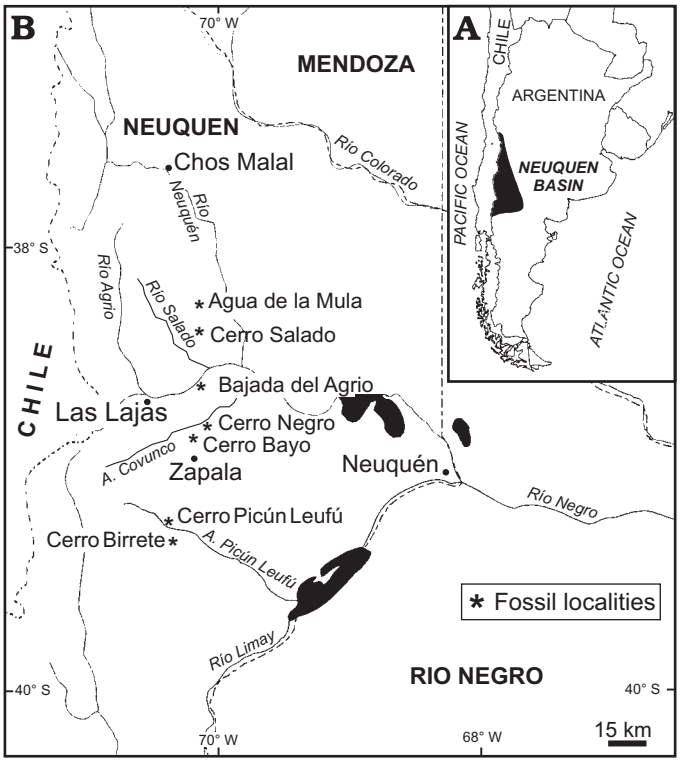


Fig. 1. **A**. Location of the Neuquén Basin in west-central Argentina, 321–401 S. **B**. Detailed map of the Neuquén Basin showing fossil localities.

members, reaching 1600 m of maximum thickness. The Pilmatué and Agua de la Mula Members consist of shales, sandstones, and limestones of marine origin, while the Avilé Member is a fluvial to aeolian sandstone that was accumulated during a major regression in the Middle Hauterivian. The marine members of the Agrio Formation represent mixed clastic-carbonate sedimentation and were interpreted as storm influenced shoreface to offshore settings (Brinkmann 1994; Spalletti et al. 2001). A refined ammonite biostratigraphy indicates for the whole unit an Early Valanginian to Early Barremian age (Aguirre-Urreta and Rawson 1997, 2003). *Pholadomya gigantea* is the only pholadomyid recorded from the Agrio Formation, in which most of the study material was obtained. It has been found in the Pilmatué and Agua de la Mula Members (Fig. 2, see Material below).

Material

The study specimens of *Pholadomya gigantea* (J. de C. Sowerby, 1836), collected by the author, come from three sections of the Agrio Formation in Neuquén province, Argentina: Agua de la Mula, Bajada del Agrio, and Cerro Birrete. Agua de la Mula is located close to the national road 40, 80 km south of Chos Malal on the western flank of Cordillera del Salado (Fig. 1B). Twenty-three bivalved specimens were collected (CPBA 19726.1–11, CPBA 19727.1–12) in the *Hoplitocrioceras gentilii* Zone, Early Hauterivian and

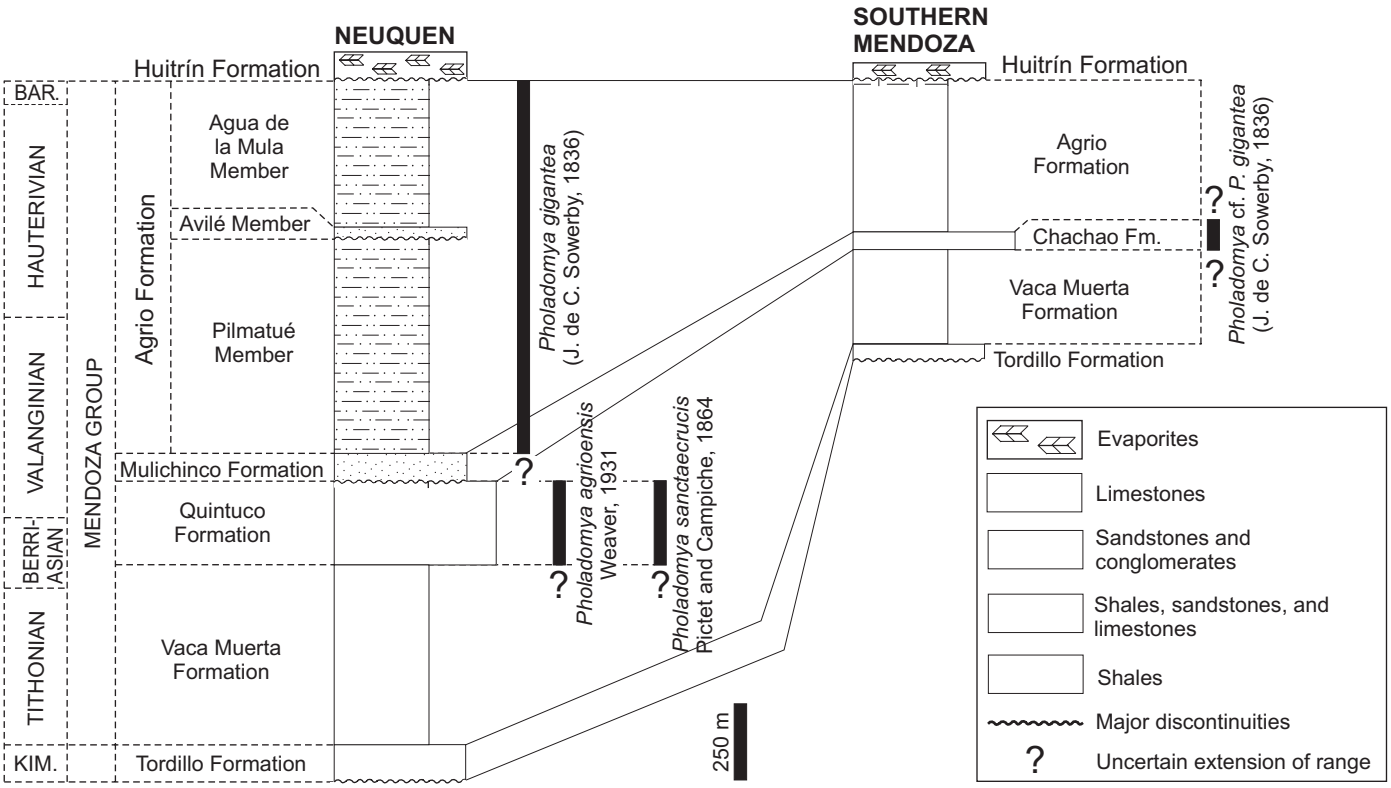


Fig. 2. Schematic correlation chart of the Mendoza Group between Neuquén and Mendoza Provinces, Early Cretaceous of the Neuquén Basin, Argentina, showing ranges of *Pholadomya* species. Modified from Uliana et al. (1977); stages from Aguirre-Urreta and Rawson (1997, 2003); ranges are based on Weaver (1931), Damborenea et al. (1979), and author's observations. Abbreviations: Bar., Barremian; Kim., Kimmeridgian.

one bivalved specimen (CPBA 20104.1) in the *Paraspiticeras groeberi* Zone, Early Barremian. Other specimens were recorded but left in the field and are indicated in Fig. 5. Bajada del Agrio is located 33 km east of Las Lajas on the provincial road 10 and on the right margin of the Agrio river (Fig. 1B). One bivalved specimen (CPBA 19728.1) was collected in the *Neocomites* sp. Subzone, Late Valanginian. Cerro Birrete is located 7 km south of Cerro Picún Leufú on road 40 (Fig. 1B). Four bivalved specimens (CPBA 20121.1–4) have been collected in the *Neocomites* sp. Subzone, Late Valanginian.

Other specimens of *Pholadomya gigantea*, housed in CPBA, were available to the author for comparisons: two bivalved specimens (CPBA 18291.1–2) collected by Marcela Lorenzo from the Agrio Formation in Cerro Salado (Fig. 1B); one bivalved specimen (CPBA 7555.1) collected by Anselmo Windhausen from the Agrio Formation at Cerro Negro (Fig. 1B); one bivalved specimen (CPBA 20120.1) collected by María B. Aguirre-Urreta from the Agrio Formation at Cerro Bayo (Fig. 1B); two bivalved specimens (CPBA 20106.1–2) from the Agrio Formation in the Early Hauterivian of Arroyo Lagunitas (Mendoza) collected by Sebastián Saavedra; one bivalved specimen (CPBA 16177.1) from the Hauterivian of Puente del Inca (Mendoza) collected by Gabriela Lo Forte; eight bivalved specimens (CPBA 20122.1–7, 7012.1) from the Agrio Formation in Neuquén; and two bivalved specimens (CPBA 228.1–2) from the Early Cretaceous of Auxerre, Yonne (France). Seven unpublished specimens of *Pholadomya agrioensis* Weaver, 1931 housed at CPBA under the numbers 7579.1–6 and 7588.1 from the Early Cretaceous of Neuquén were also studied by the author.

In addition the following type and figured specimens were examined by the author: (1) holotype of *Pholadomya candida* G.B. Sowerby, 1823 from Tortola Island, British Virgin Islands, NHM; (2) holotype of *P. gigantea* (J. de C. Sowerby, 1836) from Hythe beds (Aptian) of Lympne, Kent (U.K.) under the number NHML67764; (3) *Pholadomya gigantea* from the Early Cretaceous (Barremian?) of Oman collected by Lees (1928) under the number NHML52763; (4) holotype of *Pholadomya agrioensis* Weaver, 1931 (Weaver 1931: pl. 36: 205, 206) under the number UWBM208; and (5) hypotype of *P. gigantea* (Weaver 1931: pl. 36: 209, 210) under the number UWBM206.

Systematic palaeontology

Annotations of synonymy entries follow Matthews' (1973) and Bengtson's (1988) recommendations. Only those citations with figured specimens are listed in the synonymy. Stratigraphic range of *Pholadomya gigantea* from the Agrio Formation is based on the refined ammonite zonation proposed by Aguirre-Urreta and Rawson (1997, 2003) that correlates well with the West Mediterranean zonation (see

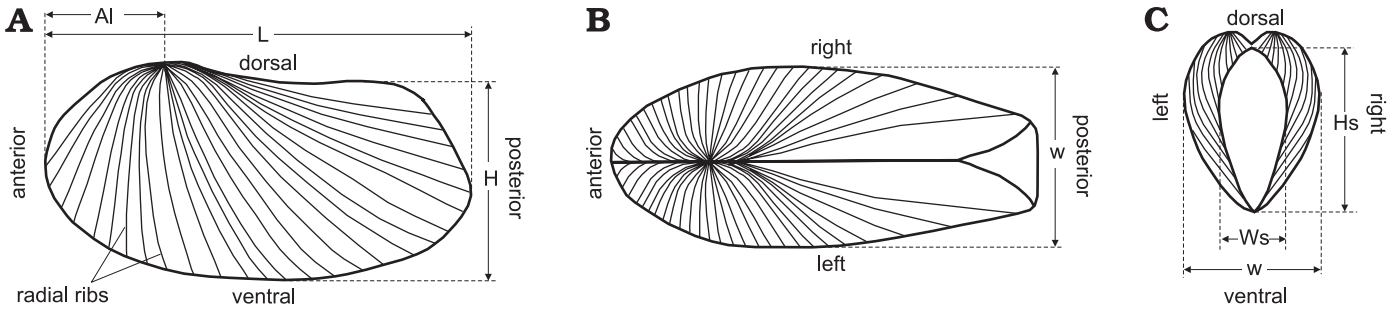


Fig. 3. Orientations of measurements in *Pholadomya*. **A**. Left lateral view. **B**. Dorsal view. **C**. Posterior view. Abbreviations: Al, anterior length; H, height; Hs, height of siphonal gape; L, length; W, width; Ws, width of siphonal gape. Measurements in Table 1.

Aguirre-Urreta et al. 1999). Measurements were made using a digital calliper (accurate to 0.1 mm) and recorded in mm (Fig. 3). They were taken on each specimen whenever possible: Length: total shell length measured parallel to the hinge axis; Height (H): total shell height perpendicular to Length; Width (W): inflation of both valves; Anterior length (Al): length measured from umbo to anterior margin; L/H: elongation; H/W: inflation; Height of siphonal gape (Hs): maximum height of siphonal gape measured perpendicular to the hinge axis; Width of siphonal gape (Ws), maximum width of siphonal gape measured parallel to shell width. For the measurements see Table 1.

Subclass Anomalodesmata Dall, 1889
Order Pholadomyoida Newell, 1965
Superfamily Pholadomyoidea Gray, 1847
Family Pholadomyidae Gray, 1847
Genus *Pholadomya* G.B. Sowerby, 1823

Type species: *Pholadomya candida* G.B. Sowerby, 1823; Recent, Tortola Island, British Virgin Islands.

Diagnosis.—See Runnegar (1972).

Remarks.—*Pholadomya candida* is the only Recent species of the nominal genus. Since living specimens had not been found since the last century this species was considered extinct, but new discoveries of recently dead shells from the Colombian Caribbean provide further evidence that the species is not extinct (Díaz and Borrero 1995). The records of these species are extremely scarce and the species is considered one of the rarest living bivalves (Runnegar 1972). It is only known from a small number of shells housed at different institutions and only two specimens had soft parts. One of them was dissected by Richard Owen in about 1839, but his illustrations were lost and the manuscript never published. The second specimen was dissected and published by Morton (1980). The shell is aragonitic and consists of three layers: an outer prismatic layer, a middle nacreous layer, and an inner sheet nacre layer (Taylor et al. 1973).

Occurrences.—Late Triassic to Recent, cosmopolitan (Cox 1969).

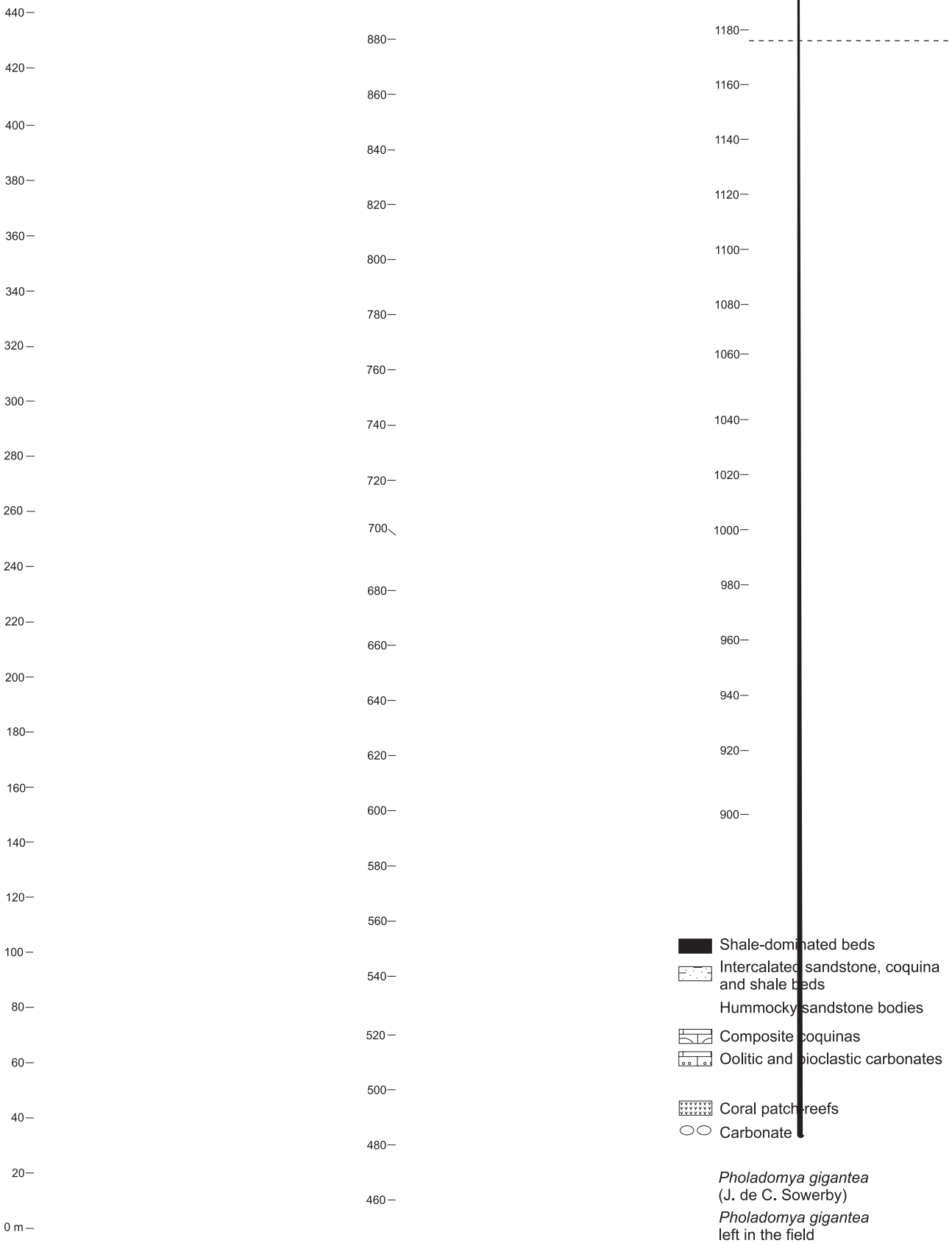
Pholadomya gigantea (J. de C. Sowerby, 1836)

Figs. 4A–E, 6A–E.

1836 *Pholas giganteus* sp. nov.; J. de C. Sowerby 1836: 338, pl. 14: 1.
1840 *Pholadomya elongata* sp. nov.; Münster in Goldfuss 1840: 270, pl. 157: 3.
1842 *Pholadomya elongata* Münster in Goldfuss 1840; Agassiz 1842: 57–58, pl. 1: 16, 17, pl. 2 (2): 1–6.
1842 *Pholadomya favrina* sp. nov.; Agassiz 1842: 59, pl. 2 (1): 1, 2.
1842 *Pholadomya scheuchzeri* sp. nov.; Agassiz 1842: 58–59, pl. 2(1): 3–7, pl. 2 (2): 7.
1844 *Pholadomya elongata* Münster in Goldfuss 1840; d'Orbigny 1844: 350–351, pl. 362: 1–3.
1852 *Pholadomya favrina* Agassiz, 1842; Pictet and Roux 1852: 403–404, pl. 29: 1a, b.
1864 *Pholadomya elongata* Münster in Goldfuss 1840; Pictet and Campiche 1864: 74–77, pl. 104: 1–4.
1884 *Pholadomya alternans* Roemer, 1841; Weerth 1884: 34, pl. 8: 1; pl. 9: 11 [?non Roemer 1841: 76].
1884 *Pholadomya* cf. *P. gigantea* (J. de C. Sowerby, 1836); Weerth 1884: 34–35, pl. 8: 2a, b.
1895 *Pholadomya elongata* Münster in Goldfuss 1840; Maas 1895: 279–280, pl. 9: 1, 2.
1897 *Pholadomya elongata* Münster in Goldfuss 1840; Karakasch 1897: 81–82, pl. 2: 9a, b.
1900 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Burckhardt 1900: 23, pl. 23: 5, 6.
1900 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Müller 1900: 44, pl. 21: 1.
1903 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Burckhardt 1903: 76, pl. 15: 1, 2.
1909 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Woods 1909: 246–249, pl. 40: 14, pl. 41: 1.
1924 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Gillet 1924: 145–146, text-fig. 90.
1928 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Lees 1928: 639.
1931 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Weaver 1931: 313–315, pl. 36: 209–211.
1940 *Pholadomya* cf. *P. gigantea* (J. de C. Sowerby, 1836); Imlay 1940: 155, pl. 18: 5.
1948 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Tavani 1948: 66, pl. 19 (10): 12.
1956 *Pholadomya* cf. *P. gigantea* (J. de C. Sowerby, 1836); Alencaster de Cserna 1956: 20–21, pl. 3: 9.
?1959 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Corvalán Díaz 1959: 35–36, pl. 2: 7.
1960 *Pholadomya gigantea* (J. de C. Sowerby, 1836); Muromtsieva and Janin 1960: 221, pl. 28: 5–7.

Table 1. Measurements (in mm) of *Pholadomya gigantea* (J. de C. Sowerby, 1836) housed at CPBA (Buenos Aires, Argentina). Abbreviations: AX, Auxerre, France; AF, Agrio Formation; AM, Agua de la Mula; BA, Bajada del Agrio; CB, Cerro Bayo; CR, Cerro Birrete; CN, Cerro Negro; CS, Cerro Salado; NQ, Neuquén Province unknown locality. For details in measurements see Systematic palaeontology and for locations see Fig. 1.

Specimen		Measurements							Rates
CPBA	Code	Length (L)	Height (H)	Width (W)	H siphonal gape	W siphonal gape	Anterior length (AL)	Number of	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520
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460
1180
1160
1140
1120
1100
1080
1060
1040
1020
1000
980
960
940
920
900
Shale-dominated beds
Intercalated sandstone, coquina and shale beds
Hummocky sandstone bodies
Composite coquinas
Oolitic and bioclastic carbonates
Coral patch-reefs
Carbonate
Pholadomya gigantea (J. de C. Sowerby)
Pholadomya gigantea left in the field

Group) and is probably Early Cretacoues in age (see Kitchin 1908: 33). *Pholadomya moeschii* Weerth, 1884 (Weerth 1884: 35, pl. 8: 4) is recorded in the Early Cretaceous of Germany and the description was based on a small-sized specimen. This proposed plexus had a somewhat different life habit from that of *P. gigantea* (see below).

Pholadomya picteti Mayer-Eymar, 1893 (Mayer-Eymar 1893: 263–264, pl. 2: 1; Tavani 1948: 146–147, pl. 10: 9) from the Early Cretaceous of Somaliland is very different from *P. gigantea*. It has a subtrigonal outline that is not posteriorly elongated and it lacks prominent radial ribbing. This species has been recorded also in the Berriasian of Tunisia, Barremian of Algeria and Aptian of Colombia and Spain (Gillet 1924: 147; Dietrich 1938: pl. 22: 4; Glaçon and Mongin 1951: 435, pl. 15: 11; Mongin 1979: 137; Etayo-Serna 1985: 21).

Pholadomya sanctaecrucis Pictet and Campiche, 1864 (Pictet and Campiche 1864: 82–83, pl. 105: 6, 7) and *Pholadomya valangiensis* Pictet and Campiche, 1864 (Pictet and Campiche 1864: 83–84, pl. 106: 1–3) from the Valanginian of Switzerland and France have an oval shape, a smaller siphonal gape, and they are ornamented only with commarginal lines. Both species are morphologically undistinguishable (personal observation, Museé Cantonal de Geologie, Lausanne) and must be placed in synonymy and probably removed to the genus *Homomya* Agassiz, 1843. *Pholadomya sanctaecrucis* was also recorded in the Quintuco Formation in Neuquén and in the Barril Viejo Shale in Coahuilla, Mexico (Weaver 1931: 317– 318, pl. 36: 202, 203; Imlay 1940: 155, pl. 12: 3–5). *Pholadomya valangiensis* has been recorded also in the Valanginian of Colombia (Etayo-Serna 1985: 22).

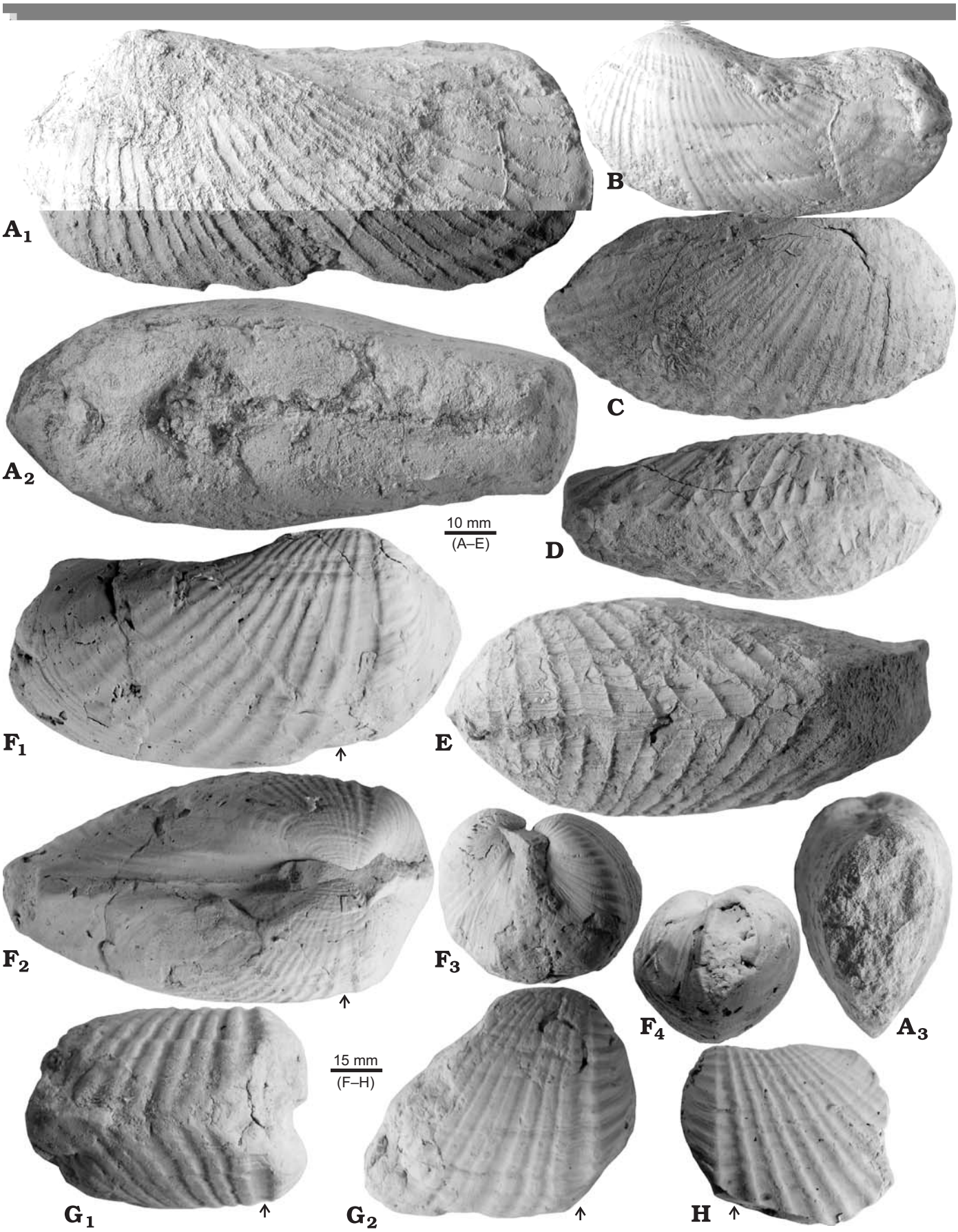
Pholadomya speetonensis Woods, 1909 (Woods 1909: 248–249, pl. 41: 4) from the Speeton Clay (probably from the C Beds, Hauterivian) of England has a suboval to rounded outline and is less elongated (L/H approximately 1.36) than *P. gigantea*. *Pholadomya* aff. *P. speetonensis* was also recorded in the Late Valanginian of Colombia (Etayo-Serna 1985: 22).

Mode of occurrence, facies relationships, and life habit

Pholadomya gigantea is a scarcely recorded species in the Agrio Formation in comparison to other infaunal bivalves. For instance *Panopea gurgitis* (Brongniart in Cuvier and Brongniart, 1822) and *Cucullaea gabrielis* Leymerie, 1842 are usually abundant in many levels. Specimens of *Pholadomya gigantea* occur in discrete levels throughout the unit, but each horizon contains a single or few specimens (Fig. 5). All recorded shells were articulated, but out of life position lying parallel to bedding. Most specimens have shell preserved, but recrystallized. The sedimentary infill of shells invariably matches the host matrix. The shell condition was generally good and in many cases the shells were pristine. Bioerosion and encrustation were not detected. The only damage present was minor external abrasion, corrosion and chipped margins. Articulated shells with low degree of taphonomic alteration suggest that lateral transport was minor and that bivalve assemblages can be regarded with confidence as slightly parautochtonous. These assemblages correspond to within habitat time-averaged associations of Kidwell (1998), spanning from days to 0.5 My, and even though there are minor discontinuities in the analyzed section, there are no records of biostratigraphically condensed assemblages.

Pholadomya gigantea was collected from high diversity bivalve assemblages. Associated bivalves were: (1) burrowers: *Trigonia carinata* Agassiz, 1840, *Steinmanella pehuenmapuensis* Leanza, 1998, *Steinmanella transitoria* (Steinmann, 1881), *Pterotrigonia* sp., *Eriphyla argentina* Burckhardt, 1903, *Ptychomya koeneni* Behrendsen, 1892, *Panopea gurgitis*, *Cucullaea gabrielis*, *Nicaniella* sp., *Disparilia* sp., *Aphrodina quintucoensis* (Weaver, 1931); (2) epifauna: *Mimachlamys robinaldina* (d'Orbigny, 1847), *Aetostreon* sp., *Amphidonte* (*Ceratostreon*) sp., *Gervillaria alatior* (Imlay, 1940), undetermined limids; and (3) semi-infauna: *Gervillella aviculoides* (J. Sowerby, 1814), *Myoconcha transatlantica* Burckhardt, 1903, *Pinna robinaldina* d'Orbigny, 1844, *Modiolus subsimplex* (d'Orbigny, 1850). Gastropods, decapods, echinoids, solitary and colonial serpulids, nautilids, and ammonites were also frequently present. Associated trace fossils were *Palaeophycus* Hall, 1847, *Thalassinoides* Ehrenberg, 1944, and *Chondrites* Sternberg, 1833.

The *Pholadomya*-bearing facies were defined in Agua de la Mula locality by grain size, sedimentary structures, and palaeontologic and taphonomic features. Generalized environmental interpretations are made for each facies. *Pholadomya gigantea* was recorded in the following facies: (1) Intercalated sandstones, coquinas, and shale beds; (2) composite coquinas; and (3) hummocky cross bedded sandstones beds (Fig. 5). In facies 1 *P. gigantea* occurred in thinly bedded sandstones and coquinas characterized by an erosional base, groove casts, poor to dense shell-packing, normal graded bedding, wave-generated cross lamination, and a mixture of fine shell debris and complete fossils. This facies is interpreted as deposited in a storm-influenced inner shelf. Facies 2 is composed of densely and loosely packed coquinas and records the accretion and amalgamation of individual coquinas up to 3.5 m-thick. They have an erosional base, planar lamination at the base and wave ripples on top. Hummocky cross-stratified shell debris is occasionally recorded. Most coquinas have a mixture of shells with different degrees of physical, biological, or chemical damage. Facies 3 is composed of amalgamated fine to medium-grained sandstones up to 17 m in thickness. The sandstones show planar lamination to low angle cross-lamination, wave and current-formed ripples, and hummocky cross-stratification. Facies 2 and 3 are interpreted as deposited in a shoreface environment under moderate to high energy levels (see Lazo et al. 2005). Associated trace fossils belong to the *Cruziana* ichnofacies that is representative of a shelf setting and indicates soft to firm well-oxygenated substrate,


A1
B
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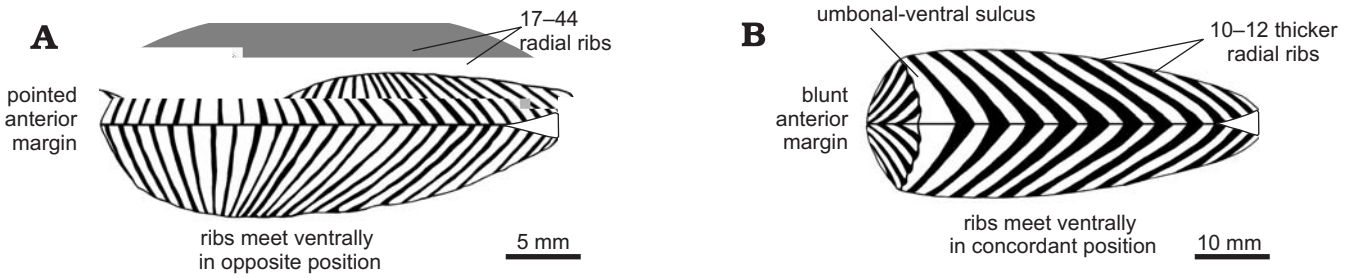

Fig. 7. Main differences between *Pholadomya gigantea* (Sowerby, 1836) (**A**) and *Pholadomya agrioensis* Weaver, 1931 (**B**). Schemes in ventral view.

lower to medium levels of energy, and moderate to low sedimentation rate.

The life habit of *Pholadomya gigantea* was similar to that of Recent *P. candida*, deep burrowing and sedentary, although some differences can be pointed out (Fig. 8). In *P. candida* the mantle fusion is nearly complete, being open only at siphons, the pedal gape and a special pallial aperture that is located immediately below the inhalant siphon. The siphons cannot be completely retracted within the shell. Since it has never been collected alive its life habit, mode of feeding, and preferred substrate remain unknown, but Morton (1980) postulated a passive deep burrowing life habit lying on its back. The presence of a pedal gape and accessory muscles suggested a pedal-feeding system. The foot would function as a piston and the pedal gape as a valve bringing sediments and water into the mantle cavity (Morton 1980). It is suspected to habit sublitoral sandy or muddy substrates in protected bays (Runnegar 1972; Morton 1980).

Pholadomya gigantea has a posteriorly elongated shell, posterior gape, and a well-developed pallial sinus. However, *P. gigantea* has neither pedal gape nor accessory muscles related to its aperture and closure. Thus a suspension-feeding habit, not a pedal-feeding system, may be inferred as it is commonly suggested in other Jurassic and Cretaceous *Pholadomya* species (e.g., Scott 1970; Freneix 1981). In modern *P. candida* the shortness of the inhalant siphon relative to the exhalant may not indicate that the animal lay on its back as suggested by Morton (1980: fig. 57). The longer siphon may function as a sort of tube or chimney to discharge waste water well-above the entrance of clean water at the inhalant siphon aperture. In addition *P. candida* could not have reached a final position lying on its back because, while digging in the sediment, the foot protrudes at the anteroventral margin and cannot turn the shell in a posterior direction.

Pholadomya gigantea is a very elongated species with an average L/H = 2.11 (see Table 1). Very elongated Recent bivalves use very little or no rocking movement with an angle of rotation less than 15° and the foot of such forms usually emerges in a direction parallel to the long axis of the shell. This direction is kept while burrowing in the sediment (Stanley 1970). It has a cylindrical shell shape plus a thin shell that may indicate a moderate to high burrowing rate (see Stanley 1970). Its radial ribs could have been of some help while digging because some are at right angles to the direction of burrowing, they show perimeter smoothening, and most are asymmetrical in cross section with the gentle slopes in the burrowing direction and the steep slopes on the leeward side. Under the influence of the ligament these ribs would have gripped the sediment when the adductor muscles relaxed, thus allowing the foot to be pushed into the sediment. However, they do not show allometric densening to compensate for the increase in shell size versus the unchanging grain size (see Seilacher 1973). Sediment could also be temporarily fluidised by the rapid closure of the shell by adductor action expelling water from the mantle into the surrounding sediment.

Pholadomya agrioensis Weaver, 1931, endemic to the Neuquén Basin, had probably the same basic palaeoecology of *P. gigantea*, a deep infaunal, siphonate, suspension-feeding burrower. However, it has a distinctly blunt anterior portion demarked by a deep umbonal-ventral sulcus that is covered only with commarginal ribs that are stronger than in the rest of the shell (Fig. 7). Once buried *P. agrioensis* could have been capable of penetrating deeper into the substrate by means of this anterior portion. In a nearly vertical position the blunt anterior margin is in wide contact with the substrate below and by opening and closure of valves the bivalve could have excavated deeper into the sediment. This mechanism is reminiscent, but probably not identical, of that of pholad boring (see Seilacher 1985: fig. 2). In addition all the study specimens of *P. agrioensis* are filled with shale. Therefore they probably burrowed in finer sediments than *P. gigantea*.

Pholadomya gigantea and *P. agrioensis* seemed to have been relatively immobile deep burrowers because they show

← Fig. 6. Anomalodesmatid bivalves from the Early Cretaceous of Argentina and France. **A**–**E**. *Pholadomya gigantea* (Sowerby, 1836). **A**. CPBA 20121.1, Late Valanginian, Cerro Birrete, in left lateral (A_1), dorsal (A_2), and posterior (A_3) views, note the presence of a posterior (siphonal) gape. **B**. CPBA 228.2, Early Cretaceous, Auxerre, France, in left lateral view. **C**. CPBA 7555.1, Valanginian–Hauterivian, Cerro Negro, in right lateral view. **D**. CPBA 20122.3, Early Cretaceous, unknown locality, Neuquén, in ventral view. **E**. CPBA 19726.10, Early Hauterivian, Agua de la Mula, in ventral view. **F**–**H**. *Pholadomya agrioensis* Weaver, 1931, Early Cretaceous, unknown locality, Neuquén. **F**. CPBA 7588.1, in right lateral (F_1), dorsal (F_2), anterior (F_3), and posterior (F_4) views, note the absence of an anterior (pedal) gape and the presence of a posterior (siphonal) gape. **G**. CPBA 7579.1, in ventral (G_1) and right lateral (G_2) views. **H**. CPBA 7579.2, in left lateral view. Arrows indicate the position of the deep umbonal-ventral sulcus. All whitened with ammonium chloride.

a permanent posterior gape and also because their modern counterpart, *P. candida*, cannot withdraw its siphons completely within the shell. Maximum burrowing depth of Recent immobile burrowers is about 2.5 to 4 times the total shell length (Kondo 1987). Using the average shell length of *P. gigantea* (92.73 mm in Table 1), its maximum burrowing depth should vary between 230 and 370 mm.

Palaeobiogeography

During the Early Cretaceous the genus *Pholadomya* reached a cosmopolitan distribution, being present in the North Temperate, Tethyan, and South Temperate Realms of Kauffman (1973). Apart from records mentioned in the Aappendix 1 there are also records in Japan (Nagao 1943), South Africa (Kitchin 1908), and the western USA (Anderson 1938). The number of recorded species is highly variable depending on location, but the highest specific diversity has been recorded in the Valanginian–Aptian of the Tethyan Realm, especially in the Mediterranean province (see Pictet and Campiche 1864: 93–95). Even though, a modern revision of type specimens is needed. The broad Early Cretaceous distribution of the genus *Pholadomya* in warm tropical and temperate subtropical settings contrasts with the modern restriction to inlets in the Caribbean Sea. It has persisted in a rather specialized infaunal niche with low abundance. The present-day restricted distribution probably resulted from a displacement by competition with more generalist bivalves as it is assumed in other Recent anomalodesmatan bivalves (see Morton 1981).

In the Neuquén Basin only two valid species of *Pholadomya* have been recorded, one is endemic and the other is globally distributed suggesting that the basin, although behind a volcanic arc, had open marine connections with other parts of the world, especially the Mediterranean until its isolation from the Pacific in the Barremian. This is supported also by the presence of other widely distributed Early Cretaceous bivalves in the Neuquén Basin. In fact about 34%, 11 of 32 recorded taxa, are shared with other parts of the world, mainly the Mediterranean Province (Lazo 2005). The species diversity is lower than in the Mediterranean indicating that environmental conditions in the Neuquén Basin, such as water temperature or salinity, had not been as favourable for settling.

In many locations the stratigraphic resolution is not precise enough to assess a stage-by-stage palaeogeographic distribution of *P. gigantea* (see Appendix 1), even though a preliminary scheme can be offered. *Pholadomya gigantea* reached quickly a wide distribution after its appearance in the Tithonian?–Early Valanginian. It occurred around South America and Africa, two continents that were already spreading apart (Fig. 9). From the Valanginian to the Barremian this species inhabited the Tethyan and South Temperate Realms, but reached the south of the North Temperate Realm, for instance southern England and northern Germany (see Appendix 1). It has not been recorded in the Antarctic Peninsula, Australia, India, Japan, New Zealand, Russia or South Africa.

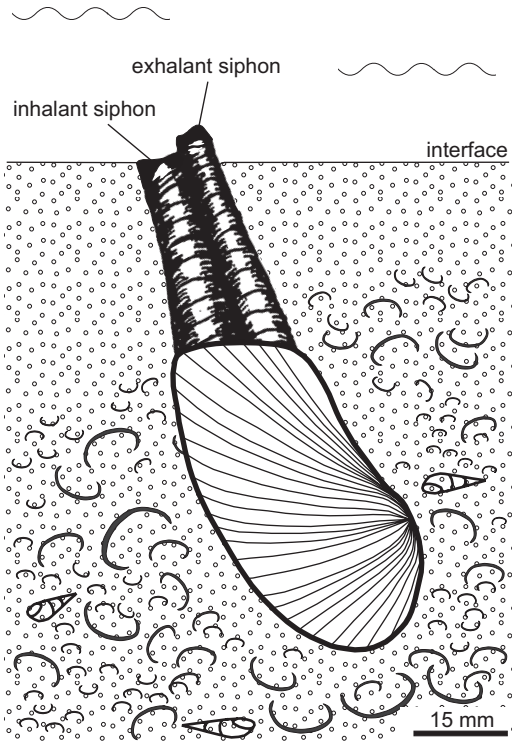

Fig. 8. Inferred life position of *Pholadomya gigantea* (Sowerby, 1836) from the Early Cretaceous of the Neuquén Basin, west-central Argentina. A passive deep burrowing habit is interpreted for this species, which has a large pallial sinus, siphonal gape, and thin posterior elongated shell. Angle between the shell and the sediment-water interface may be variable. Soft parts from Morton (1980).

From the distribution pattern it is apparent that open marine connections were established between west-central Argentina, the Mediterranean Province, and the east coast of Africa in the Valanginian–Barremian interval (Fig. 9). Marine connections may have existed from the Neuquén Basin northwards and southwards. The dispersion of *P. gingatea* took place mainly by longshore currents that run parallel to the west and north coasts of South America and the north and east coasts of Africa (Fig. 9). This is consistent with inferences made by the study of Early Cretaceous ammonites. Ammonite similarities between southern South America and South Africa-Madagascar indicate that a connecting seaway was becoming increasingly important from the Valanginian to the Aptian (Riccardi 1991).

Discussion and conclusions

The study of Early Cretaceous bivalves of the Neuquén Basin is a project that has been in progress for the last six years. Some of the species have been already studied and published (Lazo 2003a, b), and a preliminary comprehensive account given (Lazo 2004, 2005). New field work and collecting, revi-

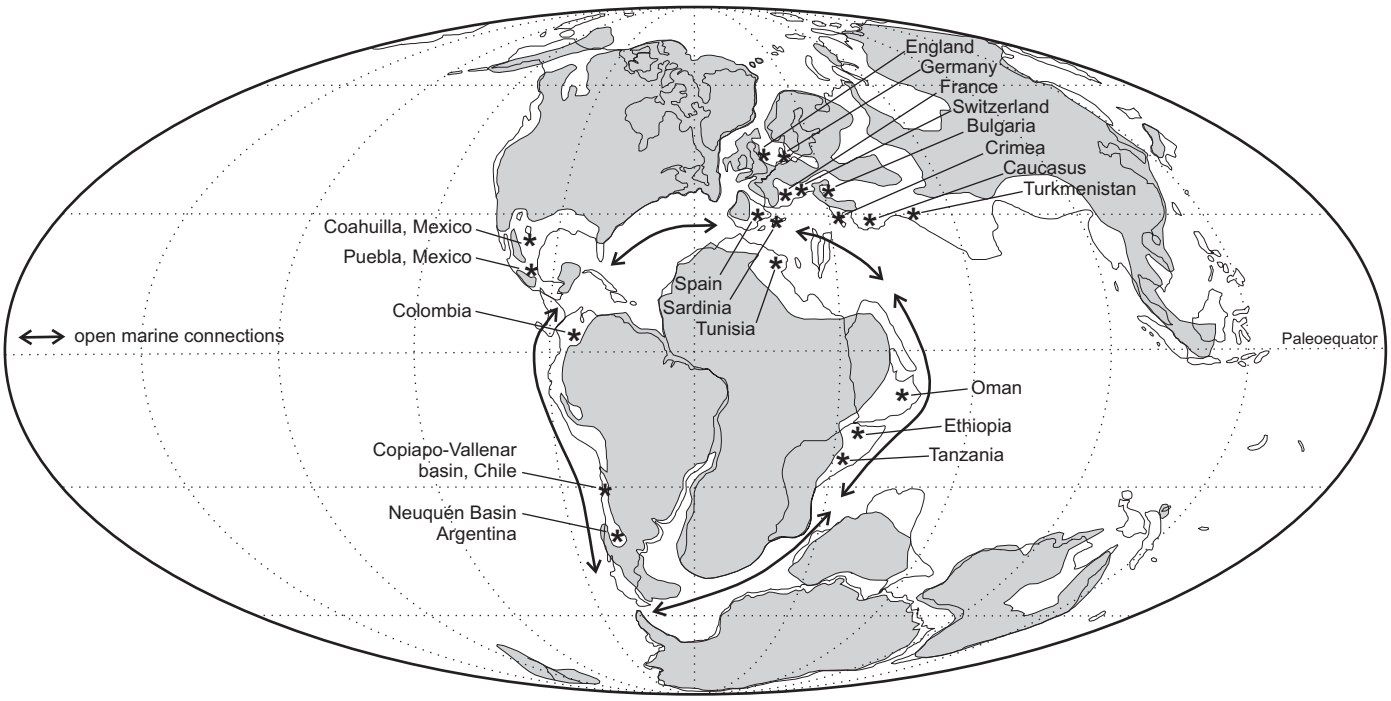

Fig. 9. Palaeobiogeography of *Pholadomya gigantea* (Sowerby, 1836) during the Early Cretaceous. Hauterivian–Barremian palaeocoastline map from Smith et al. (1994); records of *Pholadomya gigantea* are compiled in Appendix 1.

sions of former collections plus ongoing geochemical analysis will provide new insights concerning the Early Cretaceous depositional settings and their relationships with the bivalve faunas. Recent research in the Agrio formation gives a clearer emerging picture of its abundant fossil content (Lazo 2004; Lazo et al. 2005). Bivalves are abundant throughout the sequence in different lithofacies and the species diversity, approximately 32 Valanginian–Barremian taxa, is similar to that recorded in the Mediterranean. 34% of these taxa are shared with other parts of the world, 22% are endemic, and 44% have unknown affinities and remain in open nomenclature awaiting further revision (see Lazo 2005).

In Early Cretaceous beds of the Neuquén Basin the genus *Pholadomya* is represented by two species: *P. agrioensis* Weaver, 1931 and *P. gigantea* (J. de C. Sowerby, 1836). Apart from *P. gigantea*, which is revised here, the other species is poorly known and there are few published data about its stratigraphic ranges, taphonomy, and palaeoecology. Future field work in the Quintuco Formation will give a broader perspective of Early Cretaceous bivalve assemblages of the Neuquén Basin.

In this paper *Pholadomya gigantea* has been fully revised with respect to its systematics, taphonomy, palaeoecology, and palaeobiogeography based on much newly collected material and a large number of specimens housed in several institutional collections. This bivalve may have played an accessory function within bivalve assemblages of the Early Cretaceous of the Neuquén Basin because it is not abundant and shows a marked facies-dependence in comparison to other recorded bivalves. This situation is similar to that of the modern *P. candida* which is also rarely recorded. In fact the genus *Pholadomya*, even though it is a long-ranging genus has not been abundant or dominant at least since the Early Cretaceous. It has remained little changed in shell morphology and passive deep burrowing life habit since the Late Triassic. This genus managed to survive in a rather specialized niche with many constraints, but successful enough to be alive today.

Although *Pholadomya gigantea* and *P. agrioensis* have similarities and indeed some authors place them in synonymy, in this paper several morphological differences have been indicated and a different life habit has been interpreted for each one. Both species were siphonate deep burrowers, but once in life position, *P. agrioensis* was capable of further digging in the sediment by means of a blunt anterior portion ornamented with strong concentric ribs. It is also suggested that *P. agrioensis* burrowed in finer substrates than *P. gigantea*. This hypothesis is going to be tested during future field works in the Quintuco Formation.

Preference for well-oxygenated sandy or bioclastic substrates is remarkable, indicating that the larval stage of *P. gigantea* settled successfully only on those specific substrates and not on muddy bottoms that are also very common in the Agrio Formation. This is not a taphonomic bias because aragonitic bivalves are very common in muddy facies. The larvae were able to test the bottom substrate and postpone metamorphosis until they found a suitable substrate for adult life. Once the right substrate was located, metamorphosis was induced. Textural parameters of the sediment played an important role inducing metamorphosis, but the faunal and floral composition, the abundance of organic matter, and the presence of chemical compounds within the substrate may have been also important. There are other species that in

the Agrio Formation had facies restrictions, for instance *Myoconcha transatlantica* Burckhardt, 1903 (Heterodonta, Permophoridae) and *Gervillaria alatior* (Imlay, 1940) (Pteriomorphia, Bakevelliidae) were also restricted to sandy and bioclastic bottoms. In contrast, there is a number of bivalves that do not show a strong facies dependence. For instance, the genus *Steinmanella* Crickmay, 1930 (Trigonioida) colonized sandy, bioclastic, and muddy bottoms. *Steinmanella* settled periodically on muddy bottoms during increased oxygen levels and reduced net sedimentation or brief omission periods. The low net sedimentation allowed *Steinmanella* to filter-feed without clogging and changed the consistency of the substrate to become firmer and more suitable for burrowing (Lazo 2003a). Therefore, Early Cretaceous bivalves of the Neuquén Basin used different strategies to colonize the seafloor and also different ways of dispersion because there are endemic and widely distributed species.

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Appendix 1

Summary of occurrences, ages, and references to *Pholadomya gigantea* (Sowerby, 1836) used in Fig. 9.

Occurrence	Age	Reference
Crimea and northern Caucasus	Valanginian-Hauterivian	Muromtsieva and Janin (1960)
Western Turkmenistan	Valanginian-Aptian	Prozorovskii et al. (1961)
Caucasus (Russia, Georgia)	Early Cretaceous	Karakasch (1897)
Spain	Early Cretaceous	Dhondt and Dieni (1988)
Bulgaria	Early Cretaceous	Dimitrova (1974)
Italy (Eastern Sardinia)	Valanginian-Hauterivian	Dhondt and Dieni (1988)
Eastern France	Early Cretaceous	Agassiz (1842); d'Orbigny (1844); Gillet (1924)
England (Isle of Wight, South East region)	Lower Greensand, Early Aptian–Late Aptian	Woods (1909), Casey (1961)
Switzerland (Vaud, Geneva)	Early Cretaceous	Agassiz (1842); Pictet and Roux (1852); Pictet and Campiche (1864)
Northern Germany	Early Cretaceous	Weerth (1884)
Tunisia	Early Cretaceous	Dhondt and Dieni (1988)
Oman (Musandam Peninsula)	Early Cretaceous (Barremian?)	Lees (1928)
Ethiopia (Warder)	Early Cretaceous	Tavani (1948)
Tanzania (different localities)	Early Cretaceous	Müller (1900)
Mexico (Coahuilla and Puebla)	Hauterivian	Imlay (1940); Alencaster de Cserna (1956)
Colombia (Sierra Nevada del Cocuy)	Late Valanginian-Late Aptian	Etayo-Serna (1985)
Chile, Copiapó-Vallenar Basin (25°30'–31°S)	Late Barremian	Aguirre (2001)
Argentina, Neuquén Basin	Late Valanginian-Early Barremian	Burckhardt (1900, 1903), Weaver (1931), this paper