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THE GASTROPOD FAMILY APORRHAIDAE IN THE LOWER CRETACEOUS OF THE NEUQUÉN BASIN, WEST-CENTRAL ARGENTINA

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ABSTRACT—The gastropod fauna of the Lower Cretaceous of the Argentinian Neuquén Basin contains three aporrhaid species. *Protohemichenopus neuquensis* Camacho, 1953 is the most abundant, longest-lived, and most geographically widespread of the aporrhaids of this basin, and its protoconch and early teleoconch whorls were unknown until now. The new species *Dimorphosoma weaveri* features convex to subtly angular spire whorls with opisthocyrt collabral ribs that are more prominent towards the mid-whorl, a bicarinate last whorl with small rounded nodes on the adapical carina, a simple, falcate labral wing which is more or less rectangular proximally and tapering and curving towards its distal end, and a short, straight rostrum. *Tylostoma jaworskii* Weaver, 1931 is now placed in *Harpagodes*, and other previous, scattered, coeval records of this genus in the basin are now recognized as part of this single species. It is believed that whereas *H. jaworskii* preferred shallower-water carbonate settings of low to moderate energy, *P. neuquensis* and *D. weaveri* favored siliciclastic to mixed clastic-carbonate environments, in deeper waters. In spite of its endemic elements, this aporrhaid association depicts a predominantly Tethyan influence.

INTRODUCTION

THE SOUTHERN aporrhaid faunas of the Upper Jurassic to Lower Cretaceous are not as well known as the Upper Cretaceous to Cenozoic ones, which have been studied from southern South America, New Zealand, Australia and Antarctica by several workers since the beginning of the past century (e.g., Wilckens, 1907, 1910, 1921, 1922; Marwick, 1924; Zinsmeister, 1977; Zinsmeister and Camacho, 1980; Zinsmeister and Griffin, 1995; Stilwell, 2003; Nielsen, 2005). In contrast, the Early Cretaceous representation of the family in South America and Antarctica is known through a few, mostly outdated works, which depict a rather inadequately documented fauna composed of few, poorly preserved records. Most come from Aptian–Albian strata (e.g., Colombian, Venezuelan, and some Antarctic records from Alexander I Island; d'Orbigny, 1842; Gerhardt, 1897; Jaworski, 1938; Cox, 1953; von der Osten, 1957; Thomson, 1971), whereas Berriasian–Barremian gastropods were recorded so far only from Argentina, Chile, and the Antarctic Livingston Island (Weaver, 1931; Camacho, 1953; Tavera, 1956; Covacevich, 1976). Several decades past, Camacho (1953) essayed a revision of some of the southernmost Jurassic and Cretaceous records and proposed some possibilities regarding their phylogenetic relationships. A comprehensive list of all previous Early Cretaceous aporrhaid records from South America—excluding Argentina—and Antarctica is provided in online Supplemental Data File 1. It clearly shows that they are taxonomically outdated and that a revision on the basis of newly collected materials is necessary. In particular, more precision regarding their stratigraphical ranges is required since it would make them useful for taxonomic comparisons, faunistic implications, and biostratigraphic and paleobiogeographic purposes.

The oldest records of aporrhaids from the Upper Jurassic–Lower Cretaceous of the Neuquén Basin are '*Alaria*' *acutecarinata* Behrendsen, 1891 (p. 19; Tithonian, Río Malargüe, Mendoza province) and '*Alaria*' *acuta* Behrendsen, 1892 (p. 413, pl. 4, fig. 3a, 3b; 'Neocomian', Arroyo Truquico and Quili-Malal, Neuquén province). Later, Haupt (1907, p. 204) reported '*Alaria*' cf. *glaucus* (d'Orbigny, 1850; Piette, 1891) and *Harpagodes oceani* (Brongniart, 1821) from the Upper Jurassic–Lower Cretaceous of the Cerro Lotena area, Neuquén province. Other important records are those published by Weaver (1931, p. 386): *Dicroloma* cf. *obtusa* (Pictet and Campiche, 1864) and *Dicroloma glaucus* both from sections of the Agrio Formation in Neuquén and Mendoza provinces. Camacho (1953) described a new genus and species of Aporrhaidae, *Protohemichenopus neuquensis*, on the basis of a few specimens from the Agrio Formation in northern Neuquén province.

From the Lower Cretaceous outcrops of the Austral Basin in southern Argentina two aporrhaids were reported: *Aporrhais protuberatus* Stanton, 1901 (p. 32, pl. 6, figs. 13–15) and *Aporrhais*? sp. (Stanton 1901, p. 33), both from the Río Belgrano Formation (Barremian), in the Lake Pueyrredón area, Santa Cruz province. More details on both of these records can be found afterwards.

In the light of the available records, the aim of this paper is to provide a revision of the Early Cretaceous aporrhaid fauna from the Neuquén Basin, not only updating its taxonomy, but also presenting new data on their stratigraphical ranges, geographic extension and synonyms. This work intends to make a significant contribution to the knowledge of the southern aporrhaid faunas, since the information of the Early Cretaceous associations is necessary to complete the picture of the evolution of the family in the southern latitudes.

GEOLOGICAL SETTING

The aporrhaid gastropods from the Lower Cretaceous of the Argentinean Neuquén Basin come from the Mulichinco (lower Valanginian) and Agrio (upper Valanginian–upper Hauterivian/lowest Barremian) formations, both belonging to the mostly marine Mendoza Group (Upper Jurassic–Lower Cretaceous). These two units crop out extensively throughout the Neuquén province, with the Agrio Formation also cropping out in southern and western Mendoza province. Lithologically, the Mulichinco Formation shows considerable lateral variation:

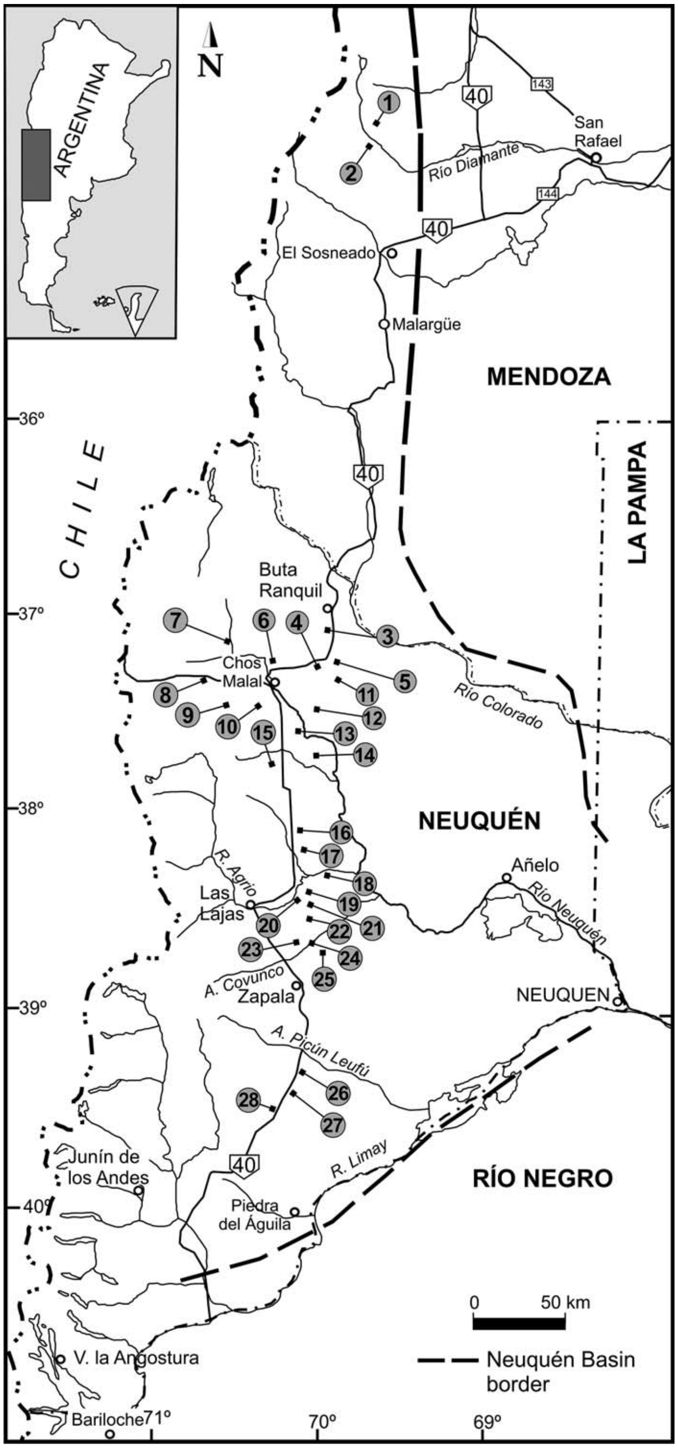

FIGURE *1*—Map of west-central Argentina showing the fossil localities with Early Cretaceous aporrhaids: *1*, Arroyo La Escondida; *2*, Lomas Bayas; *3*, Vega de Escalone; *4*, Puerta Curaco; *5*, Loma de la Torre; *6*, Chos Malal Norte; *7*, Caepe Malal; *8*, Estancia Rahueco; *9*, Cerro Caicayén; *10*, Arroyo Truquico; *11*, El Gasoducto; *12*, Mina San Eduardo; *13*, Puesto Canale; *14*, Cerro Rayoso; *15*, Pichaihue; *16*, Agua de la Mula; *17*, Salado Sur; *18*, Agrio del Medio; *19*, Bajada del Agrio; *20*, Bajada Vieja; *21*, Cañadón de los Baguales Norte; *22*, Cañadón de los Baguales Sur; *23*, Cerro Bayo; *24*, Arroyo Covunco; *25*, Cerro Mesa de Covunco; *26*, Cerro Birrete; *27*, Cerro Marucho; *28*, Estancia La Negra.

often, fluvio-deltaic sandstones and conglomerates are transitional to sandstones, mudrocks, limestones, and coquinas of marginal marine to normal marine settings (Schwarz et al., 2011). In turn, the Agrio Formation consists, to a large degree, of black shales and mudrocks with intercalations of limestones, sandstones and coquinas, which have been interpreted as mixed clastic-carbonate deposits of storm-influenced shallow-marine settings (Spalleti et al., 2001).

MATERIALS AND METHODS

This study was carried out on the basis of a large number of newly collected specimens from several Lower Cretaceous outcrops spread throughout the Neuquén Basin, as well as on the examination of the original materials of the existing records (e.g., Behrendsen, 1891, 1892; Weaver, 1931; Camacho, 1953; Damborenea et al., 1979).

More than 1,800 specimens were collected for this work, coming from 28 localities in the Neuquén Basin, which span a stratigraphical range from the lower Valanginian to the upper Hauterivian/lowest Barremian. As shown in Figure 1, the fossiliferous localities cover a wide geographic range within the basin. This geographic dispersion ensures that specimens from different facies associations within the bearing units are available for study. Collection of the material in the field was done thoroughly bed-by-bed, paying special attention to the associated ammonoid species in order to place the bearing beds in the current biostratigraphical scheme for the basin developed by Aguirre-Urreta et al. (2007) and its subsequent improvements (Aguirre-Urreta and Rawson, 2010; Rawson and Aguirre-Urreta, 2012). This allowed establishing a precise stratigraphical range for each species.

The specimens studied belong to three species, each represented by a large number of specimens, which is useful for appreciating intraspecific morphologic variation. The material is usually in a good to moderately good state of preservation, although the expansion of the outer lip is seldom preserved except in cases in which the specimens are found in coquinas or shell pavements. The apical portion of the shell was recovered only from one of the three species described herein. The material required little mechanical preparation. Photographs were taken with a digital camera after coating with ammonium chloride. Also, high-resolution images were obtained by SEM.

SYSTEMATIC PALEONTOLOGY

The institutions that house the specimens studied for this work are as follows: Colección de Paleontología de la Universidad de Buenos Aires (Buenos Aires, Argentina, CPBA); Geowissenschaftliches Museum der Universität Göttingen (Göttingen, Germany, GZG.INV); Museo de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina, MACN-Pi); Museo de Ciencias Naturales y Antropológicas J.C. Moyano (Mendoza, Argentina, MCNAM-Pi); Museo de La Plata (La Plata, Argentina, MLP); Museo Patagónico de Ciencias Naturales, (General Roca, Argentina, MPCN-PI); Paleontological Research Institution (Ithaca, U.S.A., PRI); Burke Museum of Natural History and Culture, University of Washington (Seattle, U.S.A., UWBM).

Morphologic terminology and linear and angular measurements follow the general guidelines of Cox (1960). Also, the terms used by Popenoe (1983) for the expansion of the outer lip of the Aporrhaidae were adopted. The abbreviations for measurements are as follows: H, height of teleoconch; Hlw, height of last whorl; Hap, height of aperture; D, maximum diameter of teleoconch; D/H, diameter to height rate; Hlw/H, last whorl height to teleoconch height rate; PA, pleural angle; SL, sutural slope; Ll, length of outer lip; Wl, width of outer lip; Div, amount of divergence between the lateral labral processes. The measurements taken in the outer lip are depicted in Figure 2.

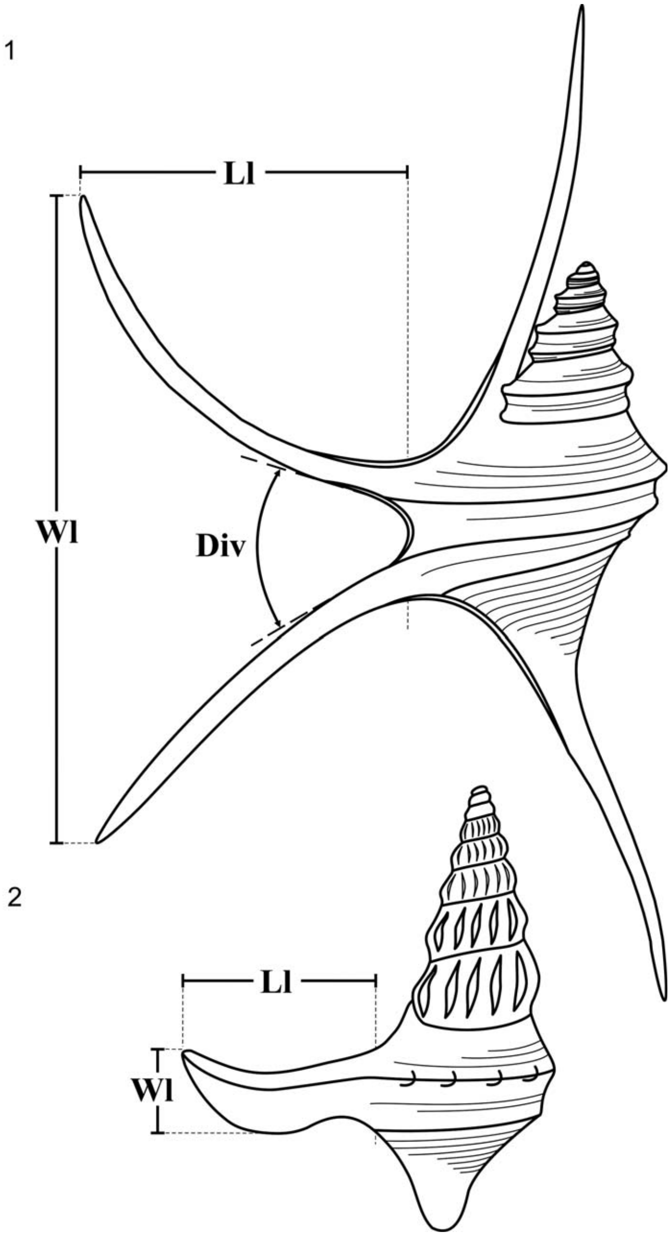

FIGURE 2—Measurements taken in the labral expansion of two of the aporrhaid species discussed herein: *1*, *Protohemichenopus neuquensis* Camacho, 1953; *2*, *Dimorphosoma weaveri* n. sp. Abbreviations: Ll=length of outer lip; Wl=width of outer lip; Div=amount of divergence between the lateral labral processes.

Superfamily STROMBOIDEA Rafinesque, 1815
Family APORRHAIDAE Gray, 1850

Remarks.—Genera are distinguished in this family on the basis of the morphology of the outer lip expansion and the rostrum—also called anterior process or anterior canal—of the adult shell, and in the presence and position of a posterior process (Loch, 1989; Bandel, 2007). Frequently, the sculpture of the spire and last whorls are considered in generic diagnoses.

The protoconch of aporrhaids is rather large, conical to dome-shaped, with rounded whorls in a variable number; the embryonic shell is smooth and the larval whorls can be smooth or finely tuberculate (Bandel, 2007); ornamentation of spiral threads or carinae and/or collabral ridges appear in the gradual transition to the juvenile teleoconch. Protoconchs similar to that of *Aporrhais pespelicani* (L.) (Bandel, 2007, pl. 1, figs. 13–16) were recorded as early as the Middle Jurassic (Bandel, 1993; Gründel, 1998).

Systematics and phylogeny of the Aporrhaidae have been studied by several workers. This resulted in a number of different classification schemes produced with sometimes very dissimilar criteria. Recently, Kollmann (2009) proposed a subdivision of the Aporrhaidae into several subfamilies based on a few morphologic characters of the teleoconch: the whorl profile and sculpture, and the shape of the outer lip expansion. Moreover, he stated that these characters are useful for delineating the phylogenetic relationships of the group if their evolution is considered. The placing of the taxa described herein in Kollmann's scheme will be discussed below.

Genus PROTOHEMICHENOPUS Camacho, 1953

Type species.—*Protohemichenopus neuquensis* Camacho, 1953 (p. 191, figs. A, B), Hauterivian, Argentina, by monotypy.

Diagnosis.—Original: teleoconch small, with the two first spire whorls smooth, then with a strong middle carina and sometimes with another, weaker one over the lower suture of the penultimate whorl. Last whorl frequently bicarinate, with a third, weaker carina and sometimes a fourth one, fine spiral cords, two thin processes and a strong callosity ascendent over the spire (translated from Camacho, 1953, p. 184).

Emended: protoconch obtusely conical to dome-shaped, with the two first whorls smooth and convex; towards two and a half whorls, fine spiral threads and collabral ribs appear gradually, forming a reticulate pattern in the first juvenile teleoconch whorls. Adult teleoconch small. Spire high, representing more than two-thirds of total shell height—excluding rostrum or anterior process. Spire whorls bicarinate, surface between carinae concave. Adapical carina located towards mid-whorl, more prominent; abapical carina close to the abapical suture. Last whorl tricarinate, the third carina very thin and close to the middle one. Outer lip extended into two long lateral processes continuous from the adapical and middle carinae of the last whorl. Posterior labral process adherent to the spire and surpassing it in length. Rostrum long, straight to more or less curved to the left. Fine spiral threads on spire and last whorl. Callus covering inner lip area and part of the apertural side of last whorl.

Occurrence.—Upper Jurassic (Tithonian)–Lower Cretaceous (Barremian/?Aptian/?Albian), Argentina, Chile and ?Colombia.

Remarks.—Camacho (1953) created this genus to group the "primitive forms", i.e., the Early Jurassic to Early Cretaceous records (Camacho, 1953, p. 183, 189, 193) of Aporrhaidae of southernmost South America. These are depicted by this author as carinate forms, with carinae on the spire as well as on the last whorl, and would constitute the ancestral stock from which the southern aporrhaids diversified during the Late Cretaceous and Paleogene. As Camacho (1953) points out, after the 'Neocomian', the "primitive forms" were substituted by forms with collabral ribs, such as *Struthioptera* Finlay and Marwick, 1937. Actually, most of Camacho's "primitive forms" belong to only one species, since the other supposedly aporrhaid species included by him in *Protohemichenopus* do not belong to the Aporrhaidae. These are '*Alaria*' *acutecarinata* and '*A.*' *acuta*. Although for both species the presence of a middle carina plus a sculpture of spiral threads was described, the examination of the specimens originally studied by O. Behrendsen revealed that their affinity to *Protohemichenopus* is apparent. '*Alaria*' *acutecarinata* probably belongs to the Campanilidae and '*A.*' *acuta* to the Mathildidae.

Camacho (1953) did not state if he included the record of '*Chenopus*' sp. by Behrendsen (1891, p. 382), from the Lower Jurassic of the Neuquén Basin, in *Protohemichenopus*. The original specimen (GZG.INV 76004) is very poorly preserved and does not show diagnostic features that would suggest its generic affinity.

Protohemichenopus received little attention since its original publication. Only Thomson (1971) mentioned the genus afterwards, stating that it is strongly similar to *Tessarolax* Gabb, 1864 and could be even synonymous with it. However, *Tessarolax* can be distinguished by the presence of a short, blunt projection of the inner lip callosity directed towards the abapertural side of the last whorl (Kase and Maeda, 1980).

The protoconch and first teleoconch whorls of the type and so far only species of *Protohemichenopus* were unknown until the present work. The obtusely conical to dome-shaped outline, the smooth first whorls and the gradual appearance of spiral and collabral sculpture match the general features of the protoconchs and early teleoconchs known of different genera of the Aporrhaidae (e.g., Kase and Maeda, 1980; Zinsmeister and Griffin, 1995; Gründel, 2001, 2005; Stilwell, 2003; Kaim, 2004; Nielsen, 2005; Bandel, 2007; Jaitly and Szabó, 2007; Gründel et al., 2009). At the same time, it can be distinguished by the details of its ornamentation: the number of spiral threads, the form of the collabral ribs, the shape of the reticulate pattern formed at the intersections, the absence of nodes or tubercles, and the ontogeny of the carinae that develop towards the teleoconch.

Given the great diversity of Aporrhaidae during the Jurassic and Cretaceous of the world, there are several genera that can be compared and contrasted with *Protohemichenopus* so as to evaluate its taxonomic independence. *Aporrhais* Da Costa, 1778 is similar to *Protohemichenopus* in the outline of the spire and last whorl, but differs in that it has unicarinate whorls and the carinae usually bear nodules or thickened collabral ribs. Also, in *Aporrhais* the outer lip expands into a wide wing bearing four or five flattened processes or lobes, gutter-like in its apertural side (Bandel, 2007). In turn, in *Protohemichenopus* the outer lip expansion does not form a wide plate, but divides rapidly into divergent, thin processes.

Dicroloma Gabb, 1868, a so far exclusively Jurassic genus (Kaim, 2004), *Hemichenopus* Steinmann and Wilckens, 1908, from the Eocene of Chile and New Zealand (Nielsen, 2005), and *Toarctocera* Gründel, Nützel, and Schulbert, 2009, from the Early Jurassic of Europe, can be separated from *Protohemichenopus* mainly by lacking a posterior labral process. *Dicroloma* also has unicarinate spire whorls and a bicarinate last whorl (Kaim, 2004, fig. 54), whereas *Protohemichenopus* has bicarinate spire whorls and a tricarinate last whorl. In *Hemichenopus* the lateral processes are shorter and thicker than in *Protohemichenopus*, and the rostrum is relatively shorter and straighter (Nielsen, 2005, fig. 2.4–2.9). *Toarctocera* also has unicarinate spire whorls, a much longer and curved rostrum, and the outer lip expands into a rectangular wing (Gründel et al., 2009, fig. 3).

Protohemichenopus and *Ceratosiphon* Gill, 1870 are similar in the general outline of the teleoconch and the outer lip expansion. However, in *Ceratosiphon* the teleoconch is fusiform, with a shorter spire made of unicarinate whorls, and the labral processes can be bifurcated and have local thickenings or lateral expansions. Besides, the rostrum is much longer and curved to the left, and the inner lip callosity is thin though very much extended over almost all the apertural surface of the teleoconch and spire (Kase and Maeda, 1980). It is worth noting that Kase and Maeda (1980) and later Kollmann (2005, 2009) retained the taxonomic independence of *Ceratosiphon*, regarded by other authors as synonym of *Tessarolax* (e.g., Cossmann, 1904; Kiel, 2006; Bandel, 2007).

Teneposita Loch, 1989 is similar to *Protohemichenopus* in the morphology of the outer lip, but it has a short process opposite to the outer lip formed by the inner lip callosity, and the teleoconch sculpture includes collabral ribs (Loch, 1989).

The recently published genus *Trilemma* Blagovetshenskiy and Shumilkin, 2006, from the Lower Cretaceous (Hauterivian–Barremian) of Russia, reunites forms with slightly different outer lip architecture but showing, in general, juvenile and adult teleoconch morphologies similar to that of *Protohemichenopus*. Although the outer lip and the apical whorls are not known in the type species of *Trilemma*, *T. striatocarinata* Sinzow, 1880 (pl. 3, figs. 1–3), Blagovetshenskiy and Shumilkin (2006, 2012) described other species in this genus in which these features can be observed at least partially. In those, the protoconch is broadly conical or dome-shaped, with three initial smooth and convex whorls, and the transitional appearance of the teleoconch sculpture of collabral ribs and spiral threads. The outer lip expands to form three processes including one posterior process more or less attached to the spire. The spire whorls are bicarinate, the last whorl is tricarinate, and the sculpture consists of numerous spiral threads that cover the entire teleoconch. In spite of the variation in outer lip and rostrum morphology, the species of *Trilemma* and *Protohemichenopus* are remarkably similar. In *Trilemma polivnense* Blagovetshenskiy, 2012 (*in* Blagovetshenskiy and Shumilkin, 2012) the outer lip is slightly more expanded than in *P. neuquensis*, forming a reduced wing, and the processes are not as thin and delicate as in the latter. In *Trilemma kremenkense* Blagovetshenskiy, 2012 (*in* Blagovetshenskiy and Shumilkin, 2012) the outer lip expansion is known only partially, showing a reduced wing divided into two lateral triangular processes and a posterior labral process apparently detached from the spire. Its rostrum is apparently short and strongly bent. *Trilemma russiense* Blagovetshenskiy and Shumilkin, 2006 shows an outer lip configuration considerably different to that of *P. neuquensis* although the teleoconch morphology is still comparable. *Trilemma tenuicarinatum* Blagovetshenskiy, 2012, actually belongs to *Ceratosiphon*. In conclusion, although the similarity between *Trilemma* and *Protohemichenopus* species is notable, its synonymy cannot be stated unmistakably since the type species of *Trilemma* is incompletely known and its type is not to be found (Blagovetshenskiy and Shumilkin, 2012).

Ten unpublished specimens from the El Way Formation (upper Hauterivian–Barremian/?Aptian; Pérez and Reyes, 1989; Mourgues, 2008) coming from the Quebrada El Way area, Antofagasta, Chile, were included in this study (CPBA 5183–5192). It is concluded that they belong to *Protohemichenopus* and likely also to *P. neuquensis*, although the outer lip and rostrum are not preserved and the latter assumption cannot be made with certainty (Fig. 3.23). Although the age of the El Way Formation deposits is not yet known with certainty, different works state that their maximum age is late Hauterivian (Mourgues, 2008) and their minimum age is Barremian (Jurgan, 1974), possibly reaching the Aptian (Alarcón and Vergara, 1964).

The three '*Rostellaria*' species recorded by d'Orbigny (1842) from the Lower Cretaceous of Colombia do not preserve the morphology of the outer lip and do not show the diagnostic features of *Protohemichenopus*. On the other hand, the aporrhaid records reported by Jaworski (1938) are better described and illustrated and allow more detailed comparisons. *Chenopus* (*Tessarolax*) *bicarinata* Deshayes var. *evolutior* Jaworski, 1938 (p. 114, pl. 23, fig. 3a–3c) shows some of the diagnostic features of *Protohemichenopus*: bicarinate spire whorls, the adapical carina more prominent than the abapical one and the latter close to the abapical suture, last whorl tricarinate and sculpture of fine spiral threads. *Chenopus* (*Tessarolax*) aff. *bicarinatoides* (Wollemann, 1903; Jaworski, 1938, p. 115, pl. 23, fig. 4), according to Jaworski (1938), differs from '*C.* (*T.*)' *bicarinata* var. *evolutior*

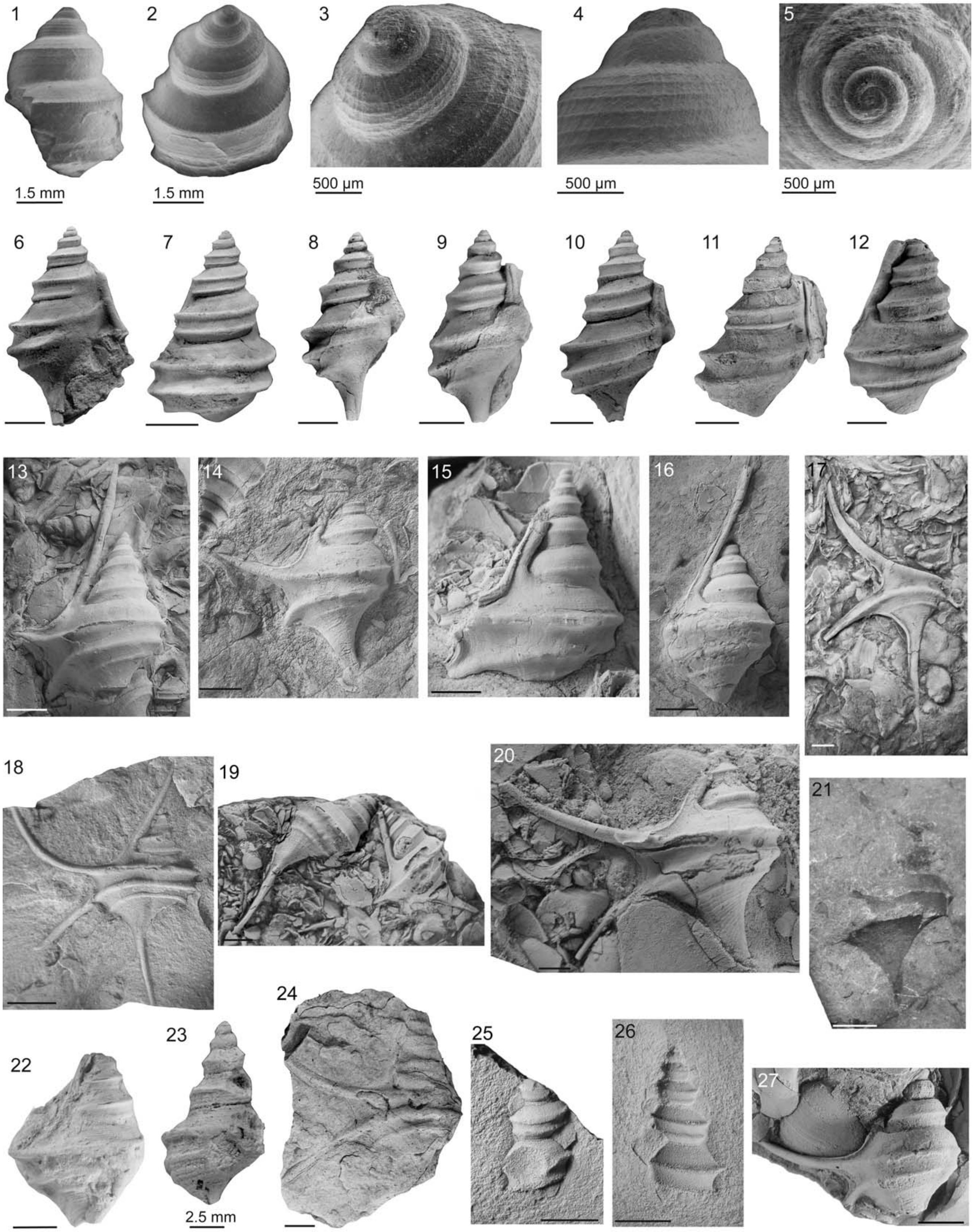

FIGURE 3—*Protohemichenopus neuquensis* Camacho, 1953. *1–4*, CPBA 21412.9, SEM pictures of protoconch and first teleoconch whorls, lateral views; *5*, CPBA 21409.1, SEM pictures of shell apex, apical view; *6*, CPBA 21409.1, apertural view; *7*, CPBA 21409.11, abapertural view; *8*, CPBA 21409.13, apertural view; *9*, CPBA 21409.63, apertural view; *10*, CPBA 21409.6, apertural view; *11*, CPBA 21408.3, apertural view; *12*, CPBA 21432.1, abapertural view; *13*, CPBA 21417.18, abapertural view, with outer lip and posterior labral process; *14*, CPBA 21417.19, abapertural view, with outer lip; *15*, CPBA 20320.1, abapertural view, with part of outer lip and posterior labral process; *16*, CPBA 21417.20, abapertural view, with posterior labral process; *17*, CPBA 21417.21, abapertural view, outer lip with lateral labral processes and rostrum; *18*, CPBA 21433, holotype, abapertural view, with labral processes and rostrum; *19*, CPBA 21417.37 (left) and CPBA 21417.33 (right), abapertural view, with rostrum (left and right) and posterior labral process (right); *20*, CPBA 20320.2, abapertural

by a more prominent spiral ornamentation and unicarinate spire whorls, but it is likely that these differences are the result of preservational modification. In every other respect the two records are alike and match the diagnostic features of *Protohemichenopus*, and therefore it could be concluded that this genus is present in the upper Lower Cretaceous of Colombia.

In the aporrhaid classification scheme of Kollmann (2009), *Protohemichenopus* may belong to the subfamily Pterocerellinae in the grounds of its long, delicate labral processes that extend from the outer lip margin and are contained in the same plane. Other genera included by Kollmann (2009) in Pterocerellinae are *Pterocerella* Meek, 1864; *Ceratosiphon* Gill, 1870; *Cultrigera* Böhm, 1885; and *Cuphosolenus* Piette, 1876.

Protohemichenopus neuquensis Camacho, 1953
Figure 3

1907 *Alaria* cf. *glaucus* (d'Orbigny); Haupt, p. 205.
1931 *Dicroloma glaucus* (d'Orbigny); Weaver, p. 386.
1953 *Protohemichenopus neuquensis* n. sp., Camacho, p. 191, figs. A, B.
1979 Aporrhaidae sp. indet. α, Damborenea, Manceñido, and Riccardi, p. 71, pl. 11, fig. 3.
?1979 Aporrhaidae sp. indet. β, Damborenea et al., p. 71.
?2001 *Dicroloma* sp., Gründel and Parent, p. 15, fig. 3E–3G.
?2006 *Dicroloma* sp., Gründel and Parent, p. 508, fig. 4F, 4G.

Diagnosis.—Emended: first teleoconch whorl with six very fine, evenly spaced spiral threads; the third spiral thread—numbered from the apex to the anteriormost point of the aperture—turning into the adapical carina towards the second teleoconch whorl; abapical carina appearing towards the third telecoconch whorl and deriving from the sixth spiral thread. Posterior labral process thin, straight to slightly curved to the left, attached to the spire and growing beyond its apex. Lateral labral processes thin, straight to slightly curved and diverging approximately 55–75°. Posterior lateral labral process bent adapically, anterior lateral labral process bent abapically. Rostrum very long and thin, straight to slightly bent towards the left.

Description.—Teleoconch small—maximum shell height 25.7 mm, excluding rostrum, more or less biconical, taller than wide—maximum diameter 16.2 mm, excluding labral processes, slightly coeloconoid, with about 10 whorls in the fully grown stage. Spire high, representing nearly three-fourths of total shell height—excluding rostrum. Protoconch with two first whorls smooth and convex. End of protoconch and beginning of teleoconch not demarcated. Spiral and collabral sculpture appearing gradually towards the third, convex whorl; six evenly spaced spiral threads appear at first, with faint, orthocline and opisthocyrt growth lines crossing and forming a fine grid of paralelograms slightly inclined to the right. Following whorl still convex and with a subtle carina slightly over mid-whorl arising from the third spiral thread. Abapical carina developing on next whorl from the sixth spiral thread and adjacent to the suture. Fourth spiral thread vanishes. In subsequent whorls new spiral threads appear above and below the first thread. Carinae rounded, sculptured with small elongated nodes formed by intersecting growth lines. Also fine spiral threads are visible on the carinae. Surface between carinae and below adapical carina flat to slightly concave; concavity emphasizing towards the last whorl. Sutural ramp wide, steep and slightly convex, limited by the adapical carina. Suture impressed, slightly grooved as a result of the depression formed below the abapical carina. Base flat to concave, limited by the abapicalmost carina of the last whorl; one strengthened spiral thread is present in few specimens abapically to the latter. On the last whorl, there are 5–8 spiral threads between the adapical suture and the adapical carina; 2–3 spiral threads between the adapical and the middle carina; 2–4 spiral threads between the middle and the abapical carina, and 10–11 spiral threads on the base. Rostrum very long and thin, straight to slightly bent to the left. Aperture narrow, elliptical. Outer lip extended into a narrow, almost unexpanded wing that readily divides into three long, thin processes, gutter-like in adapical view. Posterior labral process straight to slightly curved to the left, attached to spire and growing past the apex of the shell. Lateral labral processes diverging 55–75°; posterior lateral process bent towards the apex of the shell, anterior lateral process bent towards the rostrum. The adapical and middle carinae of the last whorl continue over the abapertural side of the lateral labral processes. Outer lip margin slightly thickened, concave and bent backwards between processes. Inner lip concave, with an extended callosity over most of the apertural side of the last whorl and reaching the base of the spire close to the posterior labral process. Very fine, opisthocyrt and orthocline to slightly opisthocline growth lines.

Types.—Holotype, CPBA 21433 (Fig. 3.18); paratype, CPBA 21434 (Fig. 3.22). According to Camacho (1953, p. 192), the holotype of *P. neuquensis* comes from "bituminous calcareous schists" of the Agrio Formation in the surroundings of the Buta Ranquil town, northern Neuquén province. The actual collector of the holotype, E. Holmberg, published later that in that area the Agrio Formation is exposed in small, scattered outcrops in which its contact with the underlying Mulichinco Formation can be observed (Holmberg, 1976). These outcrops consist of fossiliferous grayish-white marls and bituminous limestones interbedded with dark marls. Both Camacho (1953) and Holmberg (1976) pointed out a Hauterivian age.

Material.—A total of 1,345 specimens from 19 localities in Neuquén province and one locality in Mendoza province, and 25 additional specimens of different collections, from 20 localities in Neuquén and Mendoza (see online Supplemental Data File 2). Dimensions provided in online Supplemental Data File 3.

Occurrence.—Upper Jurassic (lower Tithonian)–Lower Cretaceous (upper Hauterivian). The stratigraphical range observed for the material from the Neuquén Basin studied herein goes from the *Lissonia riveroi* Zone (lower Valanginian, Mulichinco Formation) to the *Paraspiticeras groeberi* Zone (upper Hauterivian, Agrio Formation). However, specimens attributable to *P. neuquensis* have also been recorded in other units of the Mendoza Group: in lower Tithonian (Gründel and Parent, 2001, 2006), upper Tithonian and Berriasian beds (personal observ.) of the Vaca Muerta Formation, and in lower Valanginian beds of the Chachao Formation (Damborenea et al., 1979). This species also shows a wide geographical distribution, being present in 20 out of the 28 localities shown in Figure 1. *Protohemichenopus neuquensis* is generally very abundant, especially in Pichaihue, northern Neuquén province, in the *Pseudofavrella angulatiformis* Subzone, where the specimens also show a good state of preservation of the outer lip and rostrum. Also in Cerro Bayo, central Neuquén province, *P. neuquensis* is highly abundant in the *Spitidiscus riccardii* Zone.

Remarks.—The holotype and paratype of *P. neuquensis* are the specimens originally designated and illustrated by Camacho (1953, p. 192, figs. A, B) as "type and co-type". All the other studied specimens agree well in morphology with them. The

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view, with outer lip and lateral labral processes; *21*, MLP 14895, Aporrhaidae sp. indet. β in Damborenea et al. (1979), Chachao Formation (Mendoza province, Argentina); *22*, CPBA 21434, paratype, abapertural view; *23*, CPBA 5191, apertural view, El Way Formation (Chile); *24*, CPBA 21414.31, outer mold of specimen with lateral labral processes; *25*, *26*, UWBM 292, *Dicroloma glaucus* in Weaver (1931), inner (*25*) and outer (*26*) molds; *27*, CPBA 20320. 3, abapertural view, with outer lip and lateral labral process. All scale bars=5 mm except where noted.

"fourth carina" mentioned by Camacho (1953) in the original description of the species is actually a strengthened spiral thread placed abapically to the abapicalmost carina of the last whorl. This feature is not observed in every specimen but in a few. The amount of divergence of the lateral labral processes varies amongst the specimens available, which could be affected by the state of crushing of some of the specimens in which it was measured. The degree of displacement of the whorls along the coiling axis also varies, though very slightly. There are specimens in which the abapical carina is adjacent to the abapical suture and other in which it is moderately to quite detached from it. The number of spiral threads in between carinae and between these and the sutures or the base of the rostrum also displays some degree of variation, showing that one must be careful in using this feature to distinguish species of the same genus.

Camacho (1953) tentatively ascribed to *P. neuquensis* the two aporrhaid records of Weaver (1931). *Dicroloma glaucus* sensu Weaver (1931) is actually a redescription of the previous record of '*Alaria*' cf. *glaucus* by Haupt (1907), which he listed in its synonymy. Weaver (1931) attributed this record to the genus *Dicroloma* probably because the posterior labral process is not preserved in his material. Haupt (1907) did not illustrate his record and, unfortunately, the materials originally studied by him are lost and thus not available for revision. Still, several features included in his description indicate its affinity with *P. neuquensis*: bicarinate spire whorls, adapical carina with faint nodes, abapical carina less prominent and adjacent to the suture, last whorl tricarinate and partial preservation of the posterior labral process. Haupt's (1907) '*A.*' cf. *glaucus* is, consequently, included in the synonymy list of *P. neuquensis*. The examination of the specimen of *D. glaucus* studied by Weaver (1931) (UWBM 292; Fig. 3.25, 3.26) revealed that it represents a very poorly preserved fragment of teleoconch, in which only the bicarinate spire whorls are clearly visible. However, Weaver (1931) mentioned in his description the presence of two smooth apical whorls, spire whorls with a stronger middle carina and another, weaker one close to the suture, a flat and steep sutural ramp, last whorl with two strong carinae extending into labral processes, sculpture of spiral threads and faint growth lines. It is manifest that Weaver (1931) based his description in other specimens besides UWBM 292. Nonetheless, the record of *D. glaucus* sensu Weaver (1931) is attributed here to *P. neuquensis* since its description shows adequate morphologic agreement and its type locality and stratotype are comprised within the stratigraphical and geographic ranges of the species.

Gründel and Parent (2001, 2006) described poorly preserved specimens from the lower Tithonian of the Picún Leufú area, southern Neuquén province. These authors attributed the record tentatively to *Dicroloma* on the basis of the general teleoconch morphology and sculpture, pointing out that due to the lack of protoconch and the first teleoconch whorls, the generic affinity is still doubtful. In spite of the deficient preservation of the material, i.e., internal mold with some remnants of shell, the similarity of this record with *P. neuquensis* is remarkable (Gründel and Parent, 2001, fig. 3E; Gründel and Parent, 2006, fig. 4G). As was pointed out before, *P. neuquensis* is present in lower Tithonian beds of the Vaca Muerta Formation. For those reasons, *Dicroloma*? sp. is tentatively included in the synonymy list of *P. neuquensis*.

Other records of Aporrhaidae from the Lower Cretaceous of the Neuquén Basin include the specimens described as Aporrhaidae sp. indet. α and β (Fig. 3.21) by Damborenea et al. (1979, p. 71, pl. 11, fig. 3). They come from sections of the Chachao and Agrio formations in southern Mendoza province. Most of the specimens are badly preserved although some can be referred to *P. neuquensis* on the basis of the bicarinate spire whorls, more prominent adapical carina and an outer lip expanded into two lateral processes.

Amongst the three aporrhaid species reported from the Lower Cretaceous of Alexander I Island, Antarctica, *Anchura*? *antarctica* (Cox, 1953, p. 6, pl. 2, figs. 9–11; Thomson, 1971, p. 52, fig. 3a–3d) bears some resemblance to *P. neuquensis* due to its bicarinate spire whorls, tricarinate last whorl and outer lip. The labrum expands in a very short wing that rapidly extends into two diverging lateral labral processes, although not as long, thin, and delicate as in the Argentinean species. The posterior lateral labral process in *A.*? *antarctica* is bent adapically and the anterior one is shorter and bent abapically. The rostrum is also similar to that of *P. neuquensis*, although shorter and bent to the right. The main difference between these species remains in the nodose sculpture of *A.*? *antarctica* and the high turriculate spire with a lower mean spire angle. *Anchura*? sp. α (Thomson, 1971, p. 54, fig. 3e) shows a broader spire, i.e., with a greater mean spire angle, which makes it quite similar to *P. neuquensis*. Also it bears three prominent carinae on the last whorl, but again the conspicuous nodes on the adapicalmost carina distinguish *Anchura*? sp. α from the Argentinean species.

Genus DIMORPHOSOMA Gardner, 1875

Type species.—*Rostellaria calcarata* J. Sowerby, 1823 (p. 70, pl. 349, figs. 6, 7; Gardner, 1875, p. 398, pl. 5, figs. 7, 7a, 15, 15a, pl. 12, figs. 9–12b; Kollmann, 2005, p. 120), Albian, England. By original designation.

Occurrence.—Hauterivian–Maastrichtian; France, Switzerland, Netherlands, Austria, Germany, England, Argentina (Gardner, 1875; Kaunhowen, 1898; Müller, 1898; Kollmann, 1978, 2005; this paper).

Remarks.—Cossmann (1904, p. 76) pointed out that *Dimorphosoma calcarata* and *Drepanocheilus evansi* Cossmann, 1904 (pl. 6, figs. 11, 12; Sohl, 1960, pl. 11, figs. 23, 26), the type species of *Drepanocheilus* Meek, 1864, are congeneric, and that there are no distinctive features between these species. Wenz (1940), Kase (1984), Roy (1994) and Bandel (2007) also regarded *Dimorphosoma* as a subsequent synonym of *Drepanocheilus*. Both genera exhibit an outer lip expanded into a single, long wing extended perpendicularly to the coiling axis and with its distal end more or less bent adapically. Nonetheless, Kase (1984) stated the possibility that amongst the species attributed to *Drepanocheilus*, two groups can be separated on the basis of the adult teleoconch size and the morphology of the protoconch and earliest teleoconch whorls. One of these groups is represented by the type species of *Dimorphosoma*, which has a small overall size and a carina in the post-embrionary whorls of the protoconch. This could suggest an actual demarcation between these two genera.

Some diagnoses of *Drepanocheilus* given by different authors include within its variability range the diagnostic features of *Dimorphosoma* (e.g., Kiel and Bandel, 2002). This suggests a great similarity between *Dimorphosoma* and *Drepanocheilus*, although the evaluation of their affinity is complicated by a great inter- and intraspecific variability regarding the outer lip morphology, the number and spacing of collabral ribs on spire whorls and the presence/absence of nodes on the main carina of the last whorl, and the delicate nature of the labral wing of aporrhaids which lowers considerably its preservation potential.

This discussion exposes the necessity of a thorough revision of both *Dimorphosoma* and *Drepanocheilus*, on the basis of their type species and every other species ever attributed to one or the other. The description of the protoconch and juvenile teleoconch whorls of *Drepanocheilus evansi* and *Dimorphosoma calcarata* would help in the assessment of their taxonomic independency.

Kollmann (2005, 2009) kept *Dimorphosoma* and *Drepanocheilus* as independent genera, stating that in *Drepanocheilus evansi* the spire whorls are convex and the labral wing is triangular, obliquely blunt, and shorter than in *Dimorphosoma*. In this work, despite the overall morphologic similitude between both genera, the criterion of Kollmann (2005, 2009) is followed, since the Argentinian species described herein is closer to the type species of *Dimorphosoma*. Furthermore, this species conforms better with the diagnosis proposed by Kollmann (2009) for the Dimorphosominae. In this subfamily, Kollmann (2009) grouped genera with a simple, lanceolate labral wing of more or less bent distal end, convex or angulate spire whorls with collabral sculpture or nodes, last whorl bicarinate, rarely tricarinate and with diminished ornamentation, such as *Dimorphosoma*, *Pietteia* Cossmann, 1904 and *Cuphotifer* Piette, 1876.

The architecture of the outer lip in *Dimorphosoma* bears also some resemblance with that of *Struthioptera*, an emblematic genus of the Upper Cretaceous of the southern latitudes. In this genus the labral wing is trapezoidal with thickened and reflected margins and a wide and deep posterior sinus (Finlay and Marwick, 1937; Zinsmeister and Griffin, 1995). Besides, the adult teleoconch in *Struthioptera* is rather stout and somewhat larger than what is usually seen in *Dimorphosoma*, the whorls are more prominently angular and the carinae bear strong nodes.

DIMORPHOSOMA WEAVERI new species
Figure 4

1931 *Dicroloma* cf. *obtusa* Pictet and Campiche, 1864; WEAVER, p. 386.

Diagnosis.—Spire whorls convex to subtly angular, without sutural ramp. Narrow, evenly spaced, orthocline to opisthocline and opisthocyrt collabral ribs extended from suture to suture; wider and more prominent towards mid-whorl. Last whorl bicarinate; adapical carina more prominent and with small rounded nodes; continues over the wing. Labral wing simple, falcate, i.e., more or less rectangular proximally and tapering towards its distal end, where it curves adapically. Distinct callous band. Rostrum short and straight.

Description.—Teleoconch small—maximum shell height 21.2 mm, excluding rostrum, maximum diameter 9.3 mm, excluding labral wing—with up to eight whorls. Spire high, turriculate, conical to slightly cyrtoconical. Protoconch not preserved. Spire whorls convex to subtly angular, without a conspicuous sutural ramp and with maximum diameter towards the middle. Suture impressed. Last whorl bicarinate, representing nearly half of total shell height (excluding rostrum); adapical carina more prominent than the abapical one; surfaces above adapical carina, between both carinae and below abapical carinae flat to slightly concave. Aperture narrow, oblique, slightly wider posteriorly and narrowing towards the rostrum. Outer lip expanded into a single labral wing, perpendicular to the coiling axis, falcate. Inner lip forming a relatively thick, moderately extended callous band with distinct limit that extends from the adapical carina towards the base of the rostrum. Adapical carina of the last whorl continuing over the abapertural side of the labral wing and forming a prominent keel. Labral wing attached to the spire by means of a short triangular lobe that does not exceed the suture line. First three teleoconch whorls smooth, then a weak middle carina develops, and towards the fourth and a half teleoconch whorl slender nodes appear at mid-whorl. These nodes—approximately 18–20 per whorl, evenly spaced—become narrow, orthocline to opisthocline and opisthocyrt collabral ribs, extending more or less from suture to suture. Collabral ribs tend to be wider and more prominent towards mid-whorl, giving spire whorls a slightly angular profile. In some specimens the ribs—10–13 per whorl—resemble lengthened rhombs. Ribs are not present on the last whorl; instead, its adapical carina bears small rounded nodes and the abapical carina is smooth. Very fine, opisthocyrt and orthocline to slightly opisthocline growth lines on the whorl flank; more or less straight and orthocline towards the base of last whorl. All whorls with very fine spiral threads. Rostrum short and straight.

Etymology.—Named after Prof. Charles E. Weaver, for his substantial contributions to the knowledge of the Jurassic and Lower Cretaceous gastropods from the Neuquén Basin.

Types.—Holotype CPBA 21460.1 (Fig. 4.1), paratypes CPBA 21460.2–3 (Fig. 4.2–4.4), all from a coquina horizon with abundant remains of asteroids, echinoids and small bivalves—*Paraspiticeras groeberi* ammonoid Zone (late Hauterivian), Agua de la Mula Member, Agrio Formation, Agua de la Mula locality, central Neuquén province (Fig. 1).

Material.—About 393 specimens from six localities in Neuquén province and one locality in Mendoza province, and one additional specimen of the C. E. Weaver collection (UWBM) from one locality in the Neuquén province (online Supplemental Data File 2). Dimensions provided in online Supplemental Data File 3.

Occurrence.—Lower Cretaceous (upper Hauterivian–lower Barremian), comprising the *Crioceratites schlangintweiti*, *C. diamantensis* and *Sabaudiella riverorum* ammonoid zones of the Agua de la Mula Member of the Agrio Formation. This species is more abundant in central Neuquén province, e.g., in Agua de la Mula (Fig. 1), where it is also better preserved and some specimens with the labral wing were recovered. However, the stratigraphical and geographic ranges of this aporrhaid species are considerably smaller than those of *P. neuquensis*.

Remarks.—Weaver (1931) was the first to report a specimen of the new species described herein and interpreted it as a representative of *Dicroloma*. Although Weaver (1931) mentioned that the outer lip in his material is bilobate, with a central and a posterior lobe, there are actually no remains of the labral wing preserved in that specimen (UWBM 293, Figs. 4.6–7). Another feature mentioned by Weaver (1931) is the absence of spiral threads on the spire whorls. These threads are in fact present in the specimen UWBM 293 although they are extremely thin. They have been clearly observed also in almost every other specimen examined for this study.

At the species level, Weaver (1931) suggested a possible affinity with *Aporrhais obtusa* Pictet and Campiche, 1864 (p. 610, pl. 93, figs. 9–13), from the Albian of Switzerland, on the basis of their resemblance in shell outline, the convexity of the spire whorls and their sculpture, the bicarinate last whorl and the more prominent abapical carina with rounded nodes. In the original description of *A. obtusa*, Pictet and Campiche (1864) stated that the outer lip in this species is similar to that of *Aporrhais orbignyana* Pictet and Campiche, 1864 (p. 609, pl. 93, figs. 5–8), also from the Albian of Switzerland: it forms an entire, short wing with a single, long and narrow process departing from its posterior margin and curving adapically. This morphology differs from that of *Dimorphosoma weaveri* n. sp., whose labral wing is falcate. *Aporrhais obtusa* was later regarded as a representative of *Perissoptera* Tate, 1865 by Wilckens (1910), whereas Roy (1994) included this species in *Drepanocheilus*.

The morphology of the labral wing in several species of *Dimorphosoma* was shown to be variable. For instance, Gardner (1875, pl. 5, figs. 7–14) illustrated numerous specimens of *Dimorphosoma calcarata* with some differences in the labral wing. For those species that were described on the basis of a few specimens it is likely that not all of the variability in the morphology of the labral wing is yet known. In the new species described herein, more than 20 specimens show at least part of the labral wing preserved. Some variability was observed, mainly regarding the length and width of the labral wing.

The shape of the collabral ribs is also variable in *D. weaveri*. They are always arranged from suture to suture, are opisthocyrt

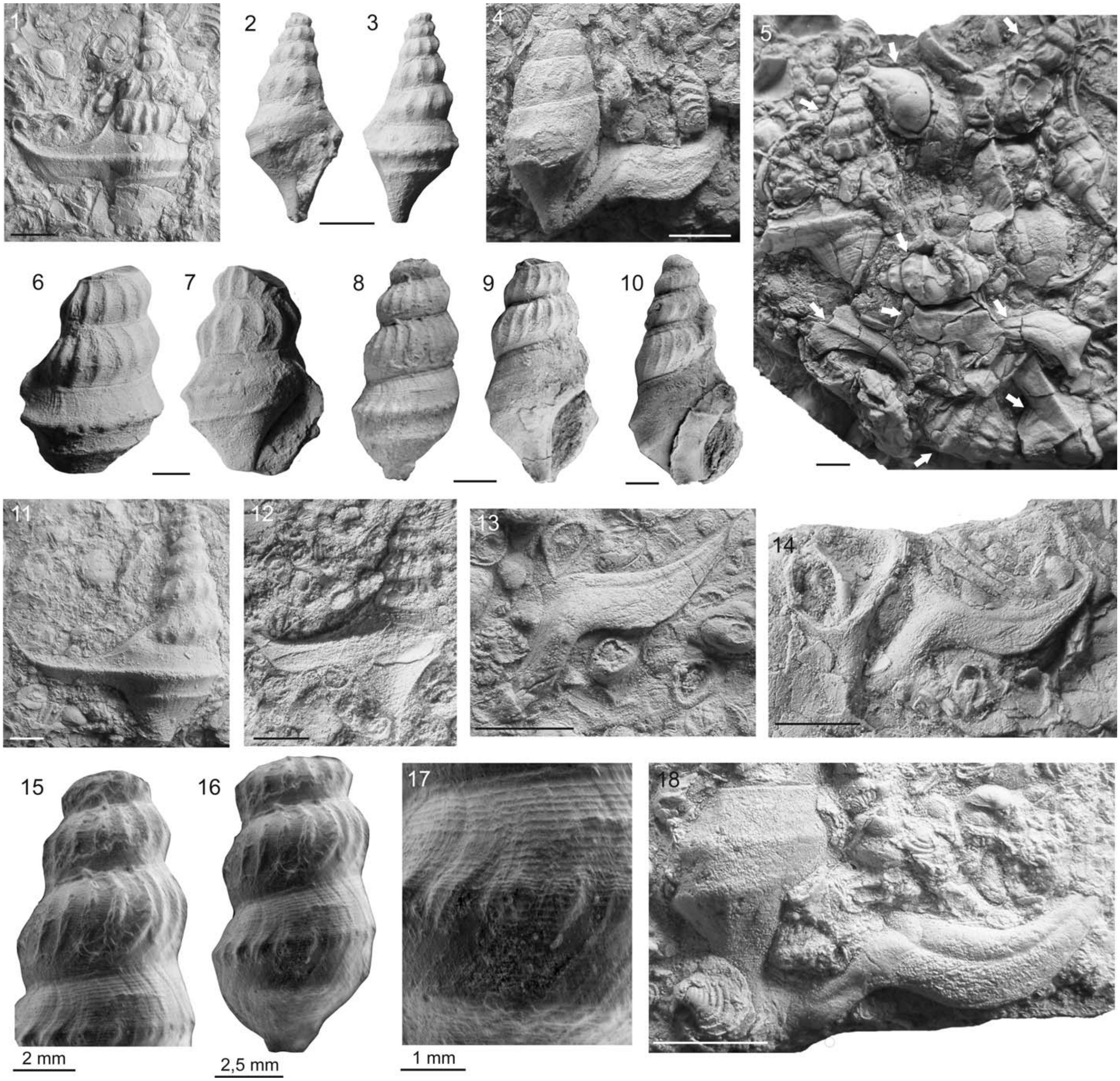

FIGURE 4—*Dimorphosoma weaveri* n. sp. *1*, CPBA 21460.1, holotype, abapertural view, with labral expansion; *2*, *3*, CPBA 21460.2, paratype, in apertural and abapertural views, respectively; *4*, CPBA 21460.3, paratype, apertural view, with labral expansion; *5*, CPBA 21428, coquina sample with several specimens of *D. weaveri*; the white arrows point to different fragments of teleoconch and labral expansions; *6*, *7*, UWBM 292, *Dicroloma* cf. *obtusa* in Weaver (1931), abapertural and apertural views, respectively; *8*, *9*, CPBA 21424.2, abapertural and apertural views, respectively; *10*, CPBA 21424.4, apertural view; *11*, CPBA 21460.6, abapertural view, with labral expansion; *12*, CPBA 21460.4, abapertural view, with labral expansion; *13*, CPBA 21460.5, loose labral expansion; *14*, CPBA 21460.8, apertural view, with labral expansion; *15–17*, CPBA 21425.2, SEM pictures, detail of spire, abapertural view, and detail of spire sculpture, respectively; *18*, CPBA 21460.7, abapertural view, with labral expansion. All scale bars=5 mm except where noted.

and orthocline to slightly opisthocline, and are more prominent at mid-whorl. In some specimens the ribs are wider in the middle and take a fairly rhombic form; in others they remain relatively thin. In those specimens with medium to high superficial wearing the ribs may appear as very thin lines of low relief. It is worth mentioning that since there are transitional forms between these morphologic ends, it is not possible to separate the specimens in distinct groups on the basis of the shape of the ribs, which suggests that this is intraspecific variability and/or differential preservation.

The systematics of the species of *Dimorphosoma* is complicated due to their homogeneity in terms of the outline of the spire and last whorl, and the whorls profile and sculpture. Nevertheless, the nature of the collabral ribs on spire whorls, the presence or absence of collabral ribs in the adapical portion of the last whorl, the presence or absence of nodes on the adapical carinae of the last whorl and their form, the length of the rostrum, the details of the shape of the labral wing and the mean spire angle are useful in the distinction of species.

Dimorphosoma weaveri differs from *D. calcarata*, also recorded in the Albian of France and Switzerland, by a taller and more slender spire, spire whorls flat to slightly convex in their abapical portion, thicker, slightly opisthocline and sinuous collabral ribs that are present on the spire whorls and the abapertural side of the last whorl, smooth adapical carina and a labral wing that is proximally broader and has narrow adapical and wide abapical sinuses. In some specimens of *D. calcarata* the labral wing has a fan-shaped expansion opposite to the bent distal end (Gardner, 1875, pl. 12, figs. 9a, 11).

Other species from the Lower Cretaceous of England described by Gardner (1875) differ from *D. weaveri* by a longer and narrower labral wing, almost in the shape of a digitiform process greatly bent distally, as is the case of *Dimorphosoma toxochila* Gardner, 1875 (p. 399, pl. 5, figs. 10, 12; pl. 12, figs. 16, 17), *D. doratochila* Gardner, 1875 (p. 399, pl. 12, figs. 18–22), and *D. vectiana* Gardner, 1875 (p. 397, pl. 12, figs. 5–7). Or else by a different sculpture, with a prominent middle carina as in *D. ancylochila* Gardner, 1875 (p. 399, pl. 12, figs. 18–22), presence of collabral ribs in the abapical portion of the last whorl as in *D. neglecta* Gardner, 1875 (p. 398, pl. 5, figs. 8, 9, 16; pl. 12, figs. 13–15; non Tate, 1865 fide Kollmann, 2005, p. 121), or absence of nodes in the main carina of the last whorl as in *D. pleurospira* Gardner, 1875 (p. 397, pl. 12, figs. 3, 3a, 4) and *D. klincispira* Gardner, 1875 (p. 397, pl. 12, fig. 1, 1a).

Kollmann (2005) revised three French species of *Dimorphosoma* described by d'Orbigny (1843), *D. calcarata* amongst them. *Dimorphosoma*? *tricostata* d'Orbigny, 1843 (p. 287, pl. 207 figs. 5, 6; Kollmann, 2005, p. 121; Albian) stands out by its bicarinate spire whorls and orthocline collabral ribs that form a reticulated pattern. The specimens of *Dimorphosoma*? *acuta* d'Orbigny, 1843 (p. 298; Hauterivian) figured by Kollmann (2005, p. 126, pl. 13, fig. 20a, 20b) resemble some specimens of the Argentinian species that seem to have a more slender spire, slightly more convex whorls and thinner collabral ribs. Unfortunately, the shape of the labral wing in *D.*? *acuta* is not as yet known, being the reason why Kollmann (2005) ascribed this species tentatively to the genus.

Aporrhais protuberatus Stanton, 1901, from the Lower Cretaceous of the Austral Basin, is similar to *D. weaveri* in general outline and sculpture. Close examination of the syntypes and other original materials (PRI 66929 and 66930) revealed that *A. protuberatus* differs from *D. weaveri* by its outer lip shaped as a broad and very thick subtriangular wing, tapering and curving towards its distal end and with the left margin thickened and reflected. This labral expansion is shorter and broader than in *D. weaveri*, has a blunter distal end and is much thicker, especially in its right margin on the apertural side. Other differences between *A. protuberatus* and *D. weaveri* are the prominent, rounded protuberance on the left side of the aperture of *A. protuberatus*, the thick inner lip callous that extends over much of the last whorl and part of the spire on the apertural side of the shell, and the absence of nodes or collabral ribs in the abapertural side of the last whorl. Stilwell (2003) reported a Campanian age for *A. protuberatus*, although the 'Belgrano Beds' that yielded this species belong to the Río Belgrano Formation, of Barremian age (Nullo et al., 1999). Stilwell (2003) tentatively ascribed this species to *Struthioptera*, whose record is so far known to begin in the Cenomanian, and indicated that it may be the predecessor of the poorly known Campanian Argentinian species *Struthioptera pastorei* Camacho, 1953. The shape of the labral wing of *A. protuberatus* indeed matches the diagnosis given by Finlay and Marwick (1937), being similar to that of the type species of *Struthioptera*. Still, the spire whorls in *A. protuberatus* are not as strongly tuberculate and the nodes are absent from the last whorl; also the protuberance of the inner lip callosity is quite distinctive. Although the generic revision of this species is pending, it can be said that it is certainly different from *D. weaveri* and that it seems to be close to the oldest species of the genus *Struthioptera*, to which it may be related.

The examination of the original material of the record from the Lower Cretaceous of the Austral Basin reported by Stanton (1901) as *Aporrhais*? sp. (PRI 66931) showed that it does not belong to the Aporrhaidae but to the Epitoniidae.

Etayo-Serna (1985) reported *Drepanocheilus* aff. *obtusa* from the upper Aptian of Sierra Nevada del Cocuy, Colombia, stating that the Colombian form differs from the European *Aporrhais obtusa* by a more oblique collabral sculpture. This record may be related to the Argentinian species *D. weaveri*, but there is not enough information to draw any conclusion at present.

Genus HARPAGODES Gill, 1870

Type species.—*Pterocera desori* Pictet and Campiche, 1864 (p. 575, pl. 90, figs. 3, 4), Hauterivian, Switzerland. By original designation (revision by Kollmann, 2005, p. 130, pl. 15, fig. 4a, 4b).

Occurrence.—Middle Jurassic (Bathonian)–Upper Cretaceous (Campanian); Europe, northern and eastern Africa, Middle East, Arabian Peninsula, and North and South America (Piette, 1891; Cossmann, 1900, 1904; Shattuck, 1903; Dacque, 1905; Yabe and Nagao, 1925; Kühn, 1929; Imlay, 1940; Cox, 1954, 1965, 1969; Alencáster, 1956; Corvalán, 1956; Hudson, 1958; Drushchits and Kudryatsev, 1960; Altinli, 1966; Busson and Albanesi, 1967; Reiner, 1968; von Hillebrandt, 1970; Dimitrova, 1974; Mourier et al., 1988; Howarth and Morris, 1998; Kollmann, 2002, 2005; Callapez, 2008; this paper).

Remarks.—At least 27 species of *Harpagodes* were described so far, 11 of them of Cretaceous age. It was Piette (1891) who first revised the genus and emended its diagnosis, paying special attention to the great intraspecific variability of the Jurassic species. Then Cossmann (1900) revised some of the species and pointed out the mistake regarding the type species. Soon after, Cossmann (1904) resumed the revision of *Harpagodes*, re-emended its diagnosis and stated that the members of this genus do not bear a true strombid notch on the outer lip, but its margin shows a slight depression between the rostrum and the anteriormost labral process.

So far, there has been no description of the protoconch or the juvenile teleoconch of a member of this genus. This may be a result of the overall very poor preservation of the specimens, i.e., mostly internal molds with some patchy remains of shell. This feature of the record of *Harpagodes* represents a problem for its systematic study, mainly when new species are described solely on the basis of such materials.

The position of the genus in suprageneric taxa has been debated, although there is a clear consensus about its place in the Stromboidea. In the last revisions of the group, by Bouchet et al. (2005) and Kollmann (2009), it was placed it in the subfamily Harpagodinae within the Aporrhaidae, along with five other similar genera, on the basis of the common presence of a narrow basal sinus, a wide subsutural sinus and a wide labral expansion with at least five processes. The representatives of the group may show variable morphologies regarding the height of the spire, the profile of the whorls, the shape of the rostrum, the number and shape of the spiral ribbons and labral processes (Kollmann, 2009).

Some members of the family Purpurinidae—superfamily Littorinoidea according to Bouchet et al. (2005), based on the Jurassic genus *Purpurina* d'Orbigny, 1849, may seem similar to the shells of *Harpagodes*. This is because they have usually large to medium-sized, thick, conical to ovoidal shells, with a rather low, conical spire, a large last whorl of angular profile, sculpture of spiral carinae and a wide aperture (Cossmann, 1906). However, the genera in this family, (e.g., *Leviathania* Golovinova and Korotkov, 1986) differ from *Harpagodes* by their wide, flat and subhorizontal subsutural ramp, limited by a prominent shoulder usually bearing strong nodes or coarse spines. Although some species of *Harpagodes* have wide sutural ramps limited by one of the posterior spiral ribbons, they do not bear nodes. Besides, purpurinids do not have an expanded outer lip, although in the state of internal mold this feature is usually lacking in *Harpagodes* shells, thus leading to misinterpretation. Another useful feature for distinguishing these taxa is the concave columellar part of the inner lip in purpurinids, whereas in *Harpagodes* the presence of a rostrum is almost always evident by the straight and long columella.

The documentation of the genus in the Neuquén Basin probably begun with the early mention of '*Pterocera*' sp. from the 'Neocomian' of Neuquén province by Burckhardt (1900). Later, Haupt (1907) recorded *H. oceani* and much later Damborenea et al. (1979, p. 70, pl. 11, fig. 4) reported *Harpagodes* cf. *americanus* Imlay, 1940 from Hauterivian beds in Mendoza province. Palma et al. (2009) reported *Harpagodes* sp. from the middle Oxfordian of Mendoza, and Mariñelarena (1959) gave account of its presence in the late Tithonian from southern Neuquén. As will be treated in detail below, many other records of *Harpagodes* from the Lower Cretaceous of the Neuquén Basin were mistaken by representatives of *Natica* Scopoli, 1777 and *Tylostoma* Sharpe, 1849, mainly as a result of the poor preservation of the materials.

HARPAGODES JAWORSKII (Weaver, 1931)
Figures 5, 6

?1900 *Pterocera* sp., BURCKHARDT, p. 32, 40.
?1907 *Harpagodes oceani* (Brongniart); HAUPT, p. 204.
1931 *Tylostoma jaworskii* n. sp., WEAVER, p. 379, pl. 41, fig. 273; pl. 43, figs. 287, 288.
1931 *Natica praelonga* Deshayes *in* Leymerie, 1842; WEAVER, p. 372.
1979 *Harpagodes* cf. *americanus* Imlay, 1940; DAMBORENEA, MANCEÑIDO AND RICCARDI, p. 70, pl. 11, fig. 4.
1979 *Tylostoma jaworskii* Weaver, 1931; DAMBORENEA et al., p. 75.
?1979 *Odostomopsis*? sp., DAMBORENEA et al., p. 76.

Diagnosis.—Emended: teleoconch subfusiform. Spire high, conical. Spire whorl convex. Last whorl large and inflated. Seven spiral striae on the spire whorls; five wide, rounded spiral ribbons in the last whorl. Area between carinae with 1–3 thinner spiral threads. Outer lip expanded into five, thick, cylindrical labral processes. The ribbons of the last whorl continue into the labral processes.

Description.—Adult teleoconch large to medium-sized—maximum shell height 157 mm, incomplete, subfusiform in outline. Usually with up to four or five whorls preserved; apical whorls not observed. Spire conical and stout, high, with convex whorls. Last whorl larger and more inflated compared with the spire whorls, representing nearly three-fourths of the total shell height, with convex profile. Five thick, cylindrical labral processes departing from the outer lip margin, the posteriormost one attached to the right side of the spire and growing parallel to the coiling axis. Rostrum thick, bent towards the left. Sculpture of seven spiral striae on spire whorls, not evenly spaced but increasing the width of interspaces from the adapicalmost to the abapicalmost striation. Towards the last whorl the striae delimit five wide and slightly swollen spiral ribbons, separated by flat to fairly convex interspaces bearing thinner spiral threads in variable numbers—ribbons numbered from the apex to the anteriormost point of the aperture: one or two between the first and second ribbon, two or three between the second and third, one between the third and fourth, one between the fourth and fifth, and several between the first and the base of the rostrum. The fifth ribbon is the less developed and is adjacent to the suture. Growth lines thin, orthocline and straight. Comma-shaped aperture, wider and rounded abapically and narrow adapically, ending in an angle to the last whorl. Parietal part of inner lip convex and callous; columellar part straight and vertical up to the base of the rostrum.

Types.—Syntypes, UWBM 281 (=282) and UWBM 283 (Fig. 6.1, 6.2, 6.6, 6.7), coming from the area of the Sierra de la Vaca Muerta (central Neuquén province), from outcrops of the Agua de la Mula Member of the Agrio Formation which bear ammonoids of the *C. diamantensis* Zone (late Hauterivian).

Material.—A total of 133 specimens from 12 localities in Neuquén province and two in Mendoza province, and 21 additional specimens of different collections, from several localities in Neuquén and Mendoza (online Supplemental Data File 2). Dimensions provided in online Supplemental Data File 3.

Occurrence.—Upper Valanginian–uppermost Hauterivian/lower Barremian. This species is present in both marine members of the Agrio Formation from slightly above the base to its top, i.e., from the *Chacantuceras ornatum* Subzone to the *Sabaudiella riverorum* Zone. It is much more abundant in the northernmost and southernmost localities of the Neuquén Basin. Corvalán (1956) and Corvalán and Pérez (1958) reported its presence in the 'Neocomian' of the Central Chile Basin.

Remarks.—The studied material of *H. jaworskii* consists mainly of internal molds, several specimens with partial preservation of the shell with high surface alteration, and a handful of specimens with well-preserved fragments of shell that show the details of the sculpture. Still, in none of the more than a hundred specimens are the labral processes preserved whole. At best, their proximal parts are present. Besides, an important part of the last whorl is lost along with the outer lip. This type of preservation is not exclusive of *H. jaworskii*, but is repeated in most species of the genus that can be found in the literature. As stated above, this represents a problem for their taxonomic treatment because many were described from internal molds. Kollmann (2005) pointed out that distinguishing species on the basis of such materials is risky, since molds do not show adequately the external morphology of the shell. They can show different shapes even for the same species depending on the thickness of the shell and its degree of taphonomic modification. Such situation leads to a probably artificial growth of the specific diversity, since different species are described on the grounds of disparities that could be owing to differential preservation or even intraspecific variability. This also complicates the comparisons between species. Some examples of *Harpagodes* species described from internal molds are *H. americanus* Imlay, 1940 (p. 158, pl. 14, fig. 9), *H. mexicanus* Imlay, 1940 (p. 158, pl. 15, fig. 9), *H. oceani* (Cossmann, 1904, pl. 7, fig. 1), *H. aranea* (d'Orbigny, 1849; Piette, 1891; pl. 67, figs. 4, 5), *H. desori*, *H. nodosus* (J. de C. Sowerby, 1823; Kollmann, 2005, p. 133, pl. 15, fig. 5) and *H. heberti* (Thomas and Peron, 1889, p. 77, pl. 21, fig. 1). Fischer and Weber (1997) and Kollmann (2005) revised some of the French Jurassic and Cretaceous species, respectively. They re-illustrated many of them with better materials, thus helping to understand their morphology beyond the original descriptions and the type specimens. Several other *Harpagodes* species from around the world would benefit much from similar revisions.

Another important issue that complicates the taxonomic treatment of the genus is that the ranges of variability that can be used to distinguish species are narrow. At least for the Cretaceous, there are few distinct species. One example is *Harpagodes beaumontianus* (d'Orbigny, 1843, p. 305, pl. 213; Kollmann, 2005, p. 133, pl. 15, fig. 5). Some species do not show enough diagnostic features that justify their distinction as

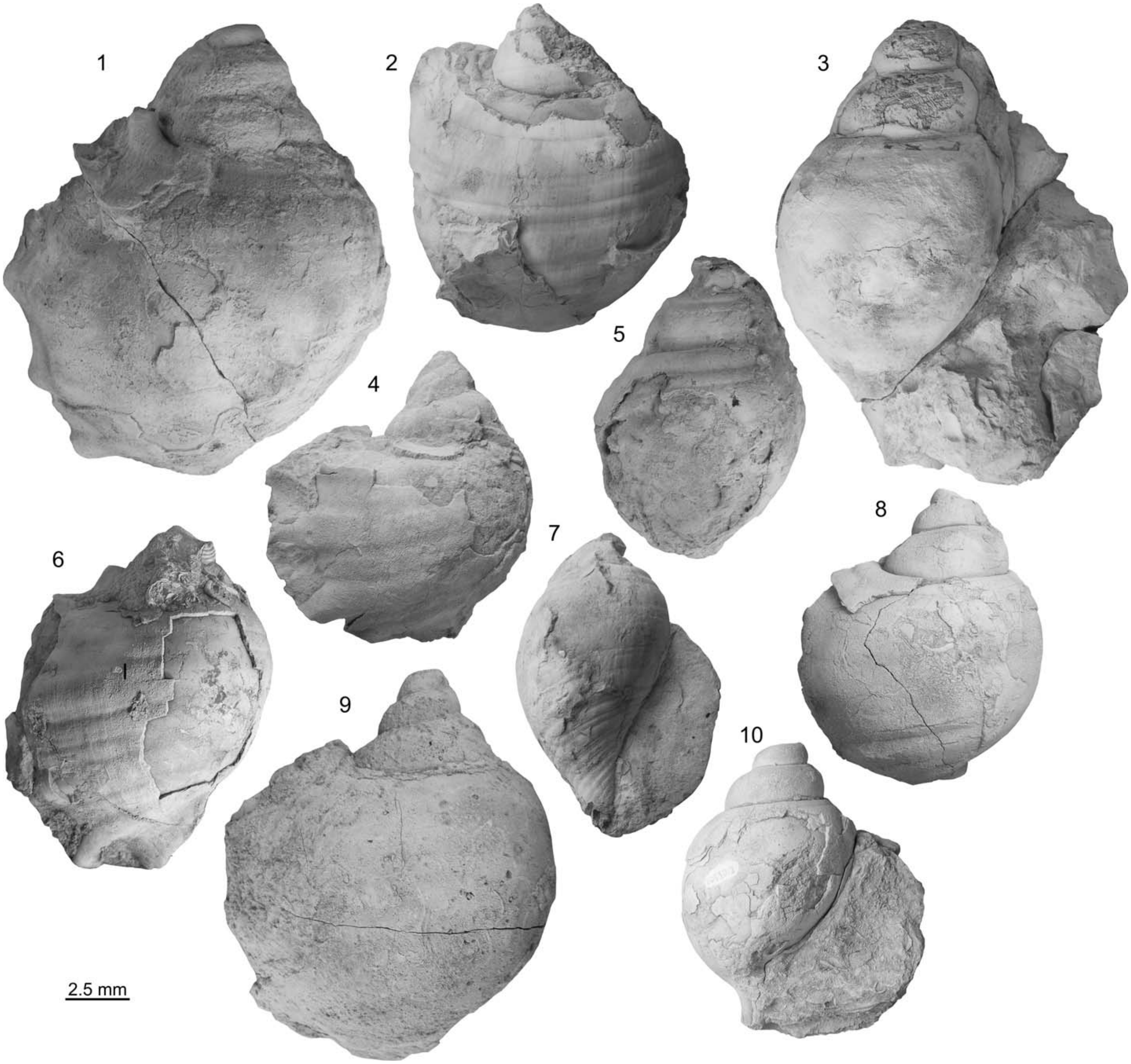

FIGURE 5—*Harpagodes jaworskii* (Weaver, 1931). *1*, *3*, CPBA 21268, abapertural and abapertural views, respectively, with part of outer lip expansion and base of labral processes; *2*, CPBA 21286, abapertural view; *4*, CPBA 20530.1, abapertural view, with part of outer lip expansion and base of labral processes; *5*, *7*, CPBA 21267, abapertural and apertural views, respectively; *6*, CPBA 21269, abapertural view, with base of some of the lateral labral processes; *8*, *10*, CPBA 20530.2, abapertural and apertural views, respectively; *9*, MCNAM-PI 24487.1, abapertural view, with part of outer lip expansion.

independent taxa. Examples of this are the aforementioned species described by Imlay (1940) from the Lower Cretaceous (Hauterivian) of Mexico: *H. mexicanus* and *H. americanus*. In addition to the poor preservation of the holotypes, which come from the same stratigraphic level, these species were described paying no attention to the possibility of variability or preservational artefact.

In the particular case of *H. jaworskii*, the large number of specimens available allows observing the large variability that the preservation may generate regarding the outline of the internal molds. Even in the same levels, specimens with very different states of preservation can be found. Weaver (1931) described this species on the basis of two specimens which lack a large part of the last whorl on the apertural area. Thus, there is no trace in the syntypes of the presence of an expanded outer lip, labral processes and a rostrum. Besides, both specimens show a considerable degree of surface alteration, thus the sculpture of spiral ribbons and threads is obliterated. The outline of the syntypes, with this degree of modification, is similar to some species of *Tylostoma*. One diagnostic feature of the shells of this genus is the presence of an internal callosity on the outer lip, repeated at regular intervals and with denticles in some species. These form collabral varices on the internal molds (Squires and Saul, 2004, p. 25, and references therein), but the varices are not always preserved, thus leading to confusion. Direct examination of the syntypes showed that one of them, the specimen UWBM

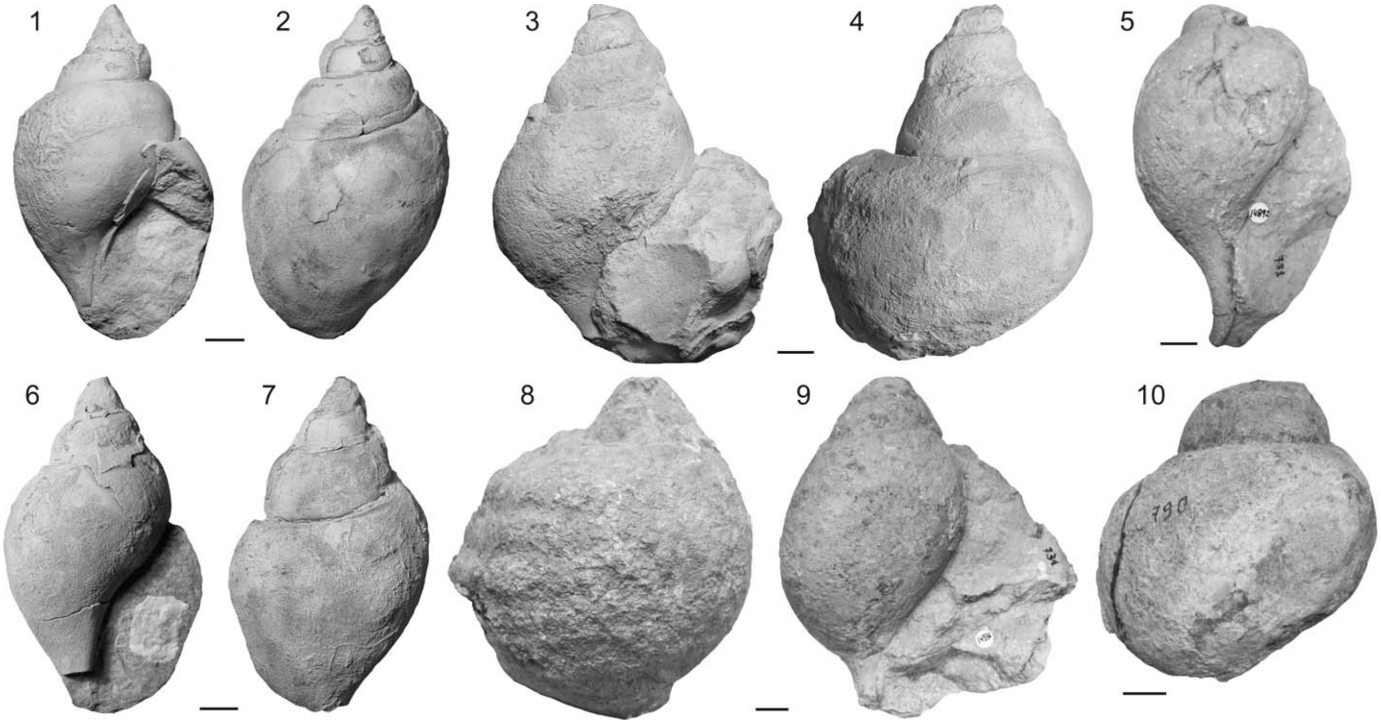

FIGURE 6—*Harpagodes jaworskii* (Weaver, 1931). *1*, *2*, UWBM 281, syntype, apertural and abapertural views, respectively; *3*, *4*, UWBM 273, *Natica praelonga* in Weaver (1931), apertural and abapertural views, respectively, with outer lip expansion; *5*, MLP 14892, apertural view, with rostrum; *6*, *7*, UWBM 283, syntype, apertural and abapertural views, respectively; *8*, *9*, MLP 14931, *Harpagodes* cf. *americanus* in Damborenea et al. (1979), abapertural and apertural views, respectively; *10*, MLP 14893, *Odostomopsis*? sp. in Damborenea et al. (1979), abapertural view. All scale bars=10 mm.

283, has a small patch of recrystallized shell in which a few spiral striae and the hint of a spiral ribbon can be seen. The observation of these features allowed the recognition of a large amount of newly collected material, previously reported as *Harpagodes* sp. (e.g., Aguirre-Urreta et al., 2011), as part of the species *jaworskii* and also the allocation of this in the genus *Harpagodes*.

Some specimens from the Agrio Formation in the Lomas Bayas section, Mendoza province (MLP 14931 and MLP 14892, Fig. 6.5, 6.8, 6.9), which were studied and published by Damborenea et al. (1979), were also examined for this study and ascribed to *H. jaworskii*. In particular, the specimen MLP 14892 shows the proximal end of the rostrum bent towards the left. On the other hand, the specimen reported by Damborenea et al. (1979) as *Odostomopsis*? sp. (MLP 14893), from the Chachao Formation (Fig. 6.10), is assigned only tentatively to *H. jaworskii* since it state of preservation precludes a more accurate assessment.

Cataldo and Lazo (2011) reported some of the material included in this study and provisionally identified it as *H.* cf. *americanus*, on the grounds of an overall similarity with the holotype of *H. americanus*. After a close examination of photographs of the holotype (UMMP 20413), housed in the Museum of Paleontology of the University of Michigan (Ann Arbor, Michigan, U.S.A.), it was concluded that a detailed evaluation of the similarities and differences between *H. americanus* and *H. jaworskii* is precluded by the state of preservation of this specimen. However, it is likely that these species are related. The holotype of *H. mexicanus* (UMMP 15976, same institution) is slightly distorted and seems to lack the area of the outer lip that is adjacent to the spire. *H. mexicanus* may be distinguished from *H. americanus* only by a smaller H/Hlw rate and apparently smooth spaces between the spiral ribbons of the last whorl.

The record of *Natica praelonga* by Weaver (1931, p. 372) is also ascribed herein to *H. jaworskii*. The examination of the single specimen available of this record, UWBM 273 (Fig. 6.3, 6.4), showed that it is an internal mold with a conical, stout spire and a large, swollen last whorl. Although the outer lip expansion is not properly preserved, there are four, wide spiral ribbons scarcely visible on the mold surface, which expand and diverge towards the aperture. The area of the fifth labral process, adjacent to the spire, is missing, much as seems to be in *H. mexicanus*.

Harpagodes jaworskii also bears some resemblance to *H. desori*, recorded from the Valanginian–Hauterivian of several peri-Tethyan localities. The two species differ in that the third spiral ribbon in *H. desori* forms a prominent carina that delimits a wide and almost horizontal sutural ramp. Also from the Valanginian–Hauterivian of the Tethys, *H. pelagi* may be distinguished from the Argentinian species by its shorter spire, the obconic shape of the last whorl, a conspicuous shoulder and sutural ramp and a different shape of the outer lip. *Harpagodes beaumontianus*, from the Barremian of France, has a shorter spire than *H. jaworskii*, a prominent sutural ramp and an outer lip with lobes instead of digitiform processes. *Harpagodes nodosus*, from the Cenomanian of several peri-Tethyan and northern localities, differs from *H. jaworskii* by a very short spire, a large number of spiral threads and a more widely expanded outer lip.

Haupt (1907, p. 204) reported an internal mold of an *Harpagodes* from the Tithonian of Cerro Lotena, Neuquén province, which he attributed to *H. oceani*. The description provided by the author lacks diagnostic features at the species level. Still, five spiral carinae on the last whorl are mentioned, with a spiral thread in each interspace and smooth spire whorls. Unfortunately, as mentioned earlier, the original material of this record is lost and thus unavailable for revision. This record may come from beds belonging to the Picún Leufú Formation (personal observ.).

PALEOECOLOGICAL NOTES AND REMARKS ON THE DISTRIBUTION OF THE TAXA

The living members of the family Aporrhaidae are adapted to burrowing in soft marine sediments and to an epifaunal habit with locomotion given by short, spasmodic movements (Yonge, 1937; Barnes and Bagenal, 1952; Perron, 1978; Morton, 1997). The amount of time spent either within the sediment or in its surface depends on the species. The feeding behavior changes seasonally in correlation with the position relative to the substrate. *Aporrhais pespelicani* and *A. serresiana* (Michaud) are suspension- and herbivore deposit-feeders (Yonge, 1937). In turn, *Arrhoges occidentalis* feeds only during the epifaunal season (Perron, 1978). During the burrowing season, these aporrhaids are sedentary, shallowly buried in soft sediment and connected with the surface by two sand tubes. During the epifaunal season, the animals move and feed actively (Perron, 1978). Several authors point out that the juveniles of these aporrhaid species remain most of their time buried in the sediment. Also the type of substrate inhabited is different amongst the living species, with *A. pespelicani* living in shallow-water firm muddy gravel bottoms, whereas *A. serresiana* inhabits fine muddy substrates of deeper waters (Yonge, 1938) and *Arrhoges occidentalis* dwells in fine muddy substrates of a wider bathymetric range (Perron, 1978).

Although the known information of habitat and feeding mode of the living species may be taken as an approximate model for the fossil ones, direct extrapolation must be done with much caution (Popenoe, 1983). If a seasonal infaunal/epifaunal behavior is inferred for the Early Cretaceous aporrhaid species considered in this work, some comments regarding the functional morphology of the shells, the type of enclosing matrix in which they were found and the taphonomic indexes are worthwhile.

Protohemichenopus neuquensis and *Dimorphosoma weaveri* n. sp. are very abundant in gray, fine-grained lithofacies. *Protohemichenopus neuquensis* is particularly abundant in the black to dark-gray shales of the *Spitidiscus ricardii* Zone of the base of the upper member—Agua de la Mula—of the Agrio Formation. These shales are up to 50 m thick (Rawson and Aguirre-Urreta, 2012) and were interpreted as suspension deposits in a very low energy setting below the storm-weather wave base. Their high organic matter content points to low oxygen concentration in the substrate (Lazo et al., 2005). The scarce benthic macrofauna in these shales is represented by a few species of small gastropods and dominated by *P. neuquensis*. *Protohemichenopus neuquensis* and *D. weaveri* shells are sometimes recorded as reworked bioclasts in coquinas (Lazo et al., 2005). *Harpagodes jaworskii* is found in a variety of lithofacies, including fine-grained limestones, sandstones and coquinas, but is much more abundant where the Agrio Formation facies consist predominantly of carbonate. In turn, *P. neuquensis* and *D. weaveri* are rather scarce in this type of settings. It is inferred here that whereas *H. jaworskii* preferred shallower-water carbonate settings of low to moderate energy, *P. neuquensis* and *D. weaveri* favored siliciclastic to mixed clastic-carbonate environments, in deeper waters.

The shells of *P. neuquensis* are almost always deprived of encrusters; only a few shells amongst several hundred show small serpulid tubes or small oysters attached. On the other hand, *D. weaveri* shows, almost as a rule, encrusting bryozoans partially or totally covering the shells. For some reason, *P. neuquensis* shells seem to have been out of reach of encrusting larvae during life and death, whereas the shells of *D. weaveri* were exposed and available for colonization either during life and/or death. Following the observations of Barnes and Bagenal (1952), it could be interpreted that individuals of *P. neuquensis* spent more the time buried in the substrate than individuals of *D. weaveri*, and the shells of the former remained buried after the death of the animal whereas the shells of the latter remained exposed.

Taking into account the functional morphology of the shells, in the case of *P. neuquensis*, where the shell is lightweight and the outer lip extends into three long, thin spines, the function of the outer lip seems related to a ‘snowshoe effect’ in soft to soupy fine-grained substrates (Savazzi, 1991). When compared with the labral architecture of the Aporrhainae or the Struthiopterinae, i.e., a broadly expanded wing with an abapical sinus (Kollmann, 2009), the outer lip of *P. neuquensis* would seem to provide limited aid in the burrowing process and in the constitution of a ventilating chamber, and would as well offer a poor shelter above the sediment-water interface. *Dimorphosoma weaveri* has a plough- or blade-shaped labral wing, which has been interpreted to aid in the burrowing process by helping the shell to enter the sediment at a low angle (Kollmann, 2009). The broad labral expansion could also be of use in supporting the shell in soft sediments as in the ‘snowshoe effect’.

The species of the genus *Harpagodes* are likely to have been epifaunal with active locomotion, similarly to the modern representatives of Strombidae, rather than infaunal or semi-infaunal. The labral design is somewhat variable amongst the species of this genus. In the case of *H. jaworskii*, it is moderately expanded and divided into five long, thick, more or less curved processes. As mentioned before, this morphology was interpreted to relate to a ‘snowshoe effect’ in soft substrates (Savazzi, 1991; Kollmann, 2009); however, the large (H>150 mm) and probably heavy shells of this species lead to think that, in spite of the ‘snowshoe effect’, the risks of sinking through the sediment was large. In the modern Strombidae, the outer lip also helps in stabilizing the shell during locomotion, although according to Savazzi (1991) this function is more compatible with shorter and thicker spines. Another function that can be associated with the labral architecture of *H. jaworskii* is the strengthening of the apertural area against the attack of predators (Savazzi, 1991).

Harpagodes and *Dimorphosoma* have several Berriasian–Barremian records in the Tethys area and farther towards the north (Fig. 7). *Harpagodes* shows a pandemic distribution, well extended across the Tethys, whereas *Dimorphosoma* shows a disjunct distribution with two centers: western Europe and south-western South America. The records of these genera in the Neuquén Basin in the same interval point to a connection between this and lower latitudes, probably through the Caribbean area.

Within the Andean basins of western South America, *Harpagodes jaworskii* was recorded in the Chilean counterpart of the Neuquén Basin, the Central Chile Basin (Corvalán, 1956; Corvalán and Pérez, 1958). *Dimorphosoma weaveri* is as yet endemic of the Neuquén Basin. The record of *Drepanochilus* aff. *obtusa* from the Aptian of Colombia by Etayo-Serna (1985) may be related to *Dimorphosoma*.

In the case of *Protohemichenopus*, the genus also has records in the Lower Cretaceous of Chile—El Way Formation, Antofagasta—and possibly as well in Colombia. However, its occurrence beyond the Neuquén Basin and the Andean Basins of western South America remains uncertain.

The aporrhaid fauna presented herein is barely diverse but significant, especially considering the relative scarcity of

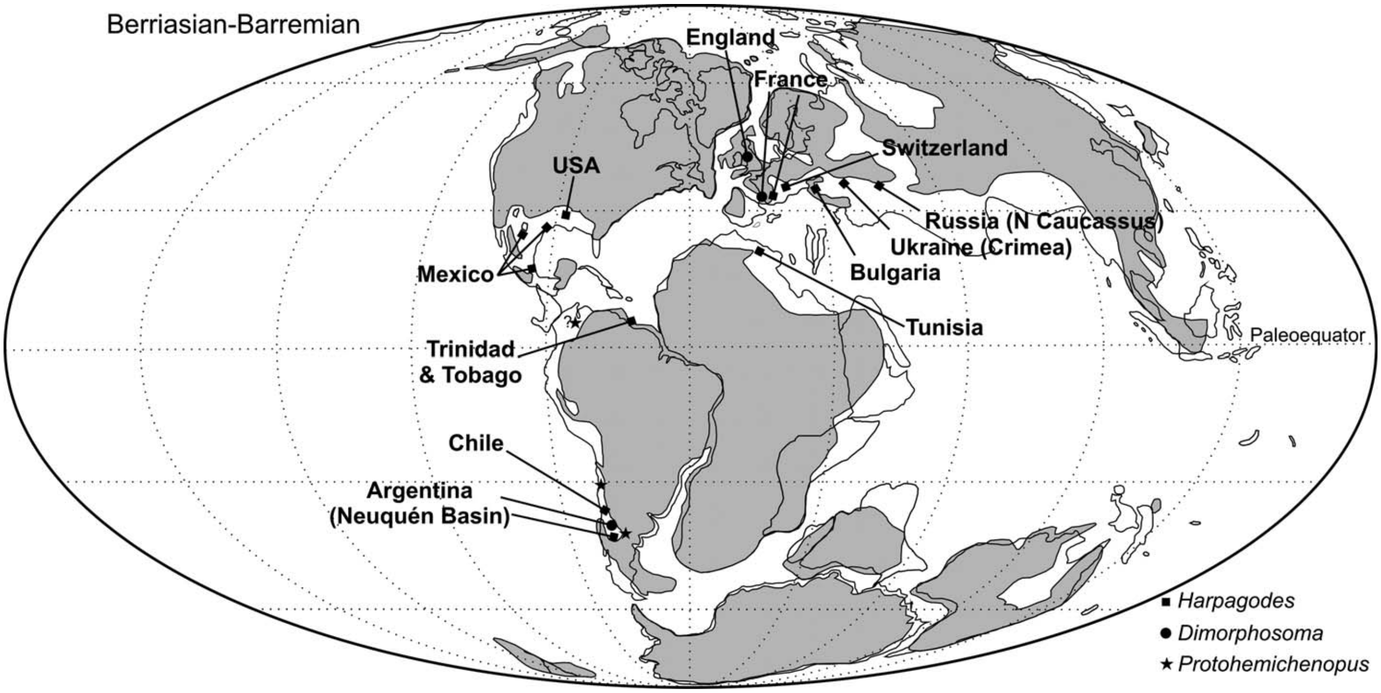

FIGURE 7—Distribution of the genera discussed in the text during the Berriasian–Barremian interval. Paleocoastline reconstruction for the Hauterivian–Barremian from Smith et al. (1994).

Valanginian–Hauterivian marine gastropod records in the Southern Hemisphere. During this interval, a faunistic exchange between the Neuquén Basin and both neighboring and remote regions was favored, probably by the configuration of continental masses and the pattern of oceanic currents, as was discussed by Aguirre-Urreta et al. (2008) for other Early Cretaceous invertebrates from the Neuquén Basin. This situation led to the development of a fauna that, in spite of its endemic elements, had a predominantly Tethyan influence. In this sense, it contrasts with the highly provincial Late Cretaceous–Paleocene austral gastropod fauna (Zinsmeister, 1982).

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: http://dx.doi.org/10.5061/dryad.pb637.

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