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Lower Cretaceous ammonites from the Neuquén Basin, Argentina: the Hauterivian genus *Holcoptychites*

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Abstract

Holcoptychites is known only from the Neuquén Basin, Argentina, but appears close to the more widespread genera *Jeanthieuloyites* and *Spitidiscus*. Thus it is placed in the subfamily Spitidiscinae (Family Holcodiscidae). Previously described *Holcoptychites* species are revised and their taxonomy clarified, while one new species is left under open nomenclature. The sequence of forms allows two subzones to be recognized. These are correlated provisionally with the lowest Hauterivian *Acanthodiscus radiatus* Zone of the Mediterranean region.

Keywords: Argentina; Neuquén Basin; Ammonites; Holcodiscidae; Spitidiscinae; *Holcoptychites*; Biostratigraphy; Lower Cretaceous; Lower Hauterivian

1. Introduction

Holcoptychites is a Lower Hauterivian (Lower Cretaceous) ammonite genus that is apparently endemic to the Neuquén Basin of west-central Argentina. It has never been monographed and its systematic position has remained uncertain. But it is one of the more frequently-figured ammonites from the Neuquén Basin, and several species have been named. It is also one of the most misunderstood, primarily because of considerable confusion over the interpretation of some key species. This has been exacerbated because the type specimens of most species are in museums in France, Germany and the United States. In addition, some species become almost smooth in more advanced growth stages, and these have often been placed in *Desmoceras* or *Holcodiscus*.

Among the forms that we now assign to *Holcoptychites*, the first to be named were *Polyptychites neuquensis*, *Holcodiscus recopei* and *Holcodiscus magdalenae.* These were among several Jurassic and Cretaceous ammonites that Douvillé (1910) described from material collected by Mr. M. Récopé from unspecified localities between the Agrio and Picún Leufú rivers in Neuquén Province. Windhausen (1914) concluded that all three species came from Cerro Negro in the Covunco area, north of Zapala (see Fig. 1). He later (Windhausen, 1918) recognized that these Covunco forms appeared to belong to a distinct, Andean genus which he referred to as 'aff *Spitidiscus*'.

Three years later, Gerth (1921) proposed the genus *Holcoptychites* to embrace '*Polyptychites*' *neuquensis* and a new species, *Holcoptychites meridionalis*, based on new material that he collected from La Mala Dormida in southern Mendoza, and comparative specimens from Arroyo Covunco given to him by Windhausen. None of the material was illustrated until 1925, when Gerth (1925b) again described *Holcoptychites* as a 'new genus'. *Holcoptychites meridionalis* was not mentioned in this paper, and the name has since disappeared from the literature. Two ammonites were figured as '*Holcoptychites neuquensis*', one from Arroyo Covunco and a

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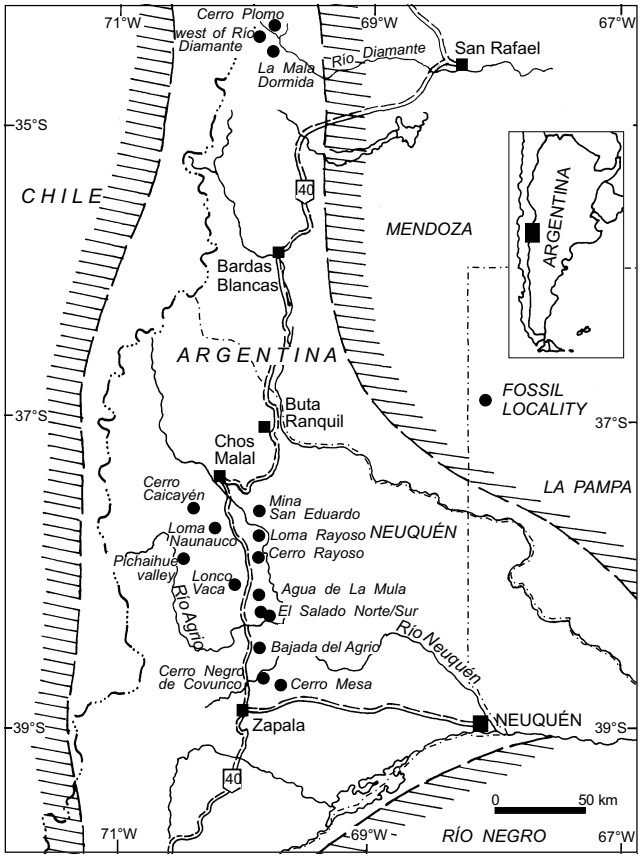

Fig. 1. Map showing *Holcoptychites* localities in the Neuquén basin.

young specimen probably from La Mala Dormida, but these forms are very different from Douvillé's holotype. Subsequently, Weaver (1931) figured several '*Holcoptychites neuquensis*' from the Río Agrio section; most of his forms are similar to the larger specimens of Gerth (1925b) and again differ considerably from the holotype. He also created a new species, *Desmoceras agrioensis*, which was overlooked by subsequent workers but also belongs to *Holcoptychites*.

Giovine (1950) was the first to realize that the '*Holcoptychites neuquensis*' described by Gerth (1921, 1925b) and most of those illustrated by Weaver (1931) were not con-specific with Douvillé's species. He proposed a new species, *H. demissus*, to accommodate these inflated, coarsely ribbed forms. Conversely, Leanza and Wiedmann (1980) erected another new species, *H. compressus* (based on a single specimen from Bajada del Agrio), for a form that is more compressed than the true *H. neuquensis*. We regard their new species as a synonym of *H. agrioensis* (Weaver).

This paper aims to resolve the taxonomic problems associated with *Holcoptychites* through a monographic description of the material, and to establish the stratigraphic sequence of faunas. It is based primarily on material that we have collected from 17 localities in the Neuquén Basin, coupled with a study of all the existing type and figured material and the more important museum collections.

2. Lithostratigraphy and fossil localities

Holcoptychites occurs in the upper part of the lower member of the Agrio Formation, recently named the Pilmatué Member (Leanza and Hugo, 2001). It ranges through many metres of sediment, here referred to informally as the *Holcoptychites* beds, though it is rare in the lower part of the sequence. Of the 17 localities recorded here (Fig. 1), the first three are in Mendoza Province and were visited by MBA-U: access is very difficult. The remaining 14 are in Neuquén, and 13 of them were visited by both of us. Detailed sections were measured at Pichaihue valley (Loc. 10) and Agua de la Mula (Loc. 12) and are described in the appendix.

2.1. Cerro Plomo

One km west of Arroyo Agua del Moro, on the northern bank of the Río Diamante. The section is a 6 km walk north-west from La Mala Dormida, crossing the Río Diamante by a precarious old wooden bridge. Half a kilometre west of the bridge bluish-grey limestones crop out. One level contains abundant *Holcoptychites agrioensis* (CPBA 19805.1-2) preserved as internal moulds, some compressed and deformed.

2.2. One km west of Río Diamante bridge

One km west of the same bridge, but on the southern bank of the Río Diamante, 6.5 km west-north-west of La Mala Dormida. Hard, grey limestones with concoidal fracture yielded one specimen of *H. magdalenae* (CPBA 19806).

2.3. La Mala Dormida

This is one of Gerth's (1925a, fig. 17) localities. It lies 10 km north of El Perdido Pass and is reached by a winding, precarious rocky track from Las Aucas settlement. A condensed section of yellowish silty limestones yielded well preserved internal moulds of *Holcoptychites* at two distinct horizons, a lower with *H. magdalenae* (CPBA 19807.1-4) and an upper with *H. agrioensis* (CPBA 19808.1-7, 19809.1-2). There are four specimens of *H. magdalenae* from this locality in Gerth's collection (SEGEMAR 9591).

2.4. Buta Ranquil

On the northern side of Buta Ranquil is a nearly complete section of the Lower Member (Aguirre-Urreta

and Rawson, 2001, p. 202). Poorly preserved *H.* sp. (CPBA 19810, 19811.1-3, 19812) occur in at least three different horizons in the middle of the section.

2.5. Cerro Caicayén

Close to Arroyo Rahueco and Puesto Contreras (Aguirre-Urreta and Rawson, 2001, p. 202). Four fragmentary specimens of *H. agrioensis* (CPBA 18142.1-4) were collected from shales exposed on the eastern bank of the Arroyo Rahueco.

2.6. Mina San Eduardo

The section is just west of secondary road 9 (Aguirre-Urreta and Rawson, 2001, p. 202). Here the *Holcoptychites* beds consist of more than 150 m of shales (partly covered) with some beds of calcareous nodules, interbedded with sandstones and calcareous coquinas; the sequence includes five levels with *H. magdalenae* (CPBA 16271) and three levels with *H. agrioensis* (CPBA 19813.1-8). *H.* sp. nov. (CPBA 19993) was loose on the lower part of the sequence.

2.7. Loma Naunauco

The section is 30 km south of Chos Malal (Aguirre-Urreta and Rawson, 2001, p. 202). One *H. magdalenae* (CPBA 19818) was collected in a calcareous nodule from a sequence of dark, silty shales. There is also at least one coquina-capped sandstone ridge that contains large *H. agrioensis*.

2.8. Loma Rayoso

Access to the locality is from Naunauco, 32 km south of Chos Malal, some 9 km east of the junction of an unpaved secondary road with national road 40. From an unspecified part of Loma Rayoso, H.A. Díaz (Panamerican Oil Company) measured a section and collected some particularly well-preserved *Holcoptychites* in 1960–61. According to his section, the lower Agrio reaches 530 m, with the base not exposed, and the *Holcoptychites* beds are 200 m thick. The material was presented to the University of Córdoba (*H. magdalenae* CORD-Pz 7475, 7476, 7480; *H. neuquensis* CORD-Pz 7483; *H. agrioensis* CORD-Pz 7484, 7497). One of us (MBA-U) visited Loma Rayoso to search for Díaz's section and collected *H. magdalenae* (CPBA 20001.1-6, 20002.1-4) from four different levels and *H. agrioensis* (CPBA 20003, 20004.1-3) from two different levels. However, the preservation is different from Díaz's material, which therefore may have come from a different part of the hill.

2.9. Cerro Rayoso

A well exposed section on the western flank of Cerro Rayoso exposes 946 m of the Agrio Formation (Ramos, 1981, pp. 21–23), down to the upper part of the *Holcoptychites* beds. Access to the locality is from the south of unpaved secondary road 9 to Paso Huitrín, some 12 km north-east of the junction with national road 40, 45 km south of Chos Malal. The lowermost beds with ammonites are two levels with *H. agrioensis* (CPBA 19815.1-4, 19816.1-2).

2.10. Pichaihue valley

The Arroyo Pichaihue cuts a valley west of the Sierra de Chorriaca (Aguirre-Urreta and Rawson, 2002, p. 765). The *Holcoptychites* beds are well exposed on both sides of the stream (the lower beds on the eastern side), 1 km south of the more southerly of two puestos. The succession (Fig. 2) is described in the appendix.

2.11. Lonco Vaca

Close to national road 40, 60 km south of Chos Malal (Aguirre-Urreta and Rawson, 2001, p. 203). There are at least four distinctive levels with *H. magdalenae* (CPBA 16997, 16998.1.4, 16999.1-5, 19825.1-2) preserved in nodules and in hard calcareous coquinas.

2.12. Agua de la Mula

Close to national road 40, 80 km south of Chos Malal. Detailed sections of the *Hoplitocrioceras* and underlying *Olcostephanus* beds were published by Aguirre-Urreta and Rawson (2001, p. 203; 2002, p. 765). The section is continued downward through the *Holcoptychites* beds in Fig. 2 and the appendix A.

2.13. El Salado Norte

Close to national road 40, 95 km south of Chos Malal (Aguirre-Urreta and Rawson, 2001, p. 205). Two incomplete phragmocones of *H. magdalenae* (CPBA 18257, 18260) were collected by M. Lorenzo from shelly sandstones interbedded in silty shales.

2.14. El Salado Sur

About 2 km south of El Salado Norte. Detailed sections of the *Olcostephanus* beds and overlying *Hoplitocrioceras* beds were published by Aguirre-Urreta and Rawson (2002, p. 765, 2001, p. 203). The underlying *Holcoptychites* beds are more than 150 m thick, and there are several levels with *H. magdalenae* (CPBA 19995.1-3, 19996, 19997) and *H. agrioensis* (CPBA 19998.1-2).

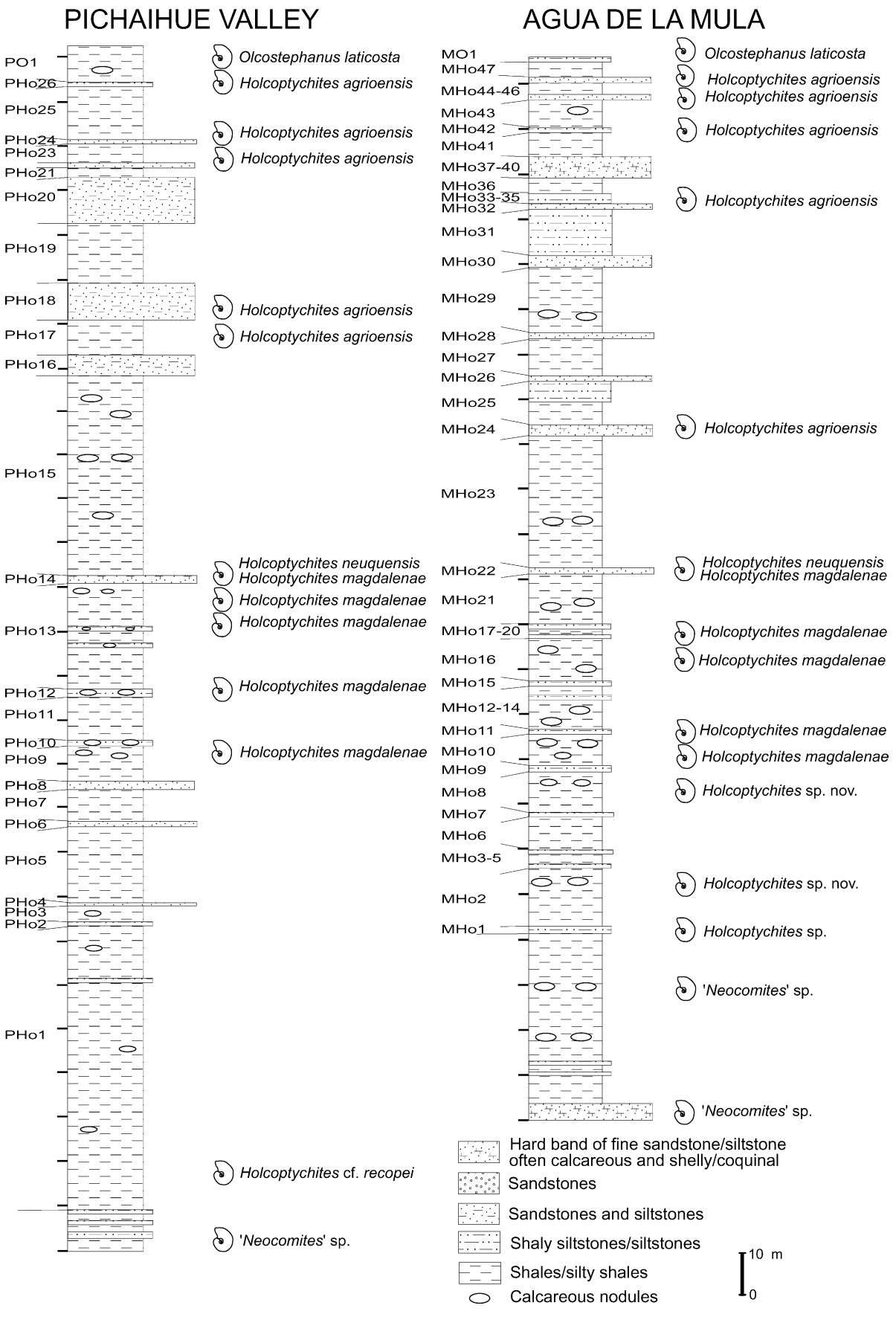

Fig. 2. The Pichaihue valley and Agua de la Mula sections.

2.15. Bajada del Agrio

The exposures are adjacent to unpaved road 10, some 5–8 km south-west of Bajada del Agrio settlement. The *Holcoptychites* beds are 110 m thick, and this is the type locality of *H. compressus* Leanza and Wiedmann (1980). *H. magdalenae* is preserved in both calcareous nodules (CPBA 19826) and coquinas (CPBA 18030) in the lower part of the sequence, while *H. agrioensis* (CPBA 18029) is more common in higher coquinas.

2.16. Cerro Negro de Covunco

Cerro Negro lies some 17 km north-east of Zapala, within the Covunco military base, and thus is of limited access to civilians. Some 200 m of the Pilmatué Member are incompletely exposed, capped by a basalt. The section was described by Windhausen (1914). The *Holcoptychites* beds are composed of grey to greenish siltstones that overlie a massive sandy oolitic limestone that forms a distinctive wide shelf in the middle of the hill. According to Windhausen (1914) this is the type locality of *H. recopei*, *H. neuquensis* and *H. magdalenae*: we collected poorly preserved examples of *Holcoptychites* cf. *recopei* (CPBA 19999.1-4) and *H.* cf. *magdalenae* (CPBA 20000.1-4) from a calcareous siltstone.

2.17. Cerro Mesa

Cerro Mesa is located some 30 km east of Cerro Negro. The Lower Member of the Agrio Formation is exposed along an anticline extending from Cerrito Maruco to Cerro Mesa. This is the type locality of *H. demissus* Giovine (1950) (=*H. magdalenae*). There are two specimens in Giovine's collection (SEGEMAR 9320, and 9324), but we were unable to find the horizon.

3. Systematic palaeontology

Superfamily: Perisphinctaceae Steinmann, 1890
Family: Holcodiscidae Spath, 1923

Discussion. *Holcoptychites* was placed in the 'Holcostephanidae' (=Olcostephanidae) by Gerth (1925b) and Giovine (1950) but was provisionally transferred to the Holcodiscidae by Wright (1957). After studying the sutural ontogeny Schindewolf (1966) confirmed that it was a holcodiscid and that view was followed by Leanza and Wiedmann (1980). However, Wright (1996) still retained it in the Holcodiscidae only provisionally. In the meantime, Tzankov and Breskowski (1982) had proposed a new family Astieridiscidae for *Holcoptychites* and *Astieridiscus*. But the two genera have no obvious features in common and are stratigraphically well separated. In fact, some early *Holcoptychites* appear so close to early *Spitidiscus* (see generic discussion, below) that we believe they must belong to the same family. Most authors, including Wright (1957), have placed *Spitidiscus* in the Holcodiscidae, though Wright (1981, 1996) later changed his view and transferred it to the Desmoceratidae. We retain both genera in the Holcodiscidae.

The suprafamilial placing of the Holcodiscidae has oscillated between the Desmoceratidae and the Perisphinctaceae. Wright (1957) placed the Holcodiscidae (including *Spitidiscus* and ?*Holcoptychites*) in the Desmoceratidae, but Wiedmann (1966) transferred them to the Perisphinctaceae on the basis of sutural ontogeny. This was followed by Leanza and Wiedmann (1980), Wright (1981, 1996) and Reboulet (1995), though Wright significantly narrowed the scope of the family by removing *Spitidiscus* and its immediate allies. Conversely, Thieuloy et al. (1990), Leanza and Wiedmann (1992) and Cecca et al. (1998) retained the Holcodiscidae in the Desmoceratidae.

The uncertainty about the family's relationships reflects at least in part the range of genera included within it, which has fluctuated considerably from author to author. Kilian (1907)–13) grouped *Holcodiscus* with *Spitidiscus* and *Astieridiscus* while indicating a polyphyletic origin for the group. Spath (1923, p. 35) proposed the Holcodiscidae without defining the family or indicating clearly its generic content. He certainly included *Holcodiscus* and *Astieridiscus*, but his discussion of *Spitidiscus* is ambiguous: on the one hand he doubted 'whether the restricted *Holcodiscus*, Uhlig emend. Kilian, and *Astieridiscus*, Kilian, are directly descended from *Spitidiscus*… or represent parallel developments of other ribbed Desmoceratids'. On the other hand he suggested that *Spitidiscus* was derived from a Valanginian desmoceratid but did not include it in his list of Lower Cretaceous Desmoceratidae.

In the first edition of the Treatise on Invertebrate Paleontology, Wright (1957, p. L371) included both *Spitidiscus* and *Plesiospitidiscus* in the Holcodiscidae, but in the second edition (Wright, 1996, p. 48) he restricted the family to embrace only *Holcodiscus, Astieridiscus, Almohadites, Parasaynoceras, Metahoplites* and, with question, *Holcoptychites* and *Gymnoplites*. This looks odd in that *Holcoptychites* is an Early Hauterivian genus in what is otherwise a group of Barremian genera.

Tzankov and Breskowski (1982, p. 491), who were unaware of the views of Wright (1981), accepted that Kilian's original informal group was polyphyletic and therefore also restricted the Holcodiscidae, but in a different way from Wright's interpretation. They included within the family *Plesiospitidiscus*, *Spitidiscus*, *Holcodiscus, Parasaynoceras* and *Almohadites*, but excluded *Astieridiscus* and *Holcoptychites* (Astieridiscidae) and *Metahoplites* (placed into a new family Metahoplitidae, possibly derived from the Neocomitinae).

Thieuloy et al. (1990) expanded the Holcodiscidae to include the genus *Jeanthieuloyites* Cooper (1981, p. 260) originally placed in the Olcostephanidae. This extended the range of the family downward into the Late Valanginian.

Hoedemaeker (1995) included *Plesiospitidiscus* and the Early Barremian forms of '*Spitidiscus*' (now *Avramidiscus* Vermeulen and *Taveraidiscus* Avram and Thieuloy) in the Holcodiscidae, and suggested that *Abrytusites* should also be placed there. If that proves correct, then the Argentine genus *Weavericeras* (Leanza and Wiedmann, 1980) may also belong in the Holcodiscidae rather than the Desmoceratidae. Cecca et al. (1998) included *Plesiospitidiscus* in the Holcodiscidae, together with a new genus *Pseudovaldedorsella*. Conversely, Vermeulen and Thieuloy (1999) regard *Plesiospitidiscus* as the direct ancestor of the Barremitidae and transfer it to that family. They also transferred *Spitidiscus* and *Jeanthieuloyites* to the Neocomitidae, placing them into a new subfamily, the Spitidiscinae.

We follow the broad interpretation of the Holcodiscidae, to include:

Abrytusites Nikolov and Breskowski, 1969
Almohadites Wiedmann, 1967
Astieridiscus Kilian, 1910
Avramidiscus Vermeulen, 1996
Holcodiscus Uhlig, 1882
Holcoptychites Gerth 1925
Jeanthieuloyites Cooper, 1981
Metahoplites Spath, 1924
Parasaynoceras Breistroffer, 1947
Plesiospitidiscus Breistroffer, 1947
Pseudovaldedorsella Cecca, Faraoni and Marini, 1998
Spitidiscus Kilian, 1910
Taveraidiscus Vermeulen and Thieuloy, 1999
? *Weavericeras* Leanza and Wiedmann, 1980

This brings into one family at least two groups of quite strongly ribbed forms. A Late Valanginian to early Late Hauterivian group embraces *Jeanthieuloyites*, *Holcoptychites* and *Spitidiscus* s.s., while a Barremian group includes *Holcodiscus* and its allies (*Astieridiscus*, *Parasaynoceras*, *Almohadites*, *Metahoplites*). We therefore suggest that the Holcodiscidae should be divided into two subfamilies. *Holcoptychites* can be placed with *Jeanthieuloyites* and *Spitidiscus* in the Spitidiscinae, while the Barremian forms are placed in the Holcodiscinae. The two groups are linked by the smoother-shelled forms *Abrytusites* and *Plesiospitidiscus*, which we also place in the Holcodiscinae. *Plesiospitidiscus* was probably derived from *Spitidiscus* (Thieuloy, 1972; Bulot, 1995; Vermeulen and Thieuloy, 1999) and *Abrytusites* could have been (Thieuloy, 1972). In turn, either *Plesiospitidiscus* (Bulot, 1995) or *Abrytusites* (Vermeulen and Thieuloy, 1999) may have been the ancestor of the later Holcodiscinae. These all have 'a distinctive feature in common, viz. on the ventral part of the conch the adapical side of the constriction is the highest and generally lined with a thickened rib, whereas near the umbilicus it is the adoral side of the constriction that is the highest and commonly raised into a bulge or thickened rib' (Hoedemaeker, 1995, p. 241). Cecca et al. (1998) confirmed this observation, which separates the Holcodiscinae from the Desmoceratidae 'which lack the adoral swelling near the umbilicus' (Hoedemaeker, 1995, p. 241).

The systematic position of the Argentine genus *Weavericeras* requires further investigation.

In conclusion, we agree with Hoedemaeker (1995) and Bulot (1995) that the family Holcodiscidae, as interpreted here, forms a link between the Perisphinctaceae and the Desmoceratacea. The strong ornament of many forms leads us to keep them in the Perisphinctaceae.

Subfamily: Spitidiscinae Vermeulen and Thieuloy, 1999

Diagnosis. Moderately evolute to moderately involute holcodiscids with inflated to moderately compressed shells. Venter normally gently rounded. Ribs quite strong, varying from coarse to fine. Constrictions generally broad and only slightly sinuous.

Discussion. *Jeanthieuloyites* is the earliest member of the subfamily. The genus was proposed by Cooper (1981, p. 260, fig. 110) for *Rogersites quinquestriatus* Besairie from the 'Upper Valanginian' of Ambiky, Malagasy Republic, and included in the Olcostephanidae. The holotype was refigured by Cooper (1981, p. 261, fig. 110). *Jeanthieuloyites* has since been figured from France (Thieuloy et al., 1990; Autran, 1993; Reboulet, 1995) and Morocco (Wippich, 2001). Thieuloy et al. (1990) and Bulot et al. (1993) showed that in France the genus ranges from high in the *verrucosum* Zone to the base of the *radiatus* Zone, i.e. through most of the Upper Valanginian to the base of the Hauterivian. They transferred *Jeanthieuloyites* to the Holcodiscidae because it is with the Early Hauterivian *Spitidiscus* that it shows the greatest ornamental similarities. Bulot (1995, p. 132) suggested that the smooth siphonal band of *Jeanthieuloyites*, the occurrence of fasciculate ribs arising from an umbilical tubercle and a clearly perisphinctid suture line suggests an origin in the Neocomitidae, possibly *Neohoploceras*. It was this apparent similarity that led Vermeulen and Thieuloy (1999) to place the Spitidiscinae in the Neocomitidae. But it is also possible that *Jeanthieuloyites* is of olcostephanid origin, and some olcostephanids also show a ventral smooth band or groove.

We agree with Bulot (1995, p. 132) that *Spitidiscus* probably evolved from *Jeanthieuloyites* at about the beginning of the Hauterivian and suggest that

Holcoptychites is a southern hemisphere derivative of the same genus, evolving at about the same time.

Genus *Holcoptychites* Gerth, 1921

Type species. *Polyptychites neuquensis* Douvillé, 1910, by subsequent designation (Gerth 1925b): see discussion below.

Description. Shell moderately evolute to moderately involute, inflated to compressed and almost discoidal. Early forms become adult by about 250 mm (macroconchs), later forms are larger, growing to at least 700 mm. Strongly ribbed, becoming almost smooth in adult stage of larger forms. Weak to strong, shallow, wide constrictions occur regularly throughout growth. Generally the rib in front of a constriction remains single, the rib behind branches at an umbilical tubercle and either both ribs branch again on the flank or the anterior one does. Other ribs are either biplicate or more varied. Umbilical bullae, when present, appear mainly on the rib or pair of ribs just behind a constriction. Suture with large, broad, trifid lateral lobe, umbilical lobe half the size of lateral, several auxiliary lobes, internal lateral lobe and dorsal lobe smaller than umbilical.

Discussion. Although *Holcoptychites* was described by Gerth (1925b, p. 79) as a new genus, he had already published the name and described the main characteristics in 1921. In the 1921 paper he included two species within *Holcoptychites* (*H. meridionalis* sp. nov. and *H. neuquensis*) but did not indicate a type species. In 1925 he described only *H. neuquensis* but in a footnote stated that the genus included other species. However, referring to *H. neuquensis*, Gerth (1925b, p. 79) said that 'new examples at my disposal induce me to establish a new genus for this singular form'. We take this to be a valid subsequent designation of *H. neuquensis*, even though the figured examples of his 'new material' do not belong to that species, but to the later-named form, *H. demissus* Giovine. Wright (1996, p. 48), mistakenly claimed that *H. neuquensis* was designated type species by Wright (1957, p. 371), but in the latter publication the designation was attributed to the original publication of Gerth (1921).

Dimorphism is seen in one species (*H. magdalenae*), where the microconchs are apparently less than 50 mm in diameter. *Holcoptychites* macroconchs shows an evolutionary tendency towards larger size and more compressed and smoother shells. Some forms are similar to *Jeanthieuloyites* in lateral view, but lack the smooth ventral band characteristic of that genus. Other, more involute forms of *Holcoptychites* appear very close to some of the strongly-ribbed early *Spitidiscus* (later *Spitidiscus* are less strongly ribbed), e.g. *Spitidiscus crimicus* in Bulot (1995, pl. 18, fig. 1) and *S. meneghinii* in Reboulet (1995, pl. 32, figs. 14–15). Although the French examples are apparently mature at a much smaller diameter than *Holcoptychites*, two larger examples of *Spitidiscus meneghinii* have been figured by Wippich (2001, pl. 12) from the *radiatus* Zone in Morocco.

While later *Spitidiscus* spread over much of the world, including to Argentina, during the mid-Hauterivian sea-level rise (Rawson, 1999), *Holcoptychites* is known with certainty only from Argentina, where it characterises the lowest part of the Hauterivian in the Neuquén Basin (section 5, below). The only other published record is from Colombia, where Royo y Gomez (1945) recorded seven poorly-preserved whorl fragments as *H.* cf. *neuquensis*. None of the material was figured and the description makes no mention of ventral features. Thus the specimens could refer to *Holcoptychites*, *Jeanthieuloyites* or even a neocomitid.

Holcoptychites magdalenae (Douvillé)
Figs. 3c–d, 4a, d–e, 5b, d–g, 6a, 7b

v*	1910	*Holcodiscus magdalenae* Douvillé 1910, p. 14, pl. 2, figs. 3, 4.
v	1910	*Polyptychites neuquensis* Douvillé, p. 10, pl. 2, figs. 5, 7.
	1921	*Holcoptychites neuquensis* Gerth, p. 143.
?	1921	*Holcoptychites meridionalis* Gerth, p. 143.
v	1925b	*Holcoptychites neuquensis* (Douvillé); Gerth, p. 80, pl. 2, figs. 3 (refigured by Windhausen 1931, pl. 34, fig. 1), 4.
	1931	*Holcoptychites neuquensis* (Douvillé); Weaver, p. 431, pl. 50, fig. 329; pl. 51, figs. 330, 331–332?, 333, pl. 52; figs. 335–336, 338.
	1931	Fragmento de un *Holcoptychites*; Windhausen, pl. 34, fig. 6.
	1950	*Holcoptychites demissus* Giovine, p. 44, pl. 4, figs 3, 4.
	1950	*Holcoptychites neuquensis* (Douvillé); Giovine, p. 42, pl. 3, figs. 2–3
v	1988	*Holcoptychites neuquensis* (Douvillé); Riccardi, pl. 6, figs. 6–7.
v	1999	*Holcoptychites neuquensis* (Douvillé); Aguirre-Urreta et al., p. 38, pl. 1, figs. 1–2.

Holotype. By original designation, the specimen figured by Douvillé (1910), which is probably from Cerro Negro de Covunco (Windhausen, 1914). UFR des Sciences de la Terre, Université Claude Bernard, Lyon, no. EM 2003 (formerly in the Laboratorie de Paléontologie de l'École des Mines, Paris). Cast: CPBA 19826.

Material. 155 specimens: 1 from west of Río Diamante bridge (CPBA 19806), 6 from La Mala Dormida (CPBA 19809.1-2), 1 from Mina San Eduardo (CPBA 16271), 1 from Loma Naunauco (CPBA 19818), 11 from Loma Rayoso (CPBA 20001.1-7, 20002.1-4), 14 from Lonco Vaca (CPBA 16997, 16998.1-4. 16999.1-7,

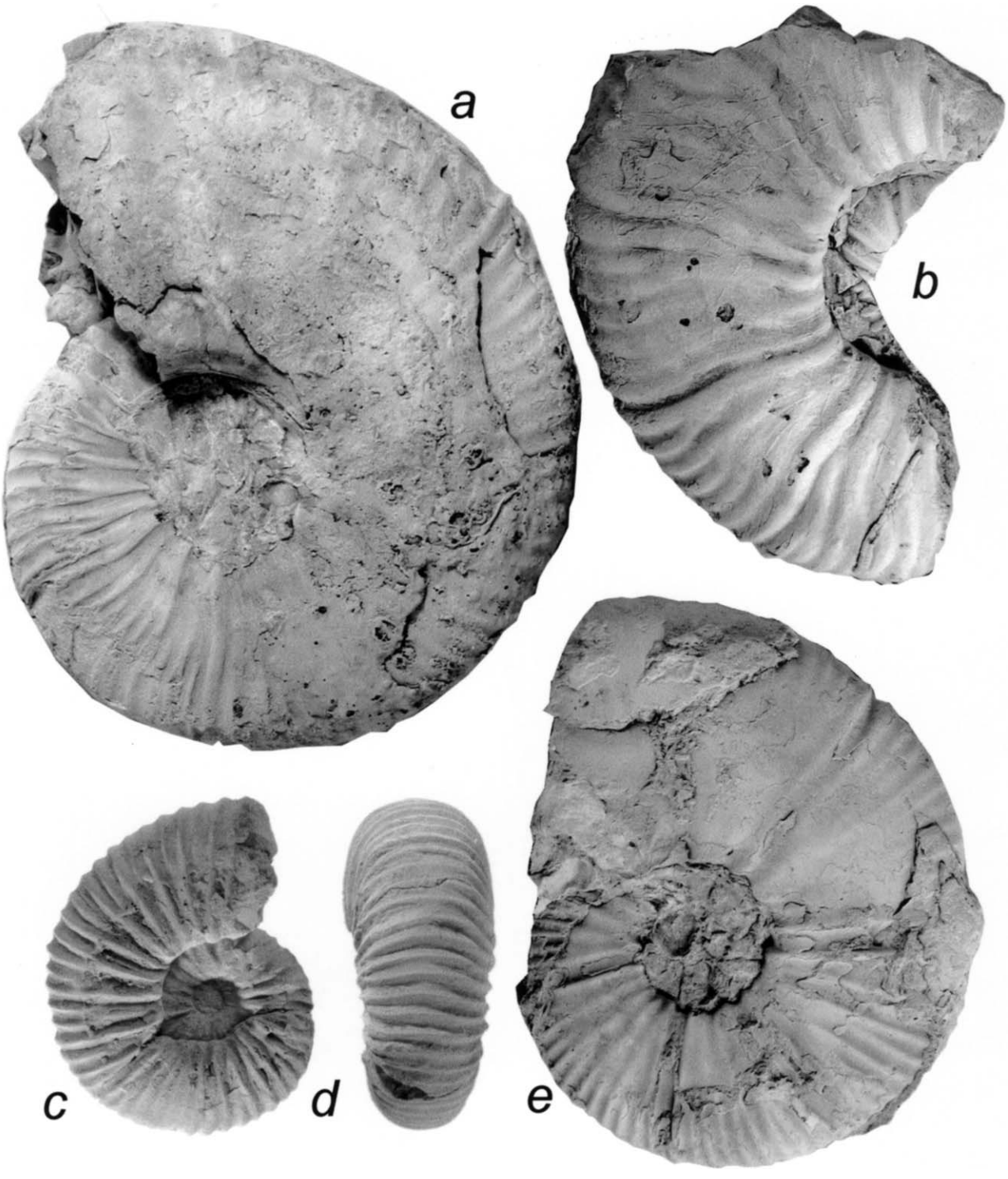

Fig. 3. a, *Holcoptychites agrioensis* (Weaver), CPBA 20011.2, bed MHo46, Agua de La Mula. b, *Holcoptychites* cf *recopei*, CPBA 19824, bed PHo 1, Pichaihue valley. c–d, *Holcoptychites magdalenae* (Douville), EM 2003 holotype (Recopé collection), probably from Cerro Negro de Covunco. e, *Holcoptychites neuquensis* (Douville), CORD-Pz 7483 (Díaz collection), Loma Rayoso. All ×1.

19825.1-2), 54 from Pichaihue (CPBA 19819.1-3, 19820.1-11, 19821.1-9, 19822.1-16, 19823.1-5, 20008.1-2, 20012.1-7, 20014), 58 from Agua de la Mula (CPBA 16988.1-14, 16990.1-13, 16992.1-6, 18355, 19985, 19986.1-3, 19987.1-2, 19988.1-4, 19989.1-2, 19990.1-3, 19991.1-7, 20013.1-2), 4 from Salado Sur (CPBA 19995.1-2, 19996, 19997) and 5 from Bajada del Agrio (CPBA 18030, 19826.1-4).

Description. A moderately large form, septate to at least 210 mm diameter, estimated maximum diameter at least 300 mm. Length of body chamber not known, but at least half a whorl. The shell is slightly to moderately evolute (wh%d=39–45%), slightly inflated to inflated, normally becoming more inflated with growth. Whorl flanks slightly curved, merging via a well-rounded ventro-lateral into a gently rounded or almost flat venter. The whorl section is subrounded to almost subquadrate, wider than high, with maximum width at the umbilical shoulder. The umbilicus is moderately shallow at first, becoming deeper with growth. The umbilical wall is almost vertical.

There are up to seven shallow constrictions per whorl. Both constrictions and ribs are more or less straight on the flanks but curve forward slightly over the venter. The shell is strongly ribbed to at least 150 mm diameter, above which the ribs sometimes weaken, at least on internal moulds. Primary ribs arise on the umbilical wall and pass straight over the umbilical margin. The rib immediately in front of each constriction normally remains single over the flank, while the rib immediately behind the next constriction often bifurcates at or just above the umbilical margin and one or more branches again at mid flank or higher. There are 1–3 intervening primary ribs, which usually extend to mid flank, where the primary bifurcates or a secondary is intercalated. The resulting rib-pattern is slightly irregular; usually two secondaries are associated with each primary; rarely, three or none. The ribs bounding the constrictions sometimes stand out slightly, especially the posterior one. Above about 40–70 mm diameter the rib immediately behind each constriction develops an umbilical swelling, which eventually develops into a large, obliquely downward-pointing, almost spinose bulla. Such swellings may extend to embrace the rib immediately behind and even cross the constriction to embrace the rib in front of it. There are 7–9 bullae, 15–23 primary ribs and 45–56 secondary ribs per whorl (sec/pr=2.4–3.0) at 90–130 mm diameter.

Dimensions of figured specimens.

	d	wh	wh%d	wt	wt%d	wu	wu%d	pr.	sec.
Holotype EM 2003	56.4	24.5	43.4	26.4	46.8	16.8	29.8	27	*c.* 50
CPBA 19985		54.9		71.3		55.0		*c.* 27	
CPBA 16999	118.8	46.0	38.7	49.3	41.5	41.2	34.7	22	*c.* 59
CPBA 20012.1	63.9	28.4	44.4	28.5	44.6	22.0	34.4		
CPBA 19823.2	62.7	26.1	41.6	29.9	47.7	19.4	30.9	21	*c.* 45
CPBA 19821.6	51.6	20.1	39.0	21.0	40.7	17.7	34.3	*c.* 25	
CPBA 19822 11	47.1	20.3	43.1	23.0	48.8	15.9	33.8		
CPBA 19821.4	41.8	17.7	42.3	17.7	42.3	14.6	34.9		
CPBA 16988.1	38.4	17.1	44.5	19.9	51.8	11.4	29.7	19	*c.* 42

Discussion. *H. magdalenae* has been overlooked almost completely since Douvillé described the species in 1910. Our material shows that it embraces those *Holcoptychites* that have a slightly to strongly inflated shell on which strong umbilical bullae appear at quite an early growth stage (40–70+ mm). Unfortunately the holotype of *H. magdalenae* represents only the earlier whorls of the species, before the distinctive large bullae developed. It is also more finely ribbed than most specimens of similar diameter. Hence its relationship to the large, bullate forms has not been recognised before – even by Douvillé, who assigned two bullate fragments of *H. magdalenae* to another of his new species, *H. neuquensis*. However, our material includes several bullate specimens that show the '*magdalenae*' morphology in the earlier whorls, i.e. they are more finely ribbed than the majority of individuals, the venter is gently rounded and the bullae do not appear until a diameter of 70 mm or more. More commonly, the earlier whorls of this species are more coarsely ribbed, the venter is almost flat, and bullae start to develop earlier, at 40–50 mm diameter. The latter variant apparently occurs more commonly in the lower part of the species' range and the *magdalenae* variant in the upper, but there is some overlap. The two variants cannot be distinguished in more advanced growth stages. On the other hand, there is considerable variation within the more advanced, bullate stage in strength of bullae, density of ribbing and inflation of shell. Some forms show particularly strong, straight ribs with well-developed constrictions, and have often been misidentified as *H. neuquensis* (*sensu* Gerth, *non* Douvillé).

Dimorphism occurs, though the evidence is limited. One specimen (CPBA 20014) of 32.7 mm diameter is septate to 24.7 mm diameter; the last two sutures are approximated and the (incomplete) body chamber shows slight retraction. There are several other small, mainly incomplete, body chambers of specimens of some 35–50 mm diameter that closely match this. Another specimen of 38.4 mm diameter shows an apparent mouth border with a strongly flared rib behind a marked constriction (CPBA 16988.1, figured by Aguirre-Urreta et al., 1999, pl. 1, figs 1–2, see also Fig. 4e). These forms indicate that the macroconch:microconch size ratio is approximately 5:1.

Gerth (1921, p. 143) proposed *H. meridionalis* for a form from Arroyo Covunco which was more strongly inflated than his '*H. neuquensis*', with large, conical, inwardly directed tubercles on the umbilical margin. The species was not illustrated and was not mentioned in the more detailed account from Gerth (1925b) of the Neuquén faunas or in any subsequent publication. Therefore it cannot be interpreted, though it is probably a variant of *H. magdalenae*.

Giovine (1950) proposed *H. demissus* for the forms previously misidentified as *H. neuquensis* by Gerth

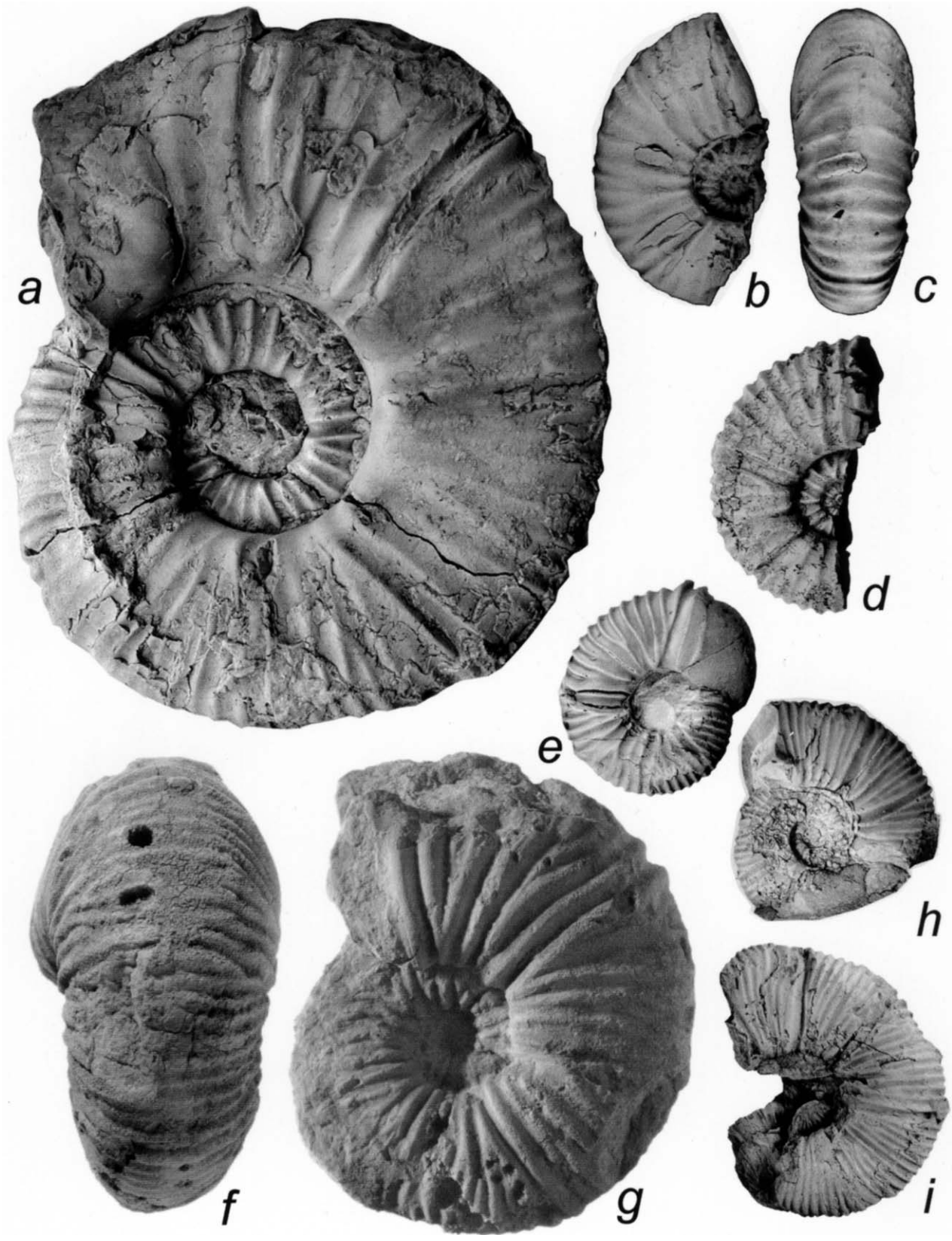

Fig. 4. a, d–e, *Holcoptychites magdalenae* (Douville), a, CPBA 16999, Agua de La Mula. d, CPBA 19822.11, bed PHo 9, Pichaihue valley. e, CPBA 16988.1, Agua de La Mula. b–c, *Holcoptychites agrioensis* (Weaver), CPBA 20004.3, Loma Rayoso. f–g, *Holcoptychites recopei* (Douville), EM 1999 holotype (Recopé collection), probably from Cerro Negro de Covunco. h–i, *Holcoptychites* sp. nov., h, CPBA 19992.2, bed MHo 8, Agua de La Mula. i, CPBA 19993, Mina San Eduardo. All ×1.

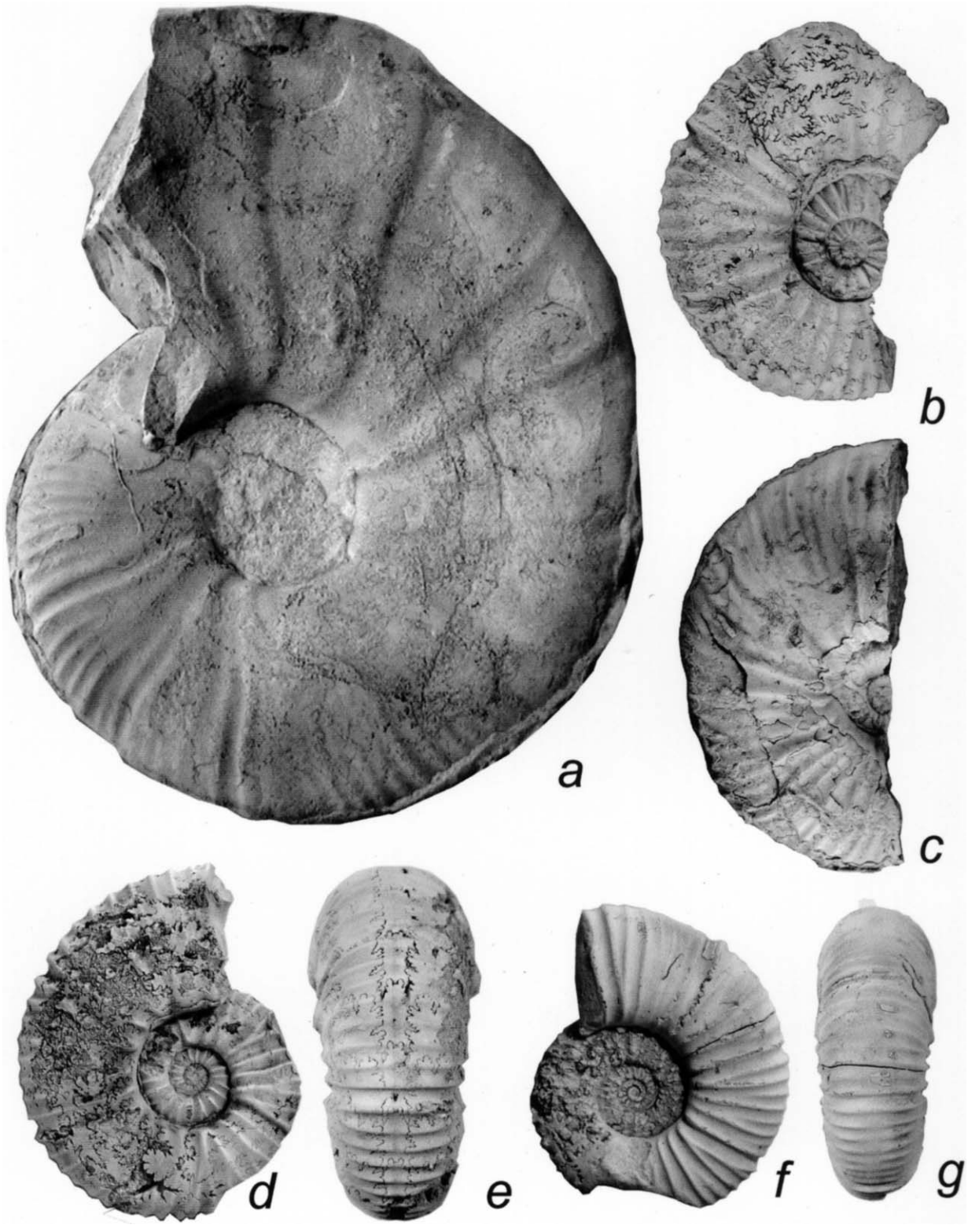

Fig. 5. a, c, *Holcoptychites agrioensis* (Weaver), a, CPBA 20011.16, c, CPBA 20011.6, bed MHo 46, Agua de La Mula. b, d–g, *Holcoptychites magdalenae* (Douville), b, CPBA 20012.1, d–e, CPBA 19823.2, bed PHo 9, f–g, CPBA 19821.6, Pichaihue valley. All ×1.

(1925b). He did not designate a holotype, but in addition to recording several examples in the Gentili collection, he also included the two specimens figured by Gerth (1925b) as *H. neuquensis* in the synonymy of his new species. All these specimens are therefore paratypes of *H. demissus*. Giovine's figured specimen is lost and was

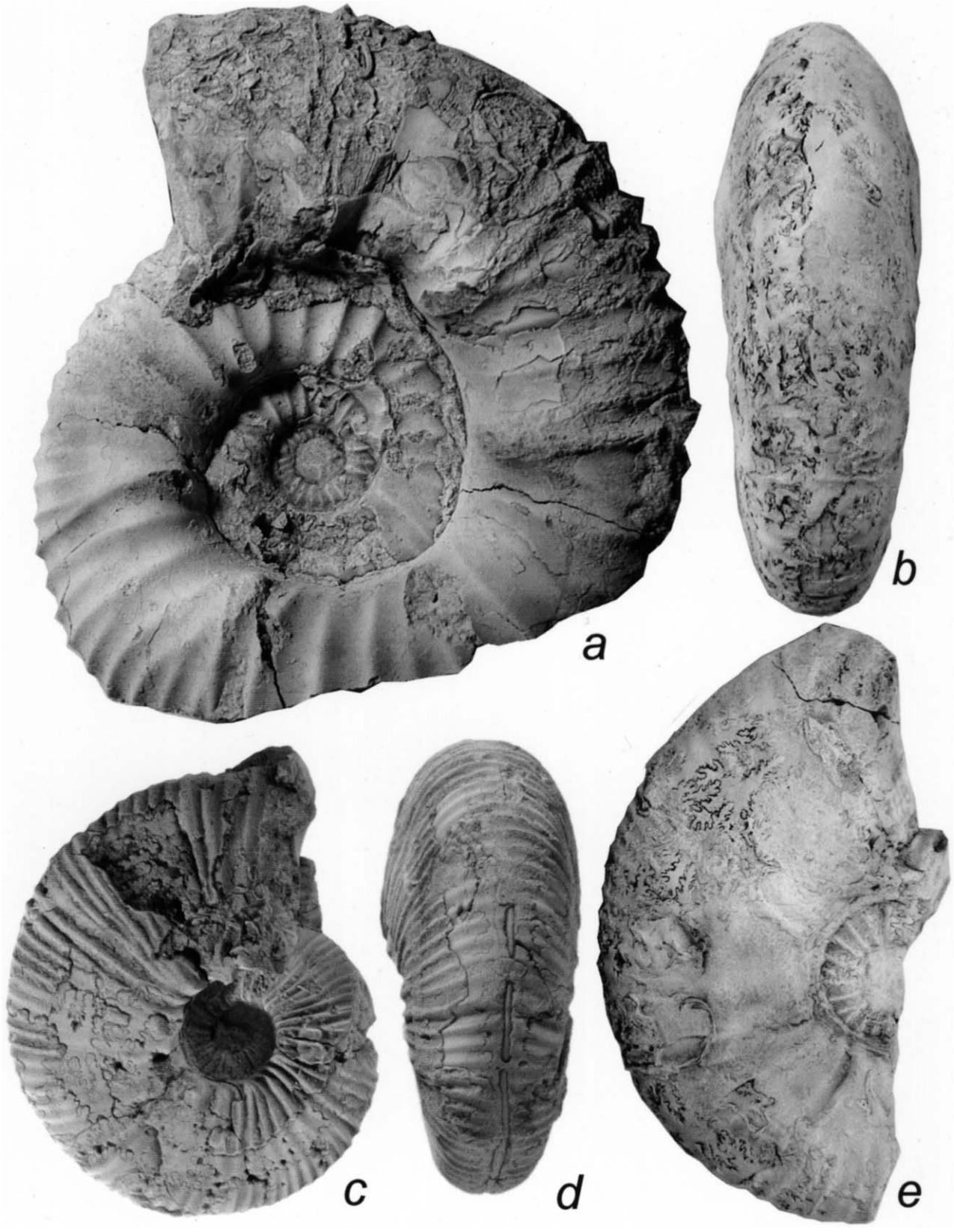

Fig. 6. a, *Holcoptychites magdalenae* (Douville), CPBA 19985, loose in bed MHo 22, Agua de La Mula. b, e, *Holcoptychites agrioensis* (Weaver), CORD-Pz 7484 (Díaz collection), Loma Rayoso. c–d, *Holcoptychites neuquensis* (Douville), EM 2001 holotype (Recopé collection), probably from Cerro Negro de Covunco. All ×1.

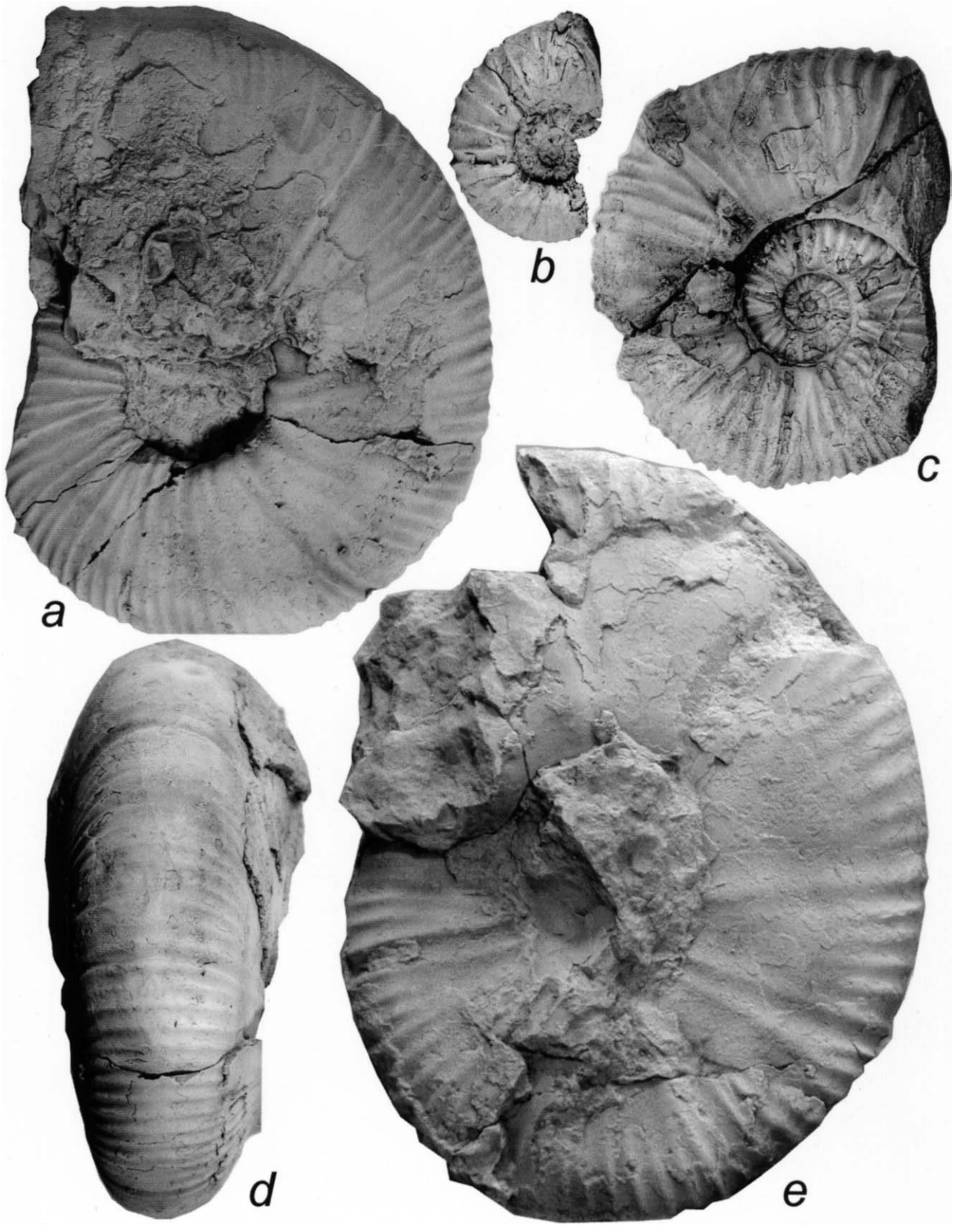

Fig. 7. a, d, *Holcoptychites neuquensis* (Douville), CPBA 19814.2, bed PHo 14, Pichaihue valley. b, *Holcoptychites madgalenae* (Douville), CPBA 19821.4, bed PHo 13, Pichaihue valley. c, *Holcoptychites* sp. nov., CPBA 20006, bed MHo 2, Agua de La Mula. e, *Holcoptychites agrioensis* (Weaver), CPBA 19827 cast of neotype (Weaver collection), Agua de La Mula. All ×1.

Fig. 8. *Holcoptychites agrioensis* (Weaver), CPBA 20011.11, bed MHo 46, Agua de La Mula, ×1.

indifferently preserved, but Gerth's (1925b, pl. 2, fig 3) larger specimen is well-preserved and is here formally selected as lectotype; it is in the Gerth collection (IPG-Gerth 11a) in the Institute for Palaeontology, Bonn University, Germany. We place *H. demissus* in *H. magdalenae*.

H. magdalenae differs from other species of *Holcoptychites* in normally having a more inflated shell in all

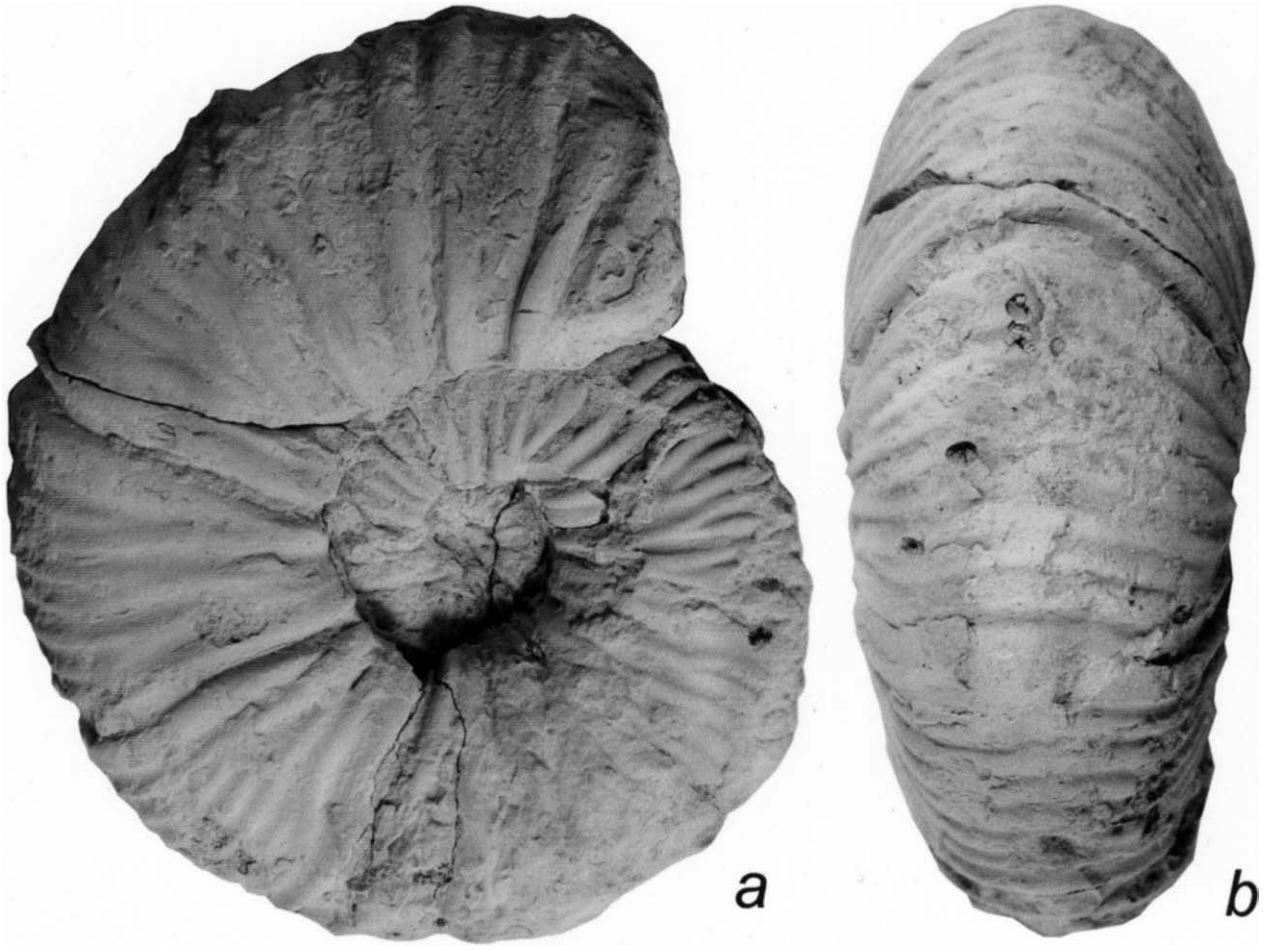

Fig. 9. a–b, *Holcoptychites* cf. *recopei*, CORD-Pz 1957 (Windhausen collection), Cerro Negro de Covunco. Both ×1.

but the earliest growth stages, and in bearing very strong umbilical bullae in intermediate to late growth stages.

Holcoptychites neuquensis (Douvillé)
Figs. 3e, 6c–d, 7a, d

v*	1910	*Polyptychites neuquensis* Douvillé 1910, p. 10, pl. 2, fig. 2 (non figs. 5, 7); text-fig. 1.
v non	1921	*Holcoptychites neuquensis* Gerth, p. 143.
v non	1925b	*Holcoptychites neuquensis* Douvillé; Gerth, p. 80, pl. 2, figs. 3 (refigured by Windhausen 1931, pl. 34, fig. 1), 4.
?	1931	*Holcoptychites neuquensis* (Douvillé); Weaver, p. 431, pl. 52, fig. 337.
non	1931	*Holcoptychites neuquensis* (Douvillé); Weaver, p. 431, pl. 50, fig. 329; pl. 51, figs. 330, 331-332?; 333, pl. 52; figs. 335–336, 338.
non	1936	*Holcoptychites neuquensis* (Douvillé); Feruglio, p. 45, pl. 8, figs. 14–15.
non	1950	*Holcoptychites neuquensis* (Douvillé); Giovine, p. 42, pl. 3, figs. 2–3
v*	1980	*Holcoptychites neuquensis* (Douvillé); Leanza and Wiedmann, p. 957, pl. 8, figs. 1-3, non? pl. 2, figs. 2–3.
non	1988	*Holcoptychites neuquensis* (Douvillé); Riccardi, pl. 6, figs. 6–7.
v non	1993	*Holcoptychites neuquensis* (Douvillé); Aguirre-Urreta, p. 63, pl. 3, figs. 5–6.
v	1997	*Holcoptychites neuquensis* (Douvillé); Aguirre-Urreta and Rawson, p. 454.
v non	1999	*Holcoptychites neuquensis* (Douvillé); Aguirre-Urreta et al., p. 38, pl. 1, figs. 1–2.

Holotype. By original designation, the specimen figured by Douvillé (1910, pl. 2, fig. 2, text-fig. 1), which is probably from Cerro Negro de Covunco (Windhausen, 1914). UFR des Sciences de la Terre, Université Claude Bernard, Lyon, no. EM 2001 (formerly in the Laboratorie de Paléontologie de l'École des Mines, Paris). Cast: CPBA 20007.

Material. Five specimens: 1 from Loma Rayoso (CORD-Pz 7483), 2 from Pichaihue (CPBA 19814.1-2)

and 2 from Agua de la Mula (CPBA 18356, Dázquez collection, CPBA 19984).

Description (of 50–100 mm diameter growth stage). Probably quite a large form, but we have found only septate whorls to a maximum estimated diameter of about 140 mm. The shell is moderately involute (wh%d=48–53%), slightly compressed, with slightly curved flanks converging towards a gently rounded, moderately narrow venter. The whorl section is arched to subtrapezoidal, higher than wide, with maximum width at the umbilical shoulder. The umbilicus is moderately shallow and the umbilical wall is slightly undercut.

There are up to six shallow constrictions per whorl; some are well marked, with a stronger rib bordering them on each side. Both constrictions and ribs bend forward slightly on the flanks and curve gently forward over the venter. The ribs are quite fine and dense. Primary ribs arise high on the umbilical wall. The rib immediately behind each constriction normally bifurcates at the umbilical margin; from about 60–80 mm diameter an umbilical tubercle develops at the point of branching. At least one of the pair branches again higher on the flank. Other primaries branch at various levels on the flank, some near the umbilical margin, most at mid-flank or above, and some more than once giving a polyptychitine appearance.

Dimensions of figured specimens.

	d	wh	wh%d	wt	wt%d	wu	wu%d	pr.	sec.
Holotype EM 2001	76.7	36.8	48.0	33.1	43.2	18.5	24.1	28	*c.* 75
CPBA 19814.2	114.2	60.4	52.9	54.4	47.6	30.4	26.6		*c.* 70
CORD-Pz 7483	88.7	45.1	50.9	34.6	39.0	23.4	26.4	*c.* 24	*c.* 53

Discussion. *H. neuquensis* is probably the most misinterpreted ammonite in the Neuquén Basin. The problem apparently stems from Douvillé's original description, where he figured along with the holotype two more inflated, strongly bullate inner whorl fragments that he assigned to the same species. Gerth (1925b) then figured as *H. neuquensis* a bullate specimen that is more inflated than the holotype, but close to Douvillé's bullate fragments. Weaver (1931) and Windhausen (1931) followed suit and it was left to Giovine (1950) to point out the error and transfer many of the previously figured '*neuquensis*' to his new species *H. demissus* (here regarded as a synonym of *H. magdalenae*). Our study of the holotype of *H. neuquensis* (not examined by Giovine) confirms Giovine's conclusions, though the specimen that he figured as *H. neuquensis* is regarded here as a compressed variety of *H. magdalenae*.

The true *H. neuquensis* lies both morphologically and stratigraphically between *H. magdalenae* and *H. agrioensis*. It is more involute and less inflated than the former species and is more finely ribbed with much less strong tubercles and a narrower venter. The occurrence of more strongly 'polyptychitine' rib bundles and a more inflated shell distinguishes it from *H. agrioensis*, though the less compressed forms of the latter are only a little more compressed than *H. neuquensis*.

We agree with Leanza (1968) that the specimens from the Austral Basin that Feruglio (1936) figured as *H. neuquensis* belong to *Phyllopachyceras aureliae* Feruglio.

Holcoptychites agrioensis (Weaver)
Figs. 3a, 4b–c, 5a, c, 6b, e, 7e, 8

vp 1931 *Desmoceras agrioensis* Weaver, p. 437, pl. 51, fig. 334.
1980 *Holcoptychites compressus* Leanza and Wiedmann, p. 958, pl. 3, fig.1, text-fig. 3.
? 1980 *Holcoptychites neuquensis* (Douvillé); Leanza and Wiedmann, p. 957, pl. 2, figs. 2–3.
v 1997 *Holcoptychites compressus* Leanza and Wiedmann; Aguirre-Urreta and Rawson, p. 454.

Types. Weaver noted that the holotype was specimen no. 371 and the paratypes specimens 372–374 in the Weaver collection, which is housed in the Burke Museum, Washington University, Seattle, Washington. The holotype and one paratype (374) are now lost (see below) but the other two paratypes (372, 373) remain in the Burke Museum and from these we have selected 373 as neotype. Cast: CPBA 19827

Material. 74 specimens: 2 from Cerro Plomo (CPBA 19805.1-2), 9 from La Mala Dormida (CPBA 19808.1-7, 19809.1-2), 4 from Cerro Caicayén (CPBA 18142.1-4), 8 from Mina San Eduardo (CPBA 19813.1-8), 6 from Loma Rayoso (CORD-Pz 7484, 7497, CPBA 20003, 20004.1-3), 6 from Cerro Rayoso (CPBA 19815.1-4, 19816.1-2), 1 from Pichaihue (CPBA 19817), 2 from Salado Sur (CPBA 19998.1-2), and 36 from Agua de la Mula (CPBA 16995, 17024, 18331, 18357-64, 19983, 20009.1-2, 20010.1-5, 20011.1-17).

Description. A large form, septate to at least 420 mm, maximum diameter at least 700 mm. The body chamber occupies about three quarters of a whorl. The shell is slightly to moderately involute (wh%d=45–48%), the whorls are often rounded at first, with sub-circular section, but soon become moderately compressed to compressed with almost flat or gently curved flanks, narrowly rounded venter, and high-arched to narrowly subtrapezoidal whorl section; maximum width at the umbilical shoulder. The umbilicus is shallow, with clearly defined umbilical margin; the umbilical wall slopes gently to steeply inward.

Shallow, often feeble, constrictions occur, normally about six per whorl, sometimes becoming more frequent in advanced growth stages (in one specimen as many as ten, CPBA 20011.16). Both constrictions and ribs are

slightly prorsiradiate on the flanks and curve gently forward over the venter. The earlier whorls (to *c*. 100–120 mm diameter) are strongly ribbed; primary ribs arise on the umbilical wall, pass straight over the umbilical margin, and most extend to mid flank; rarely, one bifurcates at or just above the umbilical margin. Secondaries branch from the primaries, or are intercalated, at about mid flank and sometimes higher. In some forms most primary ribs bifurcate at first, then above 60–70 mm diameter additional secondaries are intercalated or branch from earlier ones high on the flank, creating an irregular rib-pattern. There are 12–20 primary and 40–48 secondary ribs per whorl (sec/pr=2.25–3.33). Above 100–120 mm diameter the ribs begin to fade and the shell becomes almost smooth, especially on internal moulds. But some specimens are crossed by shallow constrictions that become closer together and more numerous with growth, bounded by slightly raised ribs that originate in a subdued umbilical tubercle. On these forms secondary ribs remain visible on the outer half of the flank and over the venter, some longer and slightly stronger than others.

Dimensions of figured specimens.

	d	wh	wh%d	wt	wt%d	wu	wu%d	pr.	sec.
CPBA 20011.11	199.0	89.2	44.8	68.7	34.5	55.0	27.6		
CPBA 20011.16	160.0	74.3	46.4	56.0	35.0	36.0	22.5		
CPBA 20011.2	114.1	55.2	48.4	45.8	40.1	28.7	25.2		*c*. 70
CORD-Pz 7484	110.3	52.0	47.1	37.0	33.5	26.5	24.0		
CPBA 20011.6	70.4	33.3	47.3	28.1	39.9	15.7	22.3		
CPBA 20004.3	50.5	23.1	45.7	20.7	41.0	14.6	28.9		

Discussion. This species varies in degree of compression and involution, and number and strength of ribs and constrictions. In general, the more compressed forms are more involute and have finer, more numerous primary and secondary ribs in the earlier whorls. Forms with predominantly biplicate ribbing and a more inflated shell in the earliest whorls are usually those with a subtrapezoidal whorl section and less involute shell.

The holotype was originally in Burke Museum but the catalogue records show that it had already disappeared in 1967. A check has also been made with the California Academy of Sciences and the University of California at Berkeley without success (Elisabeth Nesbitt, pers. comm. 2002) so the holotype is assumed to be lost. Weaver's (1931) only illustration of '*Desmoceras*' *agrioensis* was a cross-section of the holotype, which is probably why, despite his detailed description, the species has been overlooked by subsequent workers. The illustration shows that although the earliest whorls had a more rounded whorl section than most examples of the species, the intermediate growth stage has a subtrapezoidal whorl section typical of the more inflated varieties. Although the existing paratypes of *H. agrioensis* are incomplete and partially crushed they confirm that the species embraces the moderately compressed to discoidal end-members of the *Holcoptychites* lineage that Leanza and Wiedmann (1980) and Aguirre-Urreta and Rawson (1997) had assigned to *Holcoptychites compressus* Leanza and Wiedmann. The latter species was based on a single specimen (SGN 15045) from Bajada del Agrio and is here regarded as one of the more inflated and evolute examples of *H. agrioensis*, probably quite similar to the lost holotype.

Weaver (1931) did not explain why he placed his new species in *Desmoceras* rather than *Holcoptychites*, but it was presumably because of the almost smooth, compressed shell of the larger forms, sometimes crossed by constrictions bounded by flared ribs.

Inflated examples of the inner whorls of *H. agrioensis* are similar to the comparable growth stage of *H. magdalenae* and *H. neuquensis*, but *H. agrioensis* quickly becomes more compressed than these forms.

Leanza and Wiedmann (1980) put *H. neuquensis* in possible synonymy with *H. compressus* Weaver (1931, fig. 333), but Weaver's specimen has stronger umbilical tubercles on the outer whorl and his description suggests it is an inflated form. We have placed it in *H. magdalenae*.

Holcoptychites cf. recopei (Douvillé) 1910
Figs. 3b, 9 a–b

v* cf. 1910 *Holcodiscus recopei* Douvillé 1910, p. 13, pl. 2, fig. 1.
v 1931 *Holcoptychites covunquensis nom. ined.* Windhausen, p. 296, pl. 324, fig. 5.

Holotype. By original designation, the specimen figured by Douvillé (1910) which, according to Windhausen (1914), is probably from Cerro Negro de Covunco. UFR des Sciences de la Terre, Université Claude Bernard, Lyon, no. EM 1999 (formerly in the Laboratorie de Paléontologie de l'École des Mines, Paris). Refigured here, Fig. 4f–g. Cast: CPBA 20005.

Material. 5 specimens. 1 from Pichaihue (CPBA 19824), 4 from Cerro Negro de Covunco (CORD-Pz 1957, Windhausen collection; CPBA 19999.1-3).

Description. Probably a medium-sized form, septate whorls to a maximum diameter of 110 mm, body chamber when preserved occupies more than half a whorl. The shell is slightly evolute (wh%d=40–45%), with gently curved flanks converging towards the rounded ventral area. The whorl section is slightly higher than wide in the inner whorls becoming more rounded with growth. The umbilicus is moderately shallow and the umbilical wall is undercut.

There are up to eight constrictions per whorl, and these and the ribs are slightly flexuous across the flanks

and curve gently forwards over the venter. Primary ribs arise on the umbilical wall and branch at various levels on the flank, some near the umbilical margin, most at mid-flank or above, and some more than once giving a slightly polyptychitine appearance. The ribs bounding the constrictions stand out slightly.

Dimensions of figured specimens

	d	wh	wh%d	wt	wt%d	wu	wu%d	pr.	sec.
Holotype EM 1999 d max c. 84.2: at	77.7	34.6	44.5	42.0	54.1	19.2	24.7		
CORD-Pz 1957	124.9	50.4	40.4	51.8	41.5	36.9	29.6	24	*c.* 65

Discussion. Of the five specimens that we compare with *H. recopei*, one was from the lowest level at which we have found *Holcoptychites*, about 92 m below the lowest *H. magdalenae* at Pichaihue. The others are from Cerro Negro and their exact stratigraphical relationship with other species is not known. Windhausen (1931) regarded his specimen as a new species for which he used his unpublished name *H. covunquensis*. The holotype of *H. recopei* (Fig. 4f–g) has a moderately stout shell and slightly flexuous ribs, while *H.* cf. *recopei* is less stout and has more noticeably flexuous ribs. Neither form bears tubercles, and this distinguishes them from *H. magdelanae*. *H.* cf. *recopei* differs from all other *Holcoptychites* in the flexuous nature of the ribs and constrictions on the flank.

Holcoptychites sp. nov.
Figs. 4h–i, 7c

Material. Five specimens: 4 from Agua de la Mula (CPBA 19992.1-2, 19994, 20006) and 1 from Mina San Eduardo (CPBA 19993).

Description. The largest specimen, partially distorted, has an estimated original diameter of 90 mm and consists of two thirds of a whorl, of which the last fifth is body chamber. This appears to be a slightly evolute species (wh%d=42–45%) with subcircular whorl section, the whorl only slightly wider than high.

There are at least five constrictions per whorl; they are wide, shallow and slightly flexuous. The ribs extend straight across the flanks and curve forward very slightly on the venter. One specimen (CPBA 19993) shows a slight mid-ventral depression on each rib on the first quarter of a whorl (to *c.* 30 mm diameter). The rib in front of each constriction is single or bifurcates at the umbilical margin. Behind the next constriction either a single or biplicate rib occurs, branching again irregularly higher on the flank to form a group of four secondaries. Between these groups 2–3 intervening ribs arise singly or in pairs at the umbilical margin and may branch again in mid flank. The ribbing is fine through most of the preserved growth stages but becomes coarser above about 50 mm diameter.

Dimensions of figured specimens.

	d	wh	wh%d	wt	wt%d	wu	wu%d	pr.	sec.
CPBA 20006	77.5	32.8	42.3	37.7	48.7	24.4	31.5	*c.* 26	*c.* 56
CPBA 19993	48.6	21.8	44.9	24.4	50.2	14.8	30.5		

Discussion. The specimens appear to represent a new species but are too incomplete and indifferently preserved to be named formally. They differ from other *Holcoptychites* in having a subcircular whorl section and fine ribbing, at least on growth stages to about 50 mm diameter. They show some similarities with more evolute examples of *Jeanthieuloyites* (e.g. *J. keyserlingiformis* and *J. trapezoidalis* Avram and Gradinaru, 1993), though they lack the ventral interruption of the ribbing characteristic of that genus. However, the slight depression on early ribs in CPBA 19993 may indicate a link with *Jeanthieuloyites*.

Three of the specimens were found just beneath the first *H. magdalenae* at Agua de la Mula, another one lower in the section, while the other was loose on the lower part of the *Holcoptychites* beds at Mina San Eduardo. Although they have not been found at the same locality as *H.* cf. *recopei*, a comparison of the relative positions of the two forms within the *Holcoptychites* beds (Fig. 2) suggests that *H.* sp. nov. and *H.* cf. *recopei* first appear at about the same level in the lowest part of the *Holcoptychites* beds.

4. Biostratigraphy

Gerth (1925b, p. 128) proposed a biozonation for the Neocomian of the Neuquén Basin in which the 'Hauterivian' was divided into three zones; those of *Neocomites* (*Lyticoceras*) *pseudoregale*, *Holcoptychites neuquensis* and *Crioceras andinum*. He listed *Hoplitoides recopei* and *Desmoceras windhauseni* (a *nomen nudum*) as other ammonites characteristic of the *neuquensis* Zone. His scheme was followed by most subsequent workers and further taxa were recorded including *Weavericeras vacaensis*, which actually occurs much higher in the Pilmatué Member than *Holcoptychites*. Hence Aguirre-Urreta and Rawson (1997) divided this long-ranging 'zone' into four discrete zones. They retained a restricted *Holcoptychites neuquensis* Zone for the lowest division, the base of which was defined by the first appearance of the genus *Holcoptychites*. The zone was divided into three subzones (Fig. 10). *Holcoptychites* is restricted to the lowest two, while the highest subzone is characterised by an *Olcostephanus* fauna dominated by *O. laticosta* (Aguirre-Urreta and Rawson, 2002).

Within the *Holcoptychites* sequence the lower beds are characterised by the more inflated forms and the upper beds by the larger, smoother, more discoidal forms, and this formed the basis for the division into the

	NEUQUEN BASIN Aguirre-Urreta and Rawson 1997–2003		WEST MEDITERRANEAN PROVINCE Hoedemaeker, Reboulet et al. 2003	
AGE	BIOZONE	SUB-BIOZONE	BIOZONE	SUB-BIOZONE
Early Hauterivian (*pars*)	*Holcoptychites neuquensis*	*Olcostephanus (Olcostephanus) laticosta* [1]	*Crioceratites loryi*	*Olcostephanus (Jeannoticeras) jeannoti*
				Crioceratites loryi
		Holcoptychites agrioensis [2]	*Acanthodiscus radiatus*	
		Holcoptychites neuquensis		
Late Valanginian (*pars*)	*Pseudofavrella angulatiformis*	*Neocomites* sp.	*Criosarasinella furcillata*	*N. (Teschenites) callidiscus*
		Chacantuceras ornatum [3]		*Criosarasinella furcillata*
		Pseudofavrella angulatiformis		

Fig. 10. Zonation of the Valanginian/Hauterivian boundary beds of the Neuquén Basin and suggested correlation with the West Mediterranean Province. The Neuquén zonation is based on Aguirre-Urreta and Rawson (1997) modified by: [1]Aguirre-Urreta and Rawson (2002); [2]this paper; [3]Aguirre-Urreta and Rawson (1999).

neuquensis and *compressus* subzones (Aguirre-Urreta and Rawson, 1997, p. 454). However, our systematic revision of *Holcoptychites* has shown that *H. compressus* is a junior subjective synonym of *H. agrioensis*, so the name of the upper subzone has to be changed. The base of the subzone is defined by the first appearance of *H. agrioensis.* The name of the lower subzone is retained although the index species is now known to occur only in the top part of the subzone. Most of the upper part of the subzone is occupied by *H. magdalenae*, which just overlaps with the first *H. neuquensis*. Unfortunately the lower part of the subzone is very poorly fossiliferous but appears to be characterised by *H.* cf. *recopei* and *H.* sp. nov. The base of the subzone, like the base of the zone, thus has to be defined by the first appearance of the genus *Holcoptychites* rather than by a distinctive species.

Agua de la Mula is taken as the standard reference section for the *neuquensis* Zone and its three subzones. Even here, there are significant gaps in the occurrence of *Holcoptychites* and the gaps are even more pronounced at Pichaihue (Fig. 2). Further discoveries may allow the placing of subzonal boundaries within these sections to be refined.

5. Age of the *Holcoptychites* beds

Gerth's (1925b) placement of his *Holcoptychites neuquensis* Zone in the mid Hauterivian was followed by subsequent workers (e.g. Leanza and Wiedmann, 1980; Riccardi, 1988). However, four lines of evidence suggest that the lower part, the *Holcoptychites*-bearing beds, is older: probably earliest Hauterivian.

1. Aguirre-Urreta and Rawson (1997) noted that the neocomitid ammonites of the immediately preceding '*Neocomites*' sp. Subzone appear close to forms in the upper part of the *Neocomites (Techenites) callidiscus* Zone (=*callidiscus* Subzone of Hoedemaeker et al., 2003) at the top of the French Valanginian, which would suggest that the base of the overlying *Holcoptychites* beds is close to the Valanginian/Hauterivian boundary.

2. The discovery of four fragments of *Oosterella* sp. in and just beneath the lowest *Holcoptychites* beds. Two were figured by Aguirre-Urreta and Rawson (1996), one from just beneath the *Holcoptychites* beds at Arroyo Pichi Neuquén and the other in the lowest bed with *Holcoptychites* at Pichaihue. Two further fragments have been found since, one from the lowest *Holcoptychites* bed (Bed MHo1) at Agua de la Mula, the other from the *Holcoptychites* beds at Cerro Negro. *Oosterella* is best known from the Mediterranean region, where it appears in the Upper Valanginian *Saynoceras verrucosum* Zone and disappears at the base of the Lower Hauterivian *Crioceratites loryi* Zone (Reboulet, 1995, p. 138). This would indicate that the base of the *Holcoptychites* beds could be Valanginian and is certainly no younger than very early Hauterivian.

3. The close similarities noted above between some *Holcoptychites* and the earliest Hauterivian forms of *Spitidiscus*.

4. The fauna of the *Olcostephanus* (*O.*) *laticosta* Subzone, immediately above the *Holcoptychites* beds, can be correlated approximately with the *loryi* Zone of the Mediterranean Province (Aguirre-Urreta and Rawson, 2002).

Hence the 'best fit' interpretation is that the *Holcoptychites* beds are of earliest Hauterivian age (approximately equivalent to the *Acanthodiscus radiatus* Zone of the Mediterranean region). Their base is taken to mark the base of the Hauterivian, as suggested by Aguirre-Urreta and Rawson (1996). However, it should be stressed that the underlying neocomitid faunas await revision, and that the evidence outlined above does not preclude the possibility that the lowest part of the *Holcoptychites* beds is still of latest Valanginian age. On the other hand, nannofloras indicate that the base of the Hauterivian could lie lower than the *Holcoptychites* beds (Bown and Concheyro, in press).

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Appendix A.

Succession in Pichaihue valley (*Loc.10*)

(top)

Holcoptychites neuquensis Zone

Olcostephanus (*O.*) *laticosta* Subzone (pars)

PO1	Dark grey silty shales with scattered nodules at 0.9 m above base containing *Olcostephanus* (*O.*) *laticosta*.	4.5 m

(the complete succession in the *laticosta* Subzone is detailed in Aguirre-Urreta and Rawson, 2002, p. 765).

Succession in Pichaihue valley (*Loc.10*) (continued)

Holcoptychites agrioensis Subzone

PHo26	Siltstone, hard and rusty below with very sparse oysters, nautiloids (*Cymatoceras perstriatum*) and *H. agrioensis*, passing up into a softer, crumbly-weathering siltstone with poorly preserved small bivalves (including *Eriphyla* sp.) and fragments of straight burrows.	0.7 m
PHo25	Dark grey silty shales with very thin (5–10 cm), intermittently developed shelly siltstone at 8.6 m above base.	12.4 m
PHo24	Thick silty coquina/very shelly siltstone: oyster debris, *Entolium* sp. (common), *Ptychomya* sp., *Panopea* sp., fragment of *H. agrioensis*.	0.8 m
PHo23	Greenish grey, very silty shales with a thin, irregularly developed oyster coquina at 1.7 m above base. One *H. agrioensis*.	4.0 m
PHo22	Hard, pale brown, rubbly-weathering, very fine sandstone. Scattered oyster fragments.	0.7 m
PHo21	Greenish, very silty shale.	2.6 m
PHo20	Fine to very fine sandstones and interbedded siltstones forming a distinctive high ridge both sides of the stream. The lower half includes three irregular courses of sandstone, weathering a reddish purple; the lower and middle courses are laminated, and with some low angle planar cross-bedding, while the top course is more massively bedded. The upper half is more silty; an oyster-rich, hard siltstone occurs just below the top bed, the latter being a hard, pale brown fine sandstone with *Cucullaea* sp., *Myophorella* sp., scattered oyster debris, etc.	11.0 m
PHo19	Very silty, grey-green shales, grading up into shaly siltstones.	3.7 m
PHo18	Very fine sandstones, siltstones and silty shales, with a broken oyster coquina 2–2.9 m below top. One crushed *H. agrioensis* at base.	8.0 m
PHo17	Grey silty shales, weathering greenish grey, with scattered flattish nodules to *ca*. 8 cm length. Becoming more silty towards top. One *H. agrioensis* (CPBA 19817).	8.0 m

Succession in Pichaihue valley (*Loc.10*) (continued)

Holcoptychites neuquensis Subzone

PHo16	Thick rib of siltstone and fine sandstone. Lower part has reddish-weathering harder patches. The siltstones above are softer, crumbly-weathering, with numerous *Cucullaea* sp.	4.5 m
PHo15	Grey shales, weathering greenish grey. Scattered small nodules, and a nodule band at 27.5 m.	46.6 m
PHo14	Silty, oyster-debris coquina. *Cucullaea* sp. occurs; *Ptychomya* sp., *Eriphyla* sp., *H. neuquensis* (CPBA 19814.1-2), *H. magdalenae* (CPBA 20008.1-2) and nautiloids (*Cymatoceras perstriatum*) common.	0.35 m
PHo13	Greenish grey silty shales with scattered nodules, especially in top third (from 17.1–26.4 m above base). The shales are partly covered, but there appear to be four thin, harder beds: Ho13d (21.9 m above base). Medium sized (to 20 cm), rusty-weathering concretions and smaller nodules. *H. magdalenae* (CPBA 19819.1-3). Between Ho13c and Ho13d *H. magdalenae* (CPBA 19820.1-3, 19821.1-9) is common in nodules. Ho13c (17 m above base). Shelly (oyster debris) siltstone with scattered *Ptychomya* sp. and very small nodules. (0.15 m thick). Ho13b (11.9 m above base). Siltstone, in parts hard and thinly bedded, with scattered, rusty-weathering hard concretions. (0.3 m thick). Ho13a (10.5 m above base). Very thin (2–3 cm) hard, platy siltstone.	26.4 m
PHo12	Thinly bedded, yellowish siltstone with harder, well-cemented, rusty-weathering concretions. Scattered *H. magdalenae* on upper surface.	0.2 m
PHo11	Greenish-weathering silty shales with four thin, harder shelly (oyster debris) siltstone bands 3.4, 4.6, 6.5 and 7.4 m above base.	10.2 m

Succession in Pichaihue valley (*Loc.10*) (continued)

PHo10	Creamish yellow, thinly bedded siltstone, irregularly cemented to form rusty brown, harder concretions with scattered oyster debris, passing up into softer, crumbly-weathering oyster-debris coquina with scattered *Cucullaea* sp. and *Pholadomya* sp.	0.6 m
PHo9	Grey-green, silty shales, becoming slightly more silty upward. Nodules in upper part with common *H. magdalenae* (CPBA 19822, 19823).	8.2 m
PHo8	Very thinly bedded, almost laminated, fine sandstones in two courses, the lower 1.1 m thick and the upper 0.4 m thick, separated by shaly silts (0.6 m).	2.1 m
PHo7	Greenish, silty shales, becoming paler and more silty upward.	6.8 m
PHo6	Thin, silty, oyster-debris coquina.	0.3 m
PHo5	Silty shales, greenish and very silty from base to 3.3 m, then dark grey and greenish to top.	16.9 m
PHo4	Dark grey shales with three thin shelly siltstone/silty coquina horizons: at base (0.15 m thick), middle (0.25 m) and top (0.1 m). Oyster debris in all three, *Cucullaea* sp. and *Ptychomya* sp. in middle bed.	2.1 m
PH03	Dark grey shales, some nodules.	1.6 m
PHo2	Hard, rusty weathering calcareous siltstone. Scattered oyster fragments.	0.3 m
PHo1	Dark grey, occasionally almost black, silty shales with shaly siltstone streaks. Rare small, scattered nodules and, in upper half, rare reddish brown siltstone lenticles. A more continuous bed of widely spaced, reddish brown siltstone lenticles at 54.5 m above base, with scattered nodules above. (Partly covered in middle third). One *H.* cf. *recopei* (CPBA 19824) at 7.7 m above base.	67.8 m

Pseudofavrella angulatiformis Zone

'*Neocomites*' sp. Subzone

	Black shales with three brightly coloured calcareous siltstones that together form a good marker, showing as distinctive streaks on the slopes, as follows:	8.4 m
	Cream-coloured, crumbly-weathering calcareous siltstone.	1.2 m
	Black shales.	1.5 m

Succession in Pichaihue valley (*Loc.10*) (continued)

	Cream and orange, crumbly-weathering calcareous siltstone.	1.2 m
	Black shales with band of small, rather flat, silty calcareous nodules 3.5 m above base.	4.2 m
	Orange-brown-weathering, thin, hard calcareous siltstone.	0.3 m
	Many metres of black shales, with flattened '*Neocomites*' sp. at several levels. Near top are occasional large (to 0.5 m) flattened, smooth, involute neocomitids.	

(base)

Succession in Agua de la Mula (*Loc.12*)

(top)

Holcoptychites neuquensis Zone

Olcostephanus (*O.*) *laticosta* Subzone (pars)

MO1	Thin, shelly, calcareous siltstone with *Olcostephanus* (*O.*) *laticosta*.	0.20–0.25 m

Holcoptychites agrioensis Subzone

MHo 47	Bluish grey shales, weathering greenish grey.	3.5 m
MHo 46	Hard, rusty-weathering, calcareous, very fine sandstone with abundant *H. agrioensis* (CPBA 19983).	0.3 m
MHo 45	Pale, soft siltstones with common *Cucullaea*.	3.5 m
MHo 44	Pale siltstone, becoming harder and more shelly/reddish towards top. *H. agrioensis*.	0.4 m
MHo 43	Dark grey silty shales with very scattered nodules.	8.0 m
MHo 42	Pale siltstone, with harder, rusty-weathering patches, the latter with oyster debris, *H. agrioensis*, *Steinmanella*, *Cucullaea*.	1.4 m
MHo 41	Greenish-weathering, dark grey silty shales with occasional more silty streaks, the most prominent being 4.2 m above base and about 0.06 m thick.	5.6 m
MHo 40	Rusty-brown weathering, very shelly siltstone; in places almost a coquina. Occasional *Cucullaea*, much oyster debris.	2.0 m
MHo 39	Silty shale.	0.7 m
MHo 38	Rusty-brown weathering, hard shelly siltstone: *Cucullaea*, *Entolium*, *Myoconcha*, oyster debris. (MHo38 and MHo40 form a distinctive double hard band)	2.0 m
MHo 37	Pale siltstone.	0.6 m
MHo 36	Grey-green weathering silty shale with thin silty streaks.	4.0 m

Succession in Agua de la Mula (*Loc.12*) (continued)

MHo 35	Hard siltstone with very finely scattered oyster debris and *H. agrioensis*.	0.7 m
MHo 34	Medium grey shale.	0.9 m
MHo 33	Hard siltstone with very finely scattered oyster debris.	0.4 m
MHo 32	Four thin courses of fine-grained, shelly (very finely comminuted material), calcareous sandstone with softer silts between.	1.4 m
MHo 31	Siltstones and silty shales (mainly covered). Thin harder beds at 2.5, 4.2 and 5.2 m above base. From 5.9 m above base is nearly all harder siltstone.	11.3 m
MHo 30	Pale cream, fine-grained sandstone, with a harder, pale purple, central rib, *ca*. 20 cm thick, at 0.8–2.0 m above base. The top 0.15 m is again purple-weathering. The whole bed forms a distinctive pale streak and the central purple band sometimes forms a large rib.	2.8 m
MHo 29	Greenish-grey, silty shales (mainly covered). Scattered nodules at 4.6 m above base.	14.7 m
MHo 28	Silty coquina and very shelly siltstone. *Entolium*, *Myoconcha*, *Cucullaea*, oyster debris.	0.6 m
MHo 27	Medium grey-green, very silty shales.	8.6 m
MHo 26	Very hard, very calcareous, shelly (broken oysters) fine sandstone.	0.3 m
MHo 25	Yellow-green weathering, greyish silty shales, grading up into yellowish silty shales, then at about 5.6 m above base into soft siltstones, grading at about 7.5 m above base into a fine sandstone.	10.8 m
MHo 24	Shelly siltstone with *Entolium*, *Cucullaea*, *Steinmanella*: harder and red-weathering in lower part, softer above. *H. agrioensis* (CPBA 20009.1).	2.2 m

Holcoptychites neuquensis Subzone

MHo 23	Grey shales, becoming more silty in top third and forming a soft crumbly siltstone in top 2.9 m. At 8.5 m above base is a thin (0.07 m) siltstone with shell debris and at 11.3 m above base is a band of scattered large (to *ca*. 12 cm) nodules.	31.4 m

Succession in Agua de la Mula (*Loc.12*) (continued)

MHo 22	Broken oyster coquina with reddish harder patches, especially on upper surface. A poorly preserved *H. neuquensis* (CPBA 19984) on top surface; *H. magdalenae* (CPBA 19985) loose from the coquina.	1.0 m
MHo 21	Greenish-weathering, grey-black shales. Occasional small nodules in a a slightly more silty bed at 1.9 m above base; thin (0.1 m) harder rib of shelly siltstone 2.2 m above base; band of scattered nodules 2.6 m above base.	10.8 m
MHo 20	Thin hard siltstone with oyster debris and *Ptychomya*.	0.1 m
MHo 19	Greenish-weathering, grey-black shales; scattered nodules in lower part, with rare *H. magdalenae* (CPBA 19986.1-2)	1.2 m
MHo 18	Shaly silts with three harder levels, each with occasional small reddish patches, top level with many *Ptychomya* and oyster debris.	0.9 m
MHo 17	Thin siltstone, partially cemented to form reddish, harder irregular concretions. Numerous *H. magdalenae*, some large (CPBA 19987.1-2. 19988.1-2, 19989.1-2), scattered shell debris.	0.2 m
MHo 16	Shales and silty shales (partly covered), sometimes reddish-weathering. Intermittently developed harder, thin siltstone 1.1 m above base; thin (0.1 m) shaly siltstone with scattered large (to 15 cm) nodules 1.8 m above base; band of oval nodules (15 cm long) at 8.5 m above base, with *H. magdalenae* (CPBA 19990.1-3).	10.0 m
MHo 15	Siltstone, harder and rusty-weathering in places. Very scattered shell debris, *Entolium* and *Pinna*.	0.4 m
MHo 14	Silty shales.	2.1 m
MHo 13	Siltstone, harder and rusty-weathering in places. Very scattered shell debris.	0.3 m
MHo 12	Silty shales and shaly silts. Scattered nodules up to 10 cm long at 4.1, 4.6, 5.4 and 5.8 m above base.	7.2 m
MHo 11	Reddish-weathering shelly siltstone, with oyster debris and numerous *Entolium*. Loose *H. magdalenae*.	0.3 m

Succession in Agua de la Mula (*Loc.12*) (continued)

MHo 10	Greenish-weathering dark shales. Scattered nodules from 3.9–6.4 m above base, with a distinct bed of widely spaced ones at 5.7 m above base. *H. magdalenae* (CPBA 19991.1-7).	7.0 m
MHo 9	Reddish-weathering, shelly (oyster debris) siltstone.	0.3 m
MHo 8	Greenish-weathering, dark grey shales, very silty in lowest metre, and with more silty streaks from 4.3 m above base. Numerous *Cucullaea* at 5.7 m. Band of potato nodules at 10.5 m above base with *Holcoptychites* sp. nov. (CPBA 19992.1-2, 19994).	10.9 m
MHo 7	Siltstone, with very occasional harder, more rusty patches. Very few fossils.	0.6 m
MHo 6	Greenish-weathering, fairly dark grey shales. Bed of scattered nodules at 2.5 m above base, and a bed of very scattered nodules at 3.9 m above base.	6.5 m
MHo 5	Thin siltstone, sometimes cemented to form irregular reddish masses with very scattered shell debris.	0.3 m
MHo 4	Silty shales.	2.1 m
MHo 3	Hard, reddish-weathering siltstone with scattered bivalves including *Cucullaea* and *Entolium*, oyster debris, nautiloids and some serpulids.	0.3 m
MHo2	Greenish-weathering, dark grey shales with scattered nodules containing *Holcoptychites* sp. nov. (CPBA 20006), and some thin, hard siltstones; top 2 m very silty.	13.8 m
MHo 1	Yellowish-weathering clean siltstone forming a hard band, becoming rusty coloured and slightly shelly at top. *Holcoptychites* sp., *Oosterella* sp.	1.3 m

Pseudofavrella angulatiformis Zone

'*Neocomites*' sp. Subzone

	Greenish-yellow weathering silty shales in lowest 2 m, passing up into greenish-weathering, dark grey shales. At 17 m from the base, a level with small nodules with '*Neocomites*' sp.	27.8 m
	Rusty-weathering siltstone with very scattered oyster debris.	0.7 m
	Hard, blocky-weathering, very silty shales.	1.2 m

Succession in Agua de la Mula (*Loc.12*) (continued)

Very shelly, rusty-weathering siltstone. Broken oysters, scattered *Aetostreon*, *Ptychomya*, serpulid tubes.	0.7 m
Greenish brown silty shales with scattered *Aetostreon* and thin broken oyster siltstone.	4.2 m
Coquina with rare '*Neocomites*' sp.	

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