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Lower Cretaceous ammonites from the Neuquén Basin, Argentina: a Hauterivian *Olcostephanus* fauna

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The olcostephanid fauna of the *Olcostephanus* (*O.*) *laticosta* [formerly *O.* (*O.*) *leanzai*] Subzone (Agrio Formation) represents the last of four discrete invasions of olcostephanid ammonites into the Neuquén Basin of west-central Argentina. *Olcostephanus* (*O.*) *laticosta* (Gerth) dominates the fauna and is known only from the Neuquén Basin. But the co-occurrence of the distinctive subgenus *Jeannoticeras*, newly recorded from Argentina, provides a link with the 'standard' West Mediterranean sequence and indicates that the *O.* (*O.*) *laticosta* Subzone is probably of mid Early Hauterivian age. This is supported by the discovery of two specimens of the widely distributed late Early Hauterivian species *O.* (*O.*) *variegatus* (Paquier) in the overlying *Hoplitocrioceras giovinei* Subzone. *O.* (*Jeannoticeras*) *agrioensis* sp. nov. is described.

KEY WORDS: Argentina; Neuquén Basin; ammonites; Olcostephanidae; biostratigraphy; Lower Cretaceous; Lower Hauterivian.

1. Introduction

Olcostephanus is a widely-distributed ammonite genus of Early Valanginian to Early Hauterivian age. Essentially of Tethyan distribution, it spread to marginal areas of the Boreal Realm at times (Kemper *et al.*, 1981) and also invaded several peri-Gondwanan basins. In the Neuquén Basin of west-central Argentina there are four discrete levels with *Olcostephanus* in the Vaca Muerta and Agrio formations, representing four separate olcostephanid invasions alternating with neocomitids or holcodiscids (Aguirre-Urreta & Rawson, 1999). The penultimate invasion occurred in Late Valanginian times, when the fauna was dominated by very evolute *Olcostephanus* assigned to a new subgenus, *Viluceras*; *O.* (*O.*) *mingrammi* Leanza formed a minor element of this fauna. The last invasion was some three million years later, when *Olcostephanus* (*O.*) *laticosta* (Gerth) replaced the endemic genus *Holcoptychites* (Holcodiscidae) to occupy the basin for a short interval before in turn it was replaced by another endemic form, *Hoplitocrioceras* (Neocomitidae). Two examples of *O.* (*O.*) *variegatus* (Paquier) are recorded from the *Hoplitocrioceras* beds.

Only three specimens of the *O.* (*O.*) *laticosta* fauna have ever been figured, assigned to two 'species' [*O.* (*O.*) *laticosta* and *O.* (*O.*) *leanzai*] whose morphological and stratigraphical inter-relationships have not been appreciated previously. Based on newly collected material, this paper shows that the two forms are variants of a single species, describes *O.* (*O.*) *laticosta* and some previously unknown associated species, and then considers the importance of the fauna to correlation with the 'standard' West Mediterranean sequences.

2. Lithostratigraphy and fossil localities

The Agrio Formation occurs over extensive areas of Neuquén and southern Mendoza provinces. It consists of up to 1500 m of shales and silty shales with thin limestone (often coquinal), siltstone and sandstone interbeds, though much of the sequence thins and becomes more calcareous northwards. In the middle of the formation a thin non-marine sandstone, the Avilé Member, divides the remainder of the formation into Lower and Upper members. The beds with *O.* (*O.*) *laticosta* occur in the upper part of the

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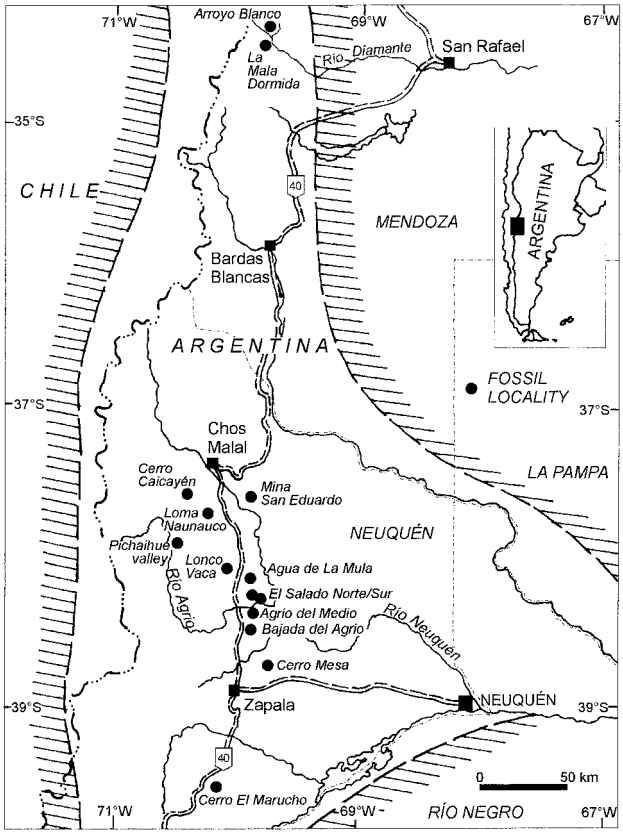


Figure 1. Map showing localities for the *Olcostephanus* (*O.*) *laticosta* fauna in the Neuquén Basin. The shaded area indicates the approximate boundaries of the basin. The western margin was formed by an island arc.

Lower Member. The fauna is widely distributed across the basin and we have collected it from 14 localities (Figure 1). It is generally represented by large, often fragmentary and abraded specimens whose morphological features are difficult to characterise. Representative samples have been collected. But at four localities (Loma Naunauco, Agua de La Mula, El Salado Sur and Agrio del Medio) we have found better preserved material, including the previously unknown inner whorls of *O.* (*O.*) *laticosta*. From the last three localities, and also from Pichaihue valley, we have collected from several different beds (detailed below). In the following account of localities, the first two are in Mendoza Province and the remainder in Neuquén. The Mendoza localities are very difficult to access, and are best reached by mule (or helicopter!).

2.1. *Arroyo Blanco*

This is the type locality of *O.* (*O.*) *laticosta* (Gerth, 1925, p. 121), on the northern bank of the Río Diamante, 2 km north-west of the mouth of the Arroyo Blanco. According to Gerth, the unique specimen was found in bluish-grey limestones, below the beds with '*Exogyra*'. One of us (MBA-U) has visited the locality to check the exact stratigraphical position of the species. In this area the '*Exogyra*' beds are composed of several beds with different concentrations of oysters. The lowermost levels are packed with large (100–120 mm) *Aetostreon* (formerly *Exogyra*); above are beds packed with smaller (40–50 mm) *Aetostreon*, whereas the upper levels have only isolated oysters in a calcareous matrix. This sequence of *Aetostreon* beds forms the lowermost outcrops of the northern bank of the Río Diamante. The bluish-grey limestones are *above* these beds and a loose, poorly preserved *O. laticosta* was collected from this horizon.

2.2. *La Mala Dormida*

This is another of Gerth's (1925) Mendoza localities. It lies some 10 km *north* of Paso El Perdido, not south of the pass as indicated on Gerth's map. The section was visited by MBA-U; four well-preserved (CPBA 19236.1–2, 19237.1–2) and two poorly preserved (CPBA 19241.1–2) *O.* (*O.*) *laticosta* were found above *Holcoptychites compressum* and below *Hoplitocrioceras* sp.

2.3. *Cerro Caicayén*

Close to Puesto Contreras, 8 km south of the Río Neuquén, on the road from Chos Malal to the Oscar mine. One fragmentary *O.* (*O.*) *laticosta* (CPBA 18143) came from shales exposed on the eastern bank of the Arroyo Rahueco.

2.4. *Mina San Eduardo*

This well-exposed section is adjacent to the abandoned San Eduardo mine, just west of secondary road 9, and 7 km west-south-west of Curacó. Inner whorls of *O.* (*O.*) *laticosta* have been collected from small ferruginous nodules in dark shales (CPBA 19239, 19240) and large specimens from overlying coquinas (CPBA 16272.1–2).

2.5. *Loma Naunauco*

The unpaved road 4 skirts the northern end of the Naunauco anticline, about 5 km west of the junction with national road 40 at Naunauco. The Lower Agrio Member is well exposed on the western flanks of the anticline to the south of the road. *O.* (*O.*) *laticosta* (CPBA 19242, 19243.1–3) was collected from a

sequence of silty shales and coquinas which lies immediately above a coquina-capped sandstone ridge that contains large *Holcoptychites compressum*.

2.6. *Pichaihue valley*

The Arroyo Pichaihue cuts a valley west of the Sierra de Chorriaca to provide extensive clear exposures of the Agrio Formation. Access is difficult; from unpaved road 4 about 12 km east of Colipilli, immediately west of a bridge crossing the Arroyo Colipilli, there is a very rough track running south-eastward to two puestos (farms) about 9 km from the road. The *Olcostephanus* beds are well exposed west of the river 1.5 km south of the more southerly puesto and about 2 km SE of Cerro León. The succession is:

(top)
Hoplitocrioceras giovinei Subzone (*pars*)

PH1	Grey, silty shales, very scattered small nodules, mainly in upper part. One large, flattened *Hoplitocrioceras* 1.2 m above base.	10.1 m

Holcoptychites neuquensis Zone
Olcostephanus (*O.*) *laticosta* Subzone

PO4	Distinctive 'triple' bed: grey silty shales with three thin siltstone/coquina horizons, of which the middle one (PO4c) is the thickest and most prominent:	
	e, broken oyster coquina, scattered *Cucullaea*.	0.2 m
	d, grey silty shales.	1.4 m
	c, broken oyster coquina; common *Olcostephanus* (*O.*) *laticosta* (CPBA 19270).	0.4 m
	b, grey silty shales. *O.* (*O.*) *laticosta* (CPBA 19269).	0.8 m
	a, thin, shelly siltstone. Oyster debris, scattered *Cucullaea*. *O.* (*O.*) *laticosta* (CPBA 19268)	0.2 m
PO3	Dark grey shales.	5.0 m
PO2	Brownish-white, crumbly-weathering, shelly siltstone with harder, brown-weathering, well-cemented lenticles.	0.2 m
PO1	Dark grey silty shales. *O.* (*O.*) *laticosta* (CPBA 19267) in scattered nodules 0.9 m above base and in lenticles and streaks of shelly siltstone at 3.1 m above base.	4.5 m

Holcoptychites compressum Subzone (*pars*)

Ho26	Siltstone, hard and rusty below with very sparse oysters, nautiloids and *Holcoptychites compressum*, passing up into a softer, crumbly-weathering siltstone with poorly preserved small bivalves (including *Eriphyla*) and fragments of straight burrows.	0.7 m

2.7. *Lonco Vaca*

Adjacent to the Puesto Casa Nuestra, close to national road 40, 60 km south of Chos Malal. *O.* (*O.*) *laticosta* is represented by a few poorly preserved specimens (e.g. CPBA 19238.1–2) preserved in dark grey to greenish silty shales.

2.8. *Agua de La Mula*

On the western flank of the Cordillera del Salado, 80 km south of Chos Malal; access is from national road 40 along a gravel road leading to a dry oil well. The whole of the Lower Agrio Member has been measured here (see summary log, with a detailed section of the *Hoplitocrioceras* beds, in Aguirre-Urreta & Rawson, 2001). This is a key section for the *O.* (*O.*) *laticosta* beds (Figure 2):

(top)
Hoplitocrioceras giovinei Subzone (*pars*)

MH1	Hard, pale rusty-brown siltstone with large bivalves (often internal moulds) on top surface; *Cucullaea*, oysters etc. *Hoplitocrioceras giovinei*.	0.25 m

Holcoptychites neuquensis Zone
Olcostephanus (*O.*) *laticosta* Subzone

MO10	Grey, silty shales with scattered lenses of shelly calcareous siltstones, and small nodules in lower part. *O.* (*O.*) *laticosta* (CPBA 19230.1–4, 19231.1–6, 19232.1–3, 19233), *O.* (*Jeannoticeras*) *agrioensis* (CPBA 19271.1–2),	10.2 m

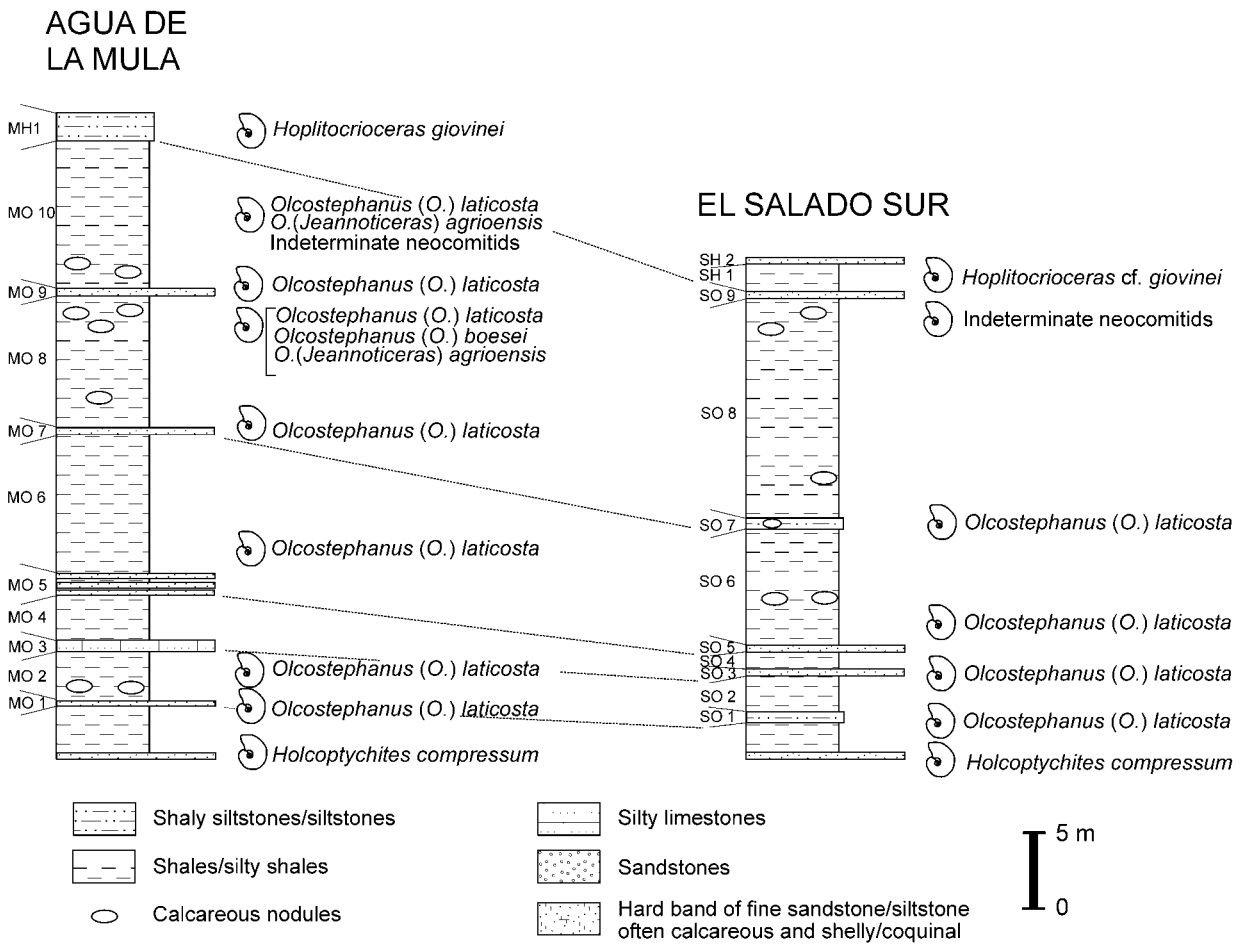


Figure 2. The Agua de La Mula and El Salado Sur sections and their correlation.

	neocomitid fragments (CPBA 18392, 18393, 19279.1–2) and *Cucullaea*.	
MO9	Grey, calcareous siltstone, weathering brown. Small shells and shell fragments, some serpulids (*Rotularia*). *O.* (*O.*) *laticosta* (CPBA 19229).	0.2 m
MO8	Blue-grey silty shales, weathering greenish. Numerous small nodules in top 2.9 m, with *O.* (*O.*) *laticosta* (CPBA 19226.1–3, 19227.1–8, 19228.1–19), *O.* (*O.*) *boesei* (CPBA 19251), *O.* (*Jeannoticeras*) *agrioensis* (CPBA 19252, 19254.1–4, 19255.1–3, 19272.1–2) and crustaceans. Scattered nodules towards base.	9.1 m
MO7	Thin, shelly (locally coquinal), rusty-weathering, very calcareous siltstone. *Cucullaea* common, oyster fragments and scattered *O.* (*O.*) *laticosta*.	0.1 m
MO6	Dark grey-green silty shales. A more silty rib at 0.6–0.8 m. At 1.7 m is a 6–8-cm silty layer, in part an oyster coquina, with scattered *O.* (*O.*) *laticosta* and *O.* (*J.*) *agrioensis* (CPBA 19253).	9.5 m
MO5	Distinctive 'triple' bed: three hard bands separated by two softer ones.	1.1 m
	e, fairly hard, slightly nodular, grey, very silty limestone, weathering brown.	0.2 m
	d, thin siltstone, forming slight cleft.	0.1 m

	c, fairly hard, slightly nodular, grey, very silty limestone, weathering brown.	0.15 m
	b, thin siltstone, forming slight cleft.	0.15 m
	a, hard, grey, very silty limestone, weathering brown. Scattered oyster debris. Bed MO5a is the hardest bed and in places forms a pavement.	0.50 m
MO4	Greenish-grey, silty shales and shaly silts, weathering greenish. Thin streaks of oyster coquina in top part.	3.8 m
MO3	Rusty-weathering, grey, very silty limestone. Weathers into small, often angular, blocks, with knobbly-weathering top surface. Very sparsely fossiliferous; scattered oyster fragments and *Entolium*.	0.5 m
MO2	Blue-grey, very silty shales, weathering greenish. At 1.3 m above base is a thin yellowish siltstone bed (0.06–0.1 m) with scattered, reddish-weathering silty calcareous nodules; sometimes forms a slight rib. *O.* (*O.*) *laticosta* (CPBA 19225.1–6) quite common.	3.3 m
MO1	Thin, shelly (mainly oyster fragments), slightly friable, calcareous siltstone. Weathers greenish-yellow, with rusty patches. Sparse *O.* (*O.*) *laticosta* (CPBA 19224.1–4).	0.20–0.25 m

Holcoptychites compressum Subzone (*pars*)

	Bluish-grey shales, weathering greenish-grey.	3.2 m
	Rusty-weathering, grey, very silty limestone, shelly (mainly oyster fragments). Numerous large *Holcoptychites compressum*, some nautiloids.	0.25–0.30 m

2.9. *El Salado Norte*

On the western flank of the Cordillera del Salado, 15 km south of Agua de la Mula, the Agrio Formation is exposed on both sides of a gravelled track leading eastward from national road 40 to the Pampa Amarga oil wells. One specimen (CPBA 19258) of *O.* (*O.*) *laticosta* was collected from a coquina.

2.10. *El Salado Sur*

The Lower Agrio Member is well exposed in a deep gulley system about 2 km south of El Salado Norte. Access is by walking southward from the track at El Salado Norte, starting from the most southerly bend, a hairpin about 3 km from national road 40. One of us (PFR) measured a detailed section through the *O.* (*O.*) *laticosta* beds (below). *Olcostephanus* is less common here than at Agua de La Mula (17 km to the north) but close correlation can be made between the two sections (Figure 2).

The overlying *Hoplitocrioceras* beds (SH1–SH25) were described by Aguirre-Urreta & Rawson (2001), who recorded a single *O.* (*O.*) cf. *variegatus* [CPBA 19256: now identified as *O.* (*O.*) *variegatus*] from bed SH9.

(top) *Hoplitocrioceras giovinei* Subzone (*pars*)

SH1	Grey silty shales. Flattened *H.* cf. *govinei*.	2.0 m

Holcoptychites neuquensis Zone
Olcostephanus (*O.*) *laticosta* Subzone

SO9	Calcareous siltstone with *Cucullaea*, *Pholadomya*, *Ostrea* and oyster debris. Straight burrows project obliquely down from base into top of bed below.	0.4 m
SO8	Grey silty shales. Very thin silty streak with scattered large nodules at 3.7 m. In middle occur large, scattered lenticular oyster debris coquinas up to 2 m thick but vanishing laterally. Scattered nodules in top 1.5 m: one fragment of an indeterminate neocomitid (CPBA 19265) loose at this level.	14.8 m
SO7	Slightly argillaceous siltstone with scattered calcareous concretions. Scattered *Cucullaea* and *Pholadomya*. *O.* (*O.*) *laticosta* (CPBA 19262).	0.25 m
SO6	Grey-black, slightly silty shales. Some thin shelly silt lenses at 3.3 m disappear	8.0 m

	laterally; hard nodules with a silty outer layer occur at the same level. *O.* (*O.*) *laticosta* (CPBA 19261) *c.* 1 m above base.	
SO5	Rubbly-weathering calcareous siltstone in irregular courses. Scattered shell debris, mainly in lower half.	0.4 m
SO4	Dark grey, slightly silty shales.	1.1 m
SO3	Calcareous siltstone with very scattered shell debris. *O.* (*O.*) *laticosta* (CPBA 19260).	0.2 m
SO2	Dark grey, slightly silty shales, more silty in top 0.7–1.2 m. Scattered nodules near top of silty part (2.5 m).	2.7 m
SO1	Thin, shaly, shelly siltstone and oyster-fragment coquina, with harder, more silty concretions. Irregular in lithology and thickness. Internal moulds of burrowing bivalves. *O.* (*O.*) *laticosta* (CPBA 19259.1–2).	0.1–0.2 m
Holcoptychites compressum Subzone (*pars*)		
	Dark grey, slightly silty shales. Very rare nodules in top third.	2.7 m
	Very shelly calcareous siltstone in two courses, with 0.1 m of silty shale between. Oyster fragments, *Cucullaea*. *Holcoptychites compressum* common in upper bed.	0.6 m

2.11. *Agrio del Medio*

The Lower Agrio Member is well exposed on the eastern flank of the Agrio Anticline, immediately west of regional road 10, about 3 km south-west of Agrio del Medio (see map in Aguirre-Urreta *et al.*, 1993, fig. 2). Here the *Olcostephanus* beds are composed of two or three coarsening-upward cycles (silty shales to siltstones/silty coquinas) with *O.* (*O.*) *laticosta* (CPBA 19244.1–3, 19246, 19248) and *O.* (*J.*) *agrioensis* (CPBA 19245, 19247).

2.12. *Bajada del Agrio*

The Agrio Formation forms the hills south of Bajada del Agrio, and is best exposed in the slopes adjacent to unpaved road 10 extending some 5–8 km south-south-west from Bajada del Agrio. *Olcostephanus* (*O.*) *laticosta* occurs in at least two levels in the *laticosta* Subzone (CPBA 19273), while a single *O.* (*O.*) *variegatus* (CPBA 19266) was found loose in the *Hoplitocrioceras giovinei* Subzone.

2.13. *Cerro Mesa*

8 km east of Mariano Moreno and 22 km north-east of Zapala, the Lower Agrio Member is well exposed along an anticline extending from Cerrito Maruco to Cerro Mesa. This is the type locality for *O.* (*O.*) *leanzai* (Giovine). In addition to the lectotype (CPBA 5144) there are two paralectotypes (SEGEMAR 9323, 9327).

2.14. *Cerro El Marucho*

The Lower Agrio member is exposed on a hillside immediately east of national road 40, 70 km south of Zapala. Large, poorly preserved *O.* (*O.*) *laticosta* (CPBA 13971.1–6, 13972, 13973.1–3, 13974.1–4) are common here.

3. Systematic palaeontology

The material described here is stored in the Palaeontological Collections of the University of Buenos Aires (CPBA), the Geological Survey of Argentina (SEGEMAR) and the Institute for Palaeontology, University of Bonn, Germany (IPB).

Dimensions of specimens are indicated as follows: d, diameter; wh, whorl height; wt, whorl thickness; wu, width of umbilicus. In the synonymy lists, v indicates that we have seen the specimen(s), and ⋆ indicates that the type specimen is figured in the cited reference.

Superfamily: Perisphinctaceae Steinmann, 1890
Family: Olcostephanidae Haug, 1910
Subfamily: Olcostephaninae Haug, 1910
Genus *Olcostephanus* Neumayr, 1875

Type species. *Ammonites astierianus* d'Orbigny, 1840, p. 115, by original designation.

Remarks. *Olcostephanus* is a long-ranging genus of Early Valanginian (top *otopeta* Zone) to Early Hauterivian age. On several occasions it suddenly 'bloomed' to form large, widely-distributed populations, a pattern of distribution that supports Cecca's (1998) suggestion that *Olcostephanus* may have been an opportunistic genus. Several important faunas

have been monographed, especially from Europe, Madagascar, Pakistan and South Africa. Over 130 species names have been proposed, despite the rather limited range of variation that the genus exhibits (especially in the subgenus *Olcostephanus s.s.*). This reflects both the extensive 'splitting' that *Olcostephanus* has been subjected to in some monographs (e.g. Spath, 1939), and the wide distribution of the genus, which has inevitably led to several regional names being proposed for some of the more widely dispersed species. When enough material is studied from one horizon, the range of variation in a single species can be assessed, and may be almost as great as that exhibited by the genus. But away from Europe the spatial and temporal variation in some of the most important faunas is impossible to ascertain as their stratigraphy is poorly known [e.g., Collignon's (1962) Madagascan and Cooper's (1981) South African faunas]. Without firm stratigraphical control it can be equally dangerous to 'lump' into synonymy superficially similar taxa from widely differing areas that may prove to be of significantly different ages.

Several *Olcostephanus* species have been named from the Neuquén Basin, some of which may be endemic to the region. This is the only area outside Europe where a succession of *Olcostephanus* faunas is well established (Aguirre-Urreta & Rawson, 1999), and where variation within successive faunas can therefore be studied. Riccardi *et al.* (1971) and Aguirre-Urreta & Rawson (1999) illustrated variation in the latest Early Valanginian *O.* (*O.*) *atherstoni* (Sharpe) and Late Valanginian *O.* (*Viluceras*) *permolestus* (Leanza) faunas respectively, while in this paper we demonstrate variation within *O.* (*O.*) *laticosta*.

Our synonymy lists refer to material previously figured from Neuquén, or to the first description of a species that was named from elsewhere. For the reasons indicated above, we do not list possible synonyms from other parts of the world, with the exception of some Colombian ammonites. However, we do indicate some possible links with other regions in our discussion of individual species and in the section on correlation below.

Subgenus *Olcostephanus* Neumayr, 1975

Olcostephanus (*Olcostephanus*) *laticosta* (Gerth)
Figures 3a–i, 4j–l, 6a–d

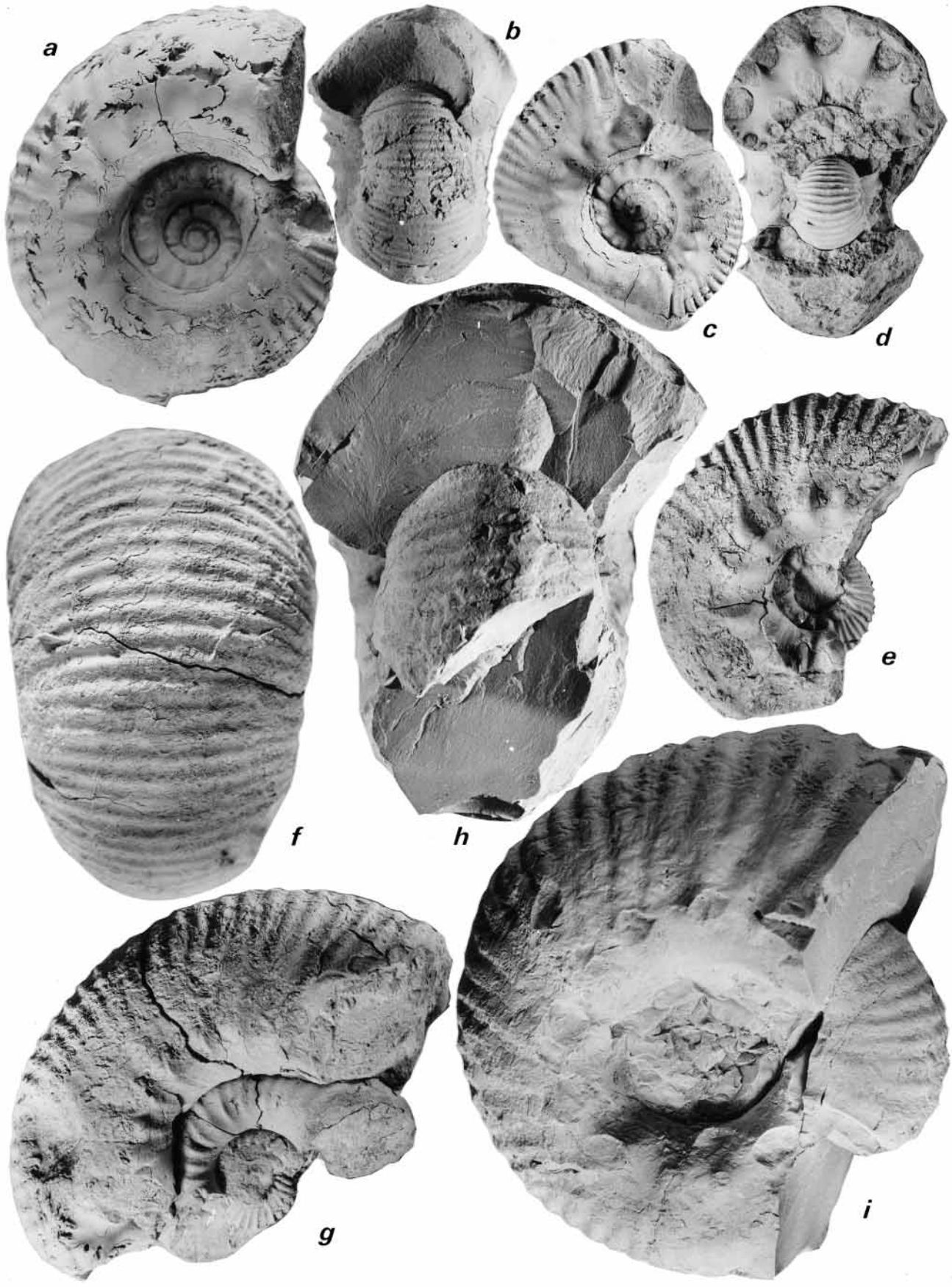
v *1925 *Astieria laticosta* Gerth, p. 62, pl. 2, fig. 8, 8a [refigured by Cooper, 1981, p. 204, fig. 47 only, as *O.* (*O.*) *bossingaulti* (d'Orbigny)].
? 1931 *Astieria laticosta* Gerth; Weaver, p. 426.
v 1950 *Holcostephanus leanzai* Giovine, p. 38, pl. 2, figs 1–3 (refigured by Cooper, 1981, p. 236, fig. 82).
v 1997 *Olcostephanus* (*O.*) *leanzai* (Giovine); Aguirre-Urreta & Rawson, fig. 6j.

Holotype. By monotypy, IPB, Gerth collection (cast: CPBA 19264), the specimen figured by Gerth (1925, pl. 2, fig. 8, 8a) from the north bank of the Río Diamante (southern Mendoza), close to the confluence with the Arroyo Blanco.

Other material. 105 specimens: 6 from La Mala Domida (CPBA 19236.1–2, 19237.1–2, 19241.1–2), 1 from Cerro Caicayén (CPBA 18143), 4 from Mina San Eduardo (16272.1–2, 19239, 19240), 4 from Loma de Naunauco (CPBA 19242, 19243.1–3), 4 from Pichaihue valley (CPBA 19267–19270), 2 from Lonco Vaca (CPBA 19238.1–2), 55 from Agua de La Mula (CPBA 19224.1–4, 19225.1–6, 19226.1–3, 19227.1–8, 19228.1–19, 19229, 19230.1–4, 19231.1–6, 19232.1–3, 19233), 1 from El Salado Norte (CPBA 19258), 5 from El Salado Sur (CPBA 19259.1–2, 19260–19262), 5 from Agrio del Medio (CPBA 19244.1–3, 19246, 19248), 1 from Bajada del Agrio (CPBA 19273), 3 from Cerro Mesa (CPBA 5144, SEGEMAR 9323, 9327) and 14 from Cerro El Marucho (CPBA 13971.1–6, 13972, 13973.1–3, 13974.1–4).

Description. Large, some specimens septate to at least 160 mm diameter; body chamber occupies at least half a whorl, so the maximum diameter must reach over 200 mm. Shell inflated to cadicone, slightly involute (wu *c.* 30% of diameter), with deep, funnel-shaped umbilicus. Whorl section subcoronate to coronate, sometimes slightly arched (Figure 6a, b). Maximum width of whorl at umbilical tubercle. Feeble primary ribs arise on the outer part of the sloping umbilical whorl, swelling into moderate to strong, slightly radially elongated tubercles (i.e., bullae) on the umbilical margin. The bullae often appear as rounded tubercles on internal moulds. They vary in number from about 13 to 19 per whorl at 50–90 mm diameter; the less frequent they are, the more widely spaced and stronger they become. Bundles of 2–5 (normally 2–3) secondary ribs are associated with each bulla. At least two secondaries branch from each bulla, but an additional one or more may branch or be intercalated higher on the whorl; in specimens where this is common there is a distinct 'polyptychitine' appearance to the rib pattern.

Constrictions occur in the innermost whorls, up to six per whorl initially, but they die out by about


a
b
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d
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i

40 mm diameter. They are narrow, shallow, and only slightly oblique to the ribbing.

Dimorphism is not apparent. Some specimens show a body chamber appearing by 60–70 mm diameter, but there is no evidence of septal approximation or of retraction of the umbilical seam.

The suture (Figure 6c, d) is typically olcostephanid, with long, narrow, deeply subdivided saddles.

Dimensions of figured specimens (in mm)

Specimen	d	wh	wh%d	wt	wt%d	wh/wt	wu	wu%d
IPB Gerth collection (holotype)	106.3	48	0.45	78*	0.73	0.61	29	0.27
CPBA 13971.1	145	53	0.36	84	0.58	0.63	53	0.36
CPBA 5144 (lectotype of *O. leanzai*)	143	68	0.47	80*	0.56	0.85	52	0.36
CPBA 19225.1	110	49	0.44	65.5	0.59	0.75	22.7	0.21
CPBA 19224.2	93.4	36.9	0.39	62.2	0.66	0.59	33.8	0.36
CPBA 19249.1	88.8	31.8	0.36	65	0.73	0.49	27.8	0.31
CPBA 19226.1	74.4	30.2	0.40	58.4	0.78	0.52	22.4	0.30
CPBA 19248	73.2	28.1	0.38	63	0.86	0.45	24.8	0.34
CPBA 19227.2	60	23.9	0.40	43.2	0.72	0.55	21.2	0.35
CPBA 19242	51.1	19.1	0.37	32.9	0.64	0.58	16.9	0.33
CPBA 19227.1	48.6	20.5	0.42	35.7	0.73	0.57	17.2	0.35

*approximate measurement

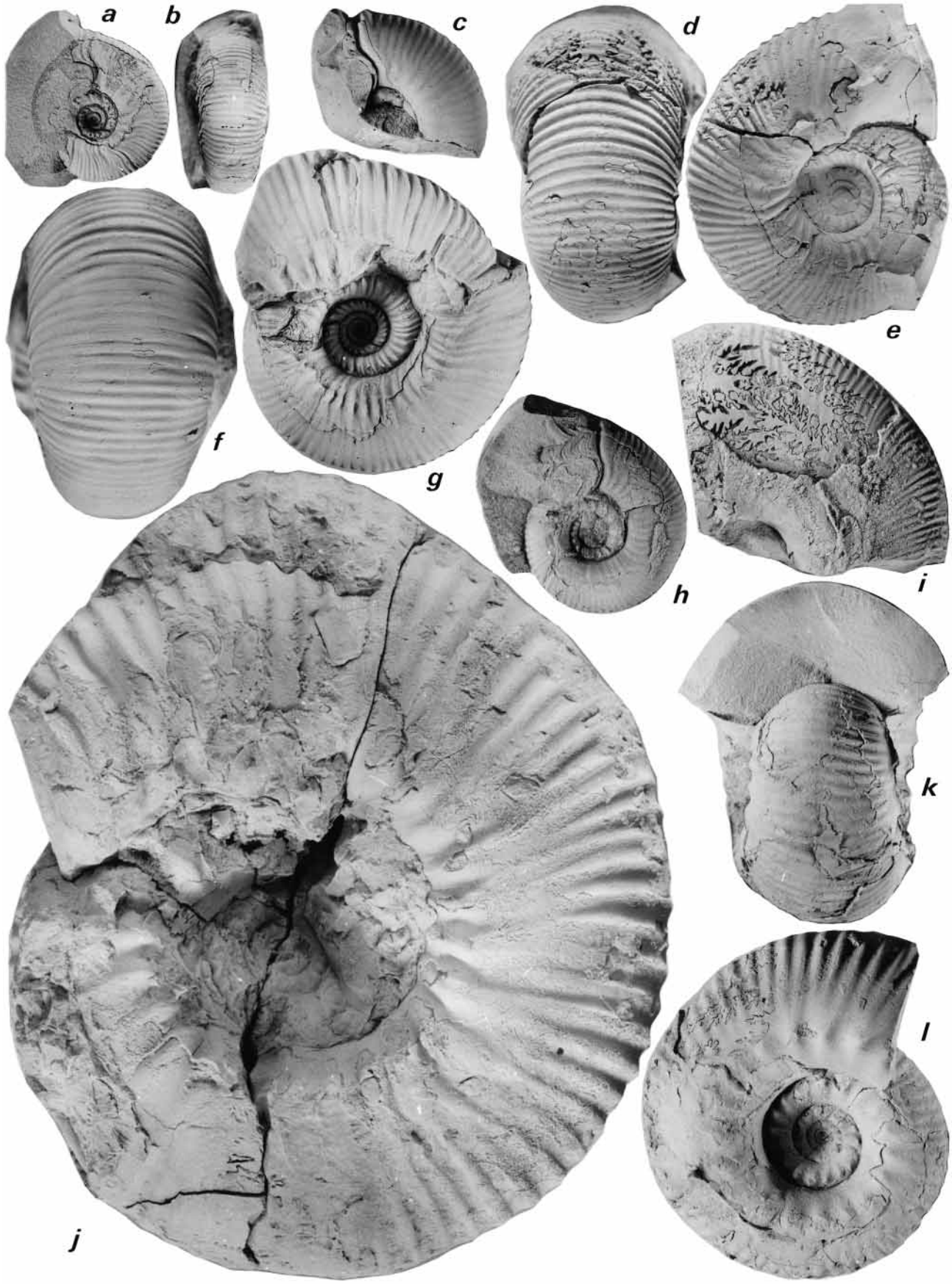
Remarks. This is a variable species, the variation embracing both *leanzai* and *laticosta* morphotypes. Typical forms are cadicone with a coronate whorl section, bullae of moderate size and occasional 'polyptychitine' rib bundles (Figures 3a–c, 4k, l). Some variants are a little less inflated, with a higher, slightly arched whorl section; they include the lectotype of *O.* (*O.*) *leanzai* (Figures 4j, 6b). Others, mainly from the lower part of the species' range, have more robust, widely spaced bullae, usually with more ribs (up to five) per bundle (Figure 3d, e). The holotype of *O.* (*O.*) *laticosta* (Figure 3h, i) is a coronate example of the latter group, with only 13 tubercles on the last whorl. In whorl proportions, it closely matches a specimen with more closely-spaced bullae (Figure 3f, g) from bed MO1 at Agua de La Mula, the lowest level at which the species appears there.

According to the original records, the types of *O.* (*O.*) *laticosta* and *O.* (*O.*) *leanzai* came from markedly different horizons. The holotype of *O.* (*O.*) *laticosta*, from the Arroyo Blanco, was supposedly from strata below the '*Exogyra*' beds. This would correspond with about the level of *Pseudofavrella angulatiformis*, if the '*Exogyra*' beds at Arroyo Blanco correlate with those at La Mala Dormida some 10 km further south. However, one of us (MBA-U) has now shown (see lithostratigraphy, above) that at Arroyo Blanco the *O.* (*O.*) *laticosta* level appears to be *above* the '*Exogyra*' beds and that at La Mala Dormida it occurs immediately above beds with *Holcoptychites compressum*. The syntypes of *O.* (*O.*) *leanzai* (the specimen figured by Giovine is here designated lectotype) are from the Cerro Maruco-Cerro Mesa anticline, north of Zapala, Neuquén, supposedly associated with *Holcoptychites*. Thus, the types of the two 'species' appear to be from similar horizons, and both morphotypes can be matched with specimens that we have collected from just above the *Holcoptychites* beds. Hence, we recognise a single variable species for which the name *O.* (*O.*) *laticosta* has priority over *O.* (*O.*) *leanzai*.

Weaver's (1931) description of a single *Astieria laticosta* from Cerro Salada appears to match the species, though his recorded horizon is anomalously low. *O.* (*O.*) *laticosta* is more involute and has fewer primary and secondary ribs per whorl than *O.* (*O.*) *mingrammi* (Leanza) from the preceding Neuquén *Olcostephanus* fauna.

Cooper (1981, pp. 204, 223, 236) regarded *O.* (*O.*) *laticosta* as a synonym of *O.* (*O.*) *bossingaulti* (d'Orbigny), originally described from Colombia, and *O.* (*O.*) *leanzai* as close to *O.* (*O.*) *rogersi* (Kitchin), originally described from South Africa. *Olcostephanus* (*O.*) *bossingaulti* appears to be less inflated than *O.* (*O.*) *laticosta* and has more numerous ribs per bundle. *Olcostephanus* (*O.*) *rogersi* is generally less coronate than *O. laticosta*, the rib bundles are less 'polyptychitine', and the constrictions are wider and extend to a larger growth stage.

Figure 3. *Olcostephanus* (*Olcostephanus*) *laticosta* (Gerth). a, CPBA 19248, Río Agrio. b, c, CPBA 19227.1, bed MO8, Agua de la Mula. d, e, CPBA 19225, bed MO2, Agua de La Mula. f, g, CPBA 19224.2, bed MO1, Agua de La Mula. h, i, holotype, IPB Gerth collection, Arroyo Blanco. All figs × 1.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Haas (1960, p. 12, figs 29, 30) figured two Colombian ammonites as *O.* (*O.*) cf. *laticosta*. In general proportions and number and spacing of umbilical bullae they compare with the '*leanzai*' morphology, but they are too poorly preserved for firm identification and their stratigraphical position is unknown. Thus at present *O.* (*O.*) *laticosta* is not known outside the Neuquén Basin.

O. (*O.*) *sulcosa* Pavlow, from England, is similar to the inner whorls of *O.* (*O.*) *laticosta* in general proportions and the number of tubercles, but has noticeably finer secondary ribbing, with 5–6 secondaries per bundle.

Olcostephanus (*Olcostephanus*) *boesei* (Riedel)
Figure 4i

*1938 *Astieria bösei* Riedel, p. 10, pl. 3, figs 1, 2; pl. 12, fig. 1 (refigured Cooper 1981, fig. 173).
1945 *Astieria boesei* Riedel; Royo y Gomez, p. 232.
1957 *Olcostephanus bösei* (Riedel); Bürgl, p. 132, pl. 4, fig. 4.
1960 *Olcostephanus bösei* (Riedel); Haas, p. 12, figs 27, 28.

Holotype. By monotypy, the specimen figured by Riedel (1938) from Cáqueza, Colombia.

Material. One fragmentary specimen from Agua de La Mula (CPBA 19251).

Description. A single whorl fragment, consisting of a partially corroded internal mould with a little shell preserved on one flank, differs considerably from the associated *Olcostephanus* in being extremely finely ribbed and moderately compressed. The venter is arched and the flanks gently rounded. On the umbilical slope and margin three feeble, slender, quite widely spaced primary ribs are visible on one side. Low on the flank, each gives rise to a bundle of about 6–7 very fine secondary ribs, and at least one rib is intercalated higher on the flank.

Remarks. In whorl shape and rib density this specimen closely matches the Colombian material figured by Riedel (1938), Royo y Gomez (1945), Bürgl (1957) and Haas (1960), all of which came from the same general area, Cáqueza (department of Cundinamarca). They have been dated as either Valanginian or Early Hauterivian, but the latter is more probable (Bürgl, 1957; Etayo-Serna, 1968). In these Colombian examples the delicate, elongate primary ribs tend to swell slightly into feeble bullae, which are missing or not preserved in the Argentine specimen. Bullae are also present in Peruvian examples of *O.* (*O.*) *boesei* in the Bulot collection.

O. (*O.*) *boesei* is close to the European group of *O.* (*O.*) *sayni* (Kilian).

Olcostephanus (*Olcostephanus*) *variegatus* (Paquier)
Figure 5a–c

*1900 *Holcostephanus variegatus* Paquier, pp. II–III, pl. 7, figs 1–2.
1938 *Astieria* aff. *atherstoni* (Sharpe); Riedel, p. 13, pl. 3, figs 5–6; pl. 12, fig. 3.
1957 *Olcostephanus* aff. *astierianus* (d'Orbigny); Bürgl, pl. 4, fig. 6a–b.
v 2001 *Olcostephanus* (*Olcostephanus*) cf. *variegatus* (Paquier); Aguirre-Urreta & Rawson, p. 206 (CPBA 19256).

Holotype. By original designation, the specimen figured by Paquier (1900, pl. 7, fig. 1) from the Lower Hauterivien of Rosans (Hautes-Alpes, France), Institut Dolomieu, Grenoble, France.

Material. Two specimens: one from El Salado Sur (CPBA 19256) and one from Bajada del Agrio (CPBA 19266).

Description. The specimens are indifferently preserved internal moulds of phragmocones. Shell only slightly inflated, slightly involute (wu *c*. 26% of diameter in CPBA 19256), with moderately shallow umbilicus. Flanks gently curved, whorl section moderately arched (Figure 5a), slightly wider than high. Maximum width of whorl at umbilical bullae. Feeble primary ribs arise on the outer part of the sloping umbilical whorl, swelling into strong, widely spaced

Figure 4. a–h, *Olcostephanus* (*Jeannoticeras*) *agrioensis* sp. nov. a, b, (m) CPBA 19255.1, bed MO8, Agua de La Mula. c, (m) CPBA 19255.3, bed MO8, Agua de La Mula. d, e, holotype (M), CPBA 19247, Río Agrio. f, g, (M) CPBA 19252, bed MO8, Agua de La Mula. h, (m) CPBA 19255.2, bed MO8, Agua de La Mula. i, *O.* (*O.*) *boesei* (Riedel), CPBA 19251, bed MO8, Agua de La Mula. j, *O.* (*O.*) *laticosta* (Gerth), CPBA 5144, Cerro Mesa [lectotype of *O.* (*O.*) *leanzai* Giovine]. k, l, *O.* (*O.*) *laticosta* (Gerth), CPBA 19227.2, bed MO8, Agua de La Mula. (M, macroconch; m, microconch). All figs × 1.

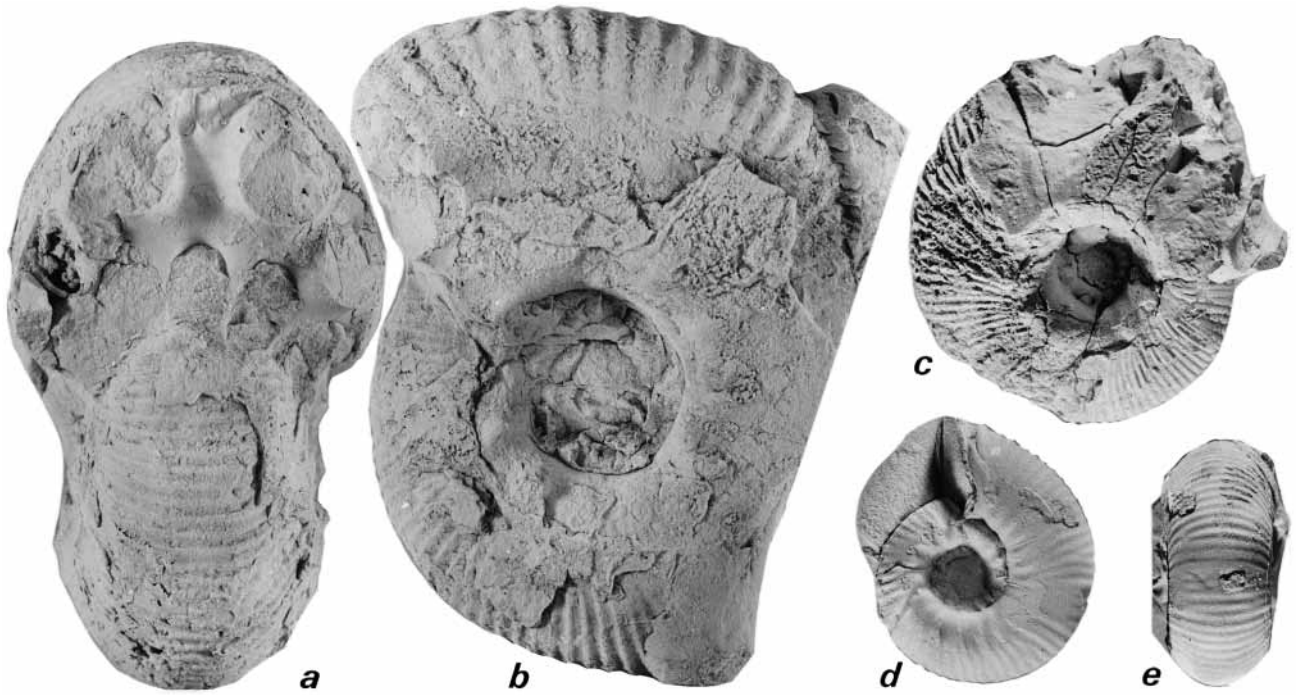

Figure 5. a, b, *O.* (*O.*) *variegatus* (Paquier), CPBA 19256, bed SH9, El Salado Sur. c, *O.* (*O.*) *variegatus* (Paquier), CPBA 19266, loose in *giovinei* Subzone, Bajada del Agrio (part of last whorl removed). d, e, *O.* (*J.*) *agrioensis* (m), CPBA 19271.1, bed MO10, Agua de La Mula. All figs × 1.

umbilical bullae close to the umbilical margin. On CPBA 19256 there are 11 bullae on the last whorl. On the earlier part of this whorl bundles of 7–9 secondary ribs are associated with each bulla, but on the last part the number has diminished to 4–5. Some secondaries branch from each bulla, but additional ones may be intercalated at the same level, or occasionally are intercalated or branch higher on the whorl, giving a slightly 'polyptychitine' rib pattern.

Remarks. These are the only specimens of *Olcostephanus* that we have found above the *O.* (*O.*) *laticosta* Subzone, and are, therefore, the youngest *Olcostephanus* known from the Neuquén Basin. CPBA 19256 is from bed SH9 (upper part of the *Hoplitocrioceras giovinei* Subzone) at El Salado Sur, 21.5 m above the top of the *O. laticosta* Subzone. CPBA 19266 was loose on the *Hoplitocrioceras giovinei* Subzone, but the matrix suggests that it came from a distinctive thin shelly siltstone near the top of the subzone. The specimens are close to some of the European variants of *O.* (*O.*) *variegatus* figured by Bulot (1992, p. 153, pl. 2, figs 1–3; pl. 3, figs 1–5: see for European synonymy). This is the last *Olcostephanus* in the European successions. However, the European forms generally have a wider umbilicus (29–40% of diameter) and a more pronounced polyptychitine rib pattern. But one French example in the Bulot collection (University of Provence) closely matches our specimens at a comparable diameter.

A medium-sized (88 mm), poorly preserved, septate specimen (CPBA 19263, A. Gutiérrez Pleimling collection) from Cerro El Marucho may also belong to *O.* (*O.*) *variegatus*. It is more compressed than the other specimens, with almost flat flanks and a high-arched whorl. The Colombian ammonites figured by Riedel (1938) as *O.* aff. *atherstoni* and by Bürgl (1957) as *O.* aff. *astierianus* represent the inner whorls of *O.* (*O.*) *variegatus*, with prominent, widely spaced umbilical tubercles and some 5–6 secondary ribs per tubercle. The poorly known Colombian species *O.* (*O.*) *bossingaulti* (d'Orbigny) may be close to *O.* (*O.*) *variegatus*, but d'Orbigny's illustration (reproduced by Cooper 1981, fig. 46) and Bürgl's (1957, pl. 4, fig. 3a, b) figured specimen shows a much more inflated shell with a wider umbilicus and more numerous, though strong, umbilical bullae.

O. (*O.*) *variegatus* has a much less inflated shell than *O.* (*O.*) *laticosta* and an arched whorl section. The umbilical bullae are more widely spaced than in most *O.* (*O.*) *laticosta*, and the ribs more closely spaced.

Subgenus *Jeannoticeras* Thieuloy, 1965

Type species. *Ammonites jeannoti* d'Orbigny, 1841

Diagnosis. A finely-ribbed subgenus of *Olcostephanus* characterised by very closely-spaced primary ribs that bear elongate bullae which normally disappear on the body chamber. Two to three secondary ribs arise from each bulla, and another may branch or be intercalated higher on the flank. Dimorphism is well marked, the microconch being much smaller than the macroconch, and bearing long, narrow lateral lappets.

Remarks. Previous descriptions of *Jeannoticeras* have indicated that the umbilical bullae are weak or even absent in the septate whorls, whereas in *Olcostephanus s.s.* they are generally strong. But both our material and European specimens of *Jeannoticeras jeannoti* show that in the microconch in particular they can be quite strong in *Jeannoticeras* too, though disappearing on the body chamber.

Jeannoticeras embraces a small group of species that appear to be widespread geographically but limited temporally to a short interval in the mid Early Hauterivian (Bulot *et al.*, 1993, p. 42). It is recorded from many parts of Europe (as far north as eastern England), Tanzania, the Pacific coast of North America, Mexico, Peru and possibly Colombia (Cooper 1981; Bulot *et al.*, 1993).

Olcostephanus (*Jeannoticeras*) *agrioensis* sp. nov.
Figures 4a–h, 5d, e

Holotype. CPBA 19247 (macroconch) from the *Olcostephanus* (*O.*) *laticosta* Subzone, Lower Agrio Member, Agrio del Medio.

Paratypes. Macroconchs: 1 specimen, from Agua de La Mula (CPBA 19252). Microconchs: 13 specimens, 12 (6 complete) from Agua de La Mula (CPBA 19253, 19254.1–4, 19255.1–3, 19271.1–2, 19272.1–2) and 1 from Agrio del Medio (CPBA 19245).

Derivation of name. From the Río Agrio, which flows by Agrio del Medio and gives its name to the Agrio Formation.

Description. Macroconchs (M): shell moderately inflated, slightly involute (wu 28–33% of diameter), with a moderately deep, funnel-shaped umbilicus. Venter gently rounded. Backward-sloping primary ribs arise on the inner part of the steeply sloping umbilical whorl, swelling slightly at the umbilical margin to form weak bullae where shell is preserved; the bullae are not visible on the internal mould. Fine, closely spaced secondaries extend radially over the whorl. Most bifurcate or, rarely, trifurcate, from the bullae or higher on the flank, but a few are intercalated close to the umbilical margin. The holotype (Figure 4d, e) is a phragmocone in which the last whorl has 33 primary ribs/bullae and about 74 secondary ribs (sec/pr. ratio=2.24). CPBA 19252 (Figure 4f, g) is of similar diameter but the whole of the last whorl is body chamber. This could be adult as slight retraction starts just before the beginning of the damaged section. On the undamaged first half of the body chamber there are 19 bullae and 44 secondary ribs (sec/pr. ratio=2.32). Constrictions are visible in the inner whorls.

Microconchs (m): the largest specimens are about 33 mm in diameter, and the body chamber occupies about two-thirds of a whorl. Shell slightly inflated and slightly involute (wu *c.* 30% of diameter), with shallow umbilicus. Whorl flanks gently rounded, merging into rounded venter. Maximum width of whorl at umbilical bullae. Feeble primary ribs arise on the outer part of the sloping umbilical whorl. Most swell into moderate to strong, quite well-spaced bullae on the umbilical margin, others remain non-bullate. The ribbing on flanks and venter is only visible on the last whorl, which is mainly body chamber. Here the ribs are sinuous on the flanks, but become straight over the ventral part of the shell. Initially, the bullate ribs give rise to bundles of 4–5 secondary ribs, but the bullae disappear by the beginning of the body chamber. Then the rib pattern changes; long, slender, closely-spaced primary ribs appear and usually bifurcate at mid-flank, though an occasional one remains single. An occasional secondary branches or is intercalated higher on the whorl. Throughout growth, shallow constrictions occur more or less parallel to the ribbing, and two of the specimens bear a deeper constriction close to the mouth border, followed by lateral lappets (Figure 4c, h).

Dimensions of figured specimens (in mm)

Specimen	d	wh	wh%d	wt	wt%d	wh/wt	wu	wu%d
CPBA 19247 (M)	56	23.2	0.41	32.2	0.57	0.72	17.0	0.30
CPBA 19245 (m)	30.2	12.1	0.40	12.6	0.42	0.96	8.4	0.28
CPBA 19255.1 (m)	27.3	11.1	0.41	12.0	0.44	0.92	8.6	0.31
CPBA 19255.2 (m)	33.7	12.5	0.37	14.6	0.43	0.86	10.1	0.30

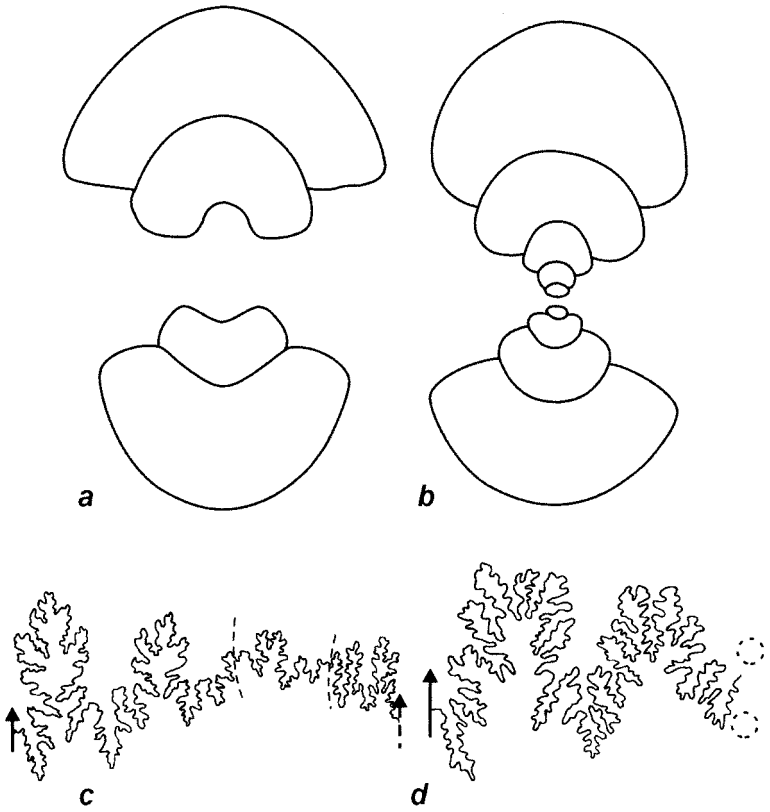

Figure 6. *O.* (*O.*) *laticosta* (Gerth). a, b, whorl sections of CPBA 19260 and CPBA 5144 [lectotype of *O.* (*O.*) *leanzai*], × 0.5; c, d, suture lines of CPBA 19244 and IPB, Gerth collection [holotype of *O.* (*O.*) *laticosta*]; × 1.

Remarks. In whorl shape and rib pattern the macroconch clearly fits into *Jeannoticeras*, though CPBA 19252 remains weakly bullate on the (adult?) body chamber, whereas other *Jeannoticeras* lose their bullae during growth. The difference may partly reflect preservation, since many of the European forms are internal moulds, and the internal moulds of the Argentine forms are also without bullae.

The microconchs occur in the same beds as three macroconch forms [*O.* (*O.*) *laticosta*, *O.* (*O.*) *boesei* and *O.* (*J.*) *agrioensis* (M)]. They are assigned to *Jeannoticeras* because: (1) they are so similar in size and general morphology to *Jeannoticeras* microconchs from other areas; (2) their shell is much more compressed than that of *O.* (*O.*) *laticosta*, and by comparison with other *Olcostephanus* species one could expect a large form like *O.* (*O.*) *laticosta* to have a larger microconch; (3) similar microconchs are not known in the *O.* (*O.*) *boesei*/*O.* (*O.*) *sayni* group.

Although *O.* (*J.*) *agrioensis* is more involute than typical *O.* (*J.*) *jeannoti*, it differs from more tightly coiled examples of the latter only in being slightly more coarsely ribbed, especially in the more advanced growth stages of the macroconch form. It is also more involute than the dimorphic pair *O.* (*J.*) *frequens* (Zwierzycki)/*O.* (*J.*) *auriculata* (Zwierzycki) from Tanzania, which was regarded by Bulot *et al.* (1993, p. 41) as a synonym of *O.* (*O.*) *jeannoti*. The Colombian *O.* (*J.*?) *delicatecostatus* Haas is much more finely ribbed than the Argentine species. Some Mexican ammonites figured by Böse (1923) and Imlay (1938) indicate that *Jeannoticeras* occurs there, but they are too small or incomplete for satisfactory comparison with our form.

4. Biostratigraphy

With the exception of two specimens of *O.* (*O.*) *variegatus*, the fauna described here is limited to, and characterises, a thin interval in the Lower Agrio Member, sandwiched between the *Holcoptychites* beds below and the *Hoplitocrioceras* beds above. The *O.* (*O.*) *laticosta* Subzone is 12.7 m thick in the centre of the basin at the Pichaihue Valley, thickening south-eastward to 28 m at El Salado Sur and 38 m at Agua de La Mula.

The subzone may coincide with the upper of two subdivisions of the '*O.* (*O.*) *curacoensis* Zone' [=*O.*

<table>
<tr><th></th><th colspan="2">NEUQUEN BASIN</th><th colspan="3">WEST MEDITERRANEAN PROVINCE</th></tr>
<tr><th>AGE</th><th colspan="2">BIOZONE/
SUB-BIOZONE</th><th>BIOZONE</th><th>SUB-BIOZONE</th><th>BIOHORIZON</th></tr>
<tr><td rowspan="6">EARLY HAUTERIVIAN</td><td colspan="2">Weavericeras vacaensis</td><td rowspan="3">Lyticoceras nodosoplicatum</td><td rowspan="3"></td><td rowspan="2"></td></tr>
<tr><td rowspan="2">gentilii</td><td>Hoplitocrioceras gentilii</td></tr>
<tr><td>Hoplitocrioceras giovinei</td><td>Olcostephanus (O.) variegatus</td></tr>
<tr><td rowspan="3">neuquensis</td><td rowspan="2">Olcostephanus (O.) laticosta</td><td rowspan="2">Crioceratites loryi</td><td>Olcostephanus (J.) jeannoti</td><td rowspan="2"></td></tr>
<tr><td>Crioceratites loryi</td></tr>
<tr><td>Holcoptychites compressum</td><td rowspan="2">Acanthodiscus radiatus</td><td rowspan="2"></td><td></td></tr>
<tr><td>Holcoptychites neuquensis</td><td>Breistrofferella castellanensis</td></tr>
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Figure 7. Correlation of the Argentine and West Mediterranean successions. Mediterranean zonal scheme from Hoedemaeker & Rawson (2000).

(*O.*) *atherstoni* Zone] recognised by Riccardi *et al.* (1993) in Mendoza as characterised by *O.* (*O.*) aff. *laticostatus*. The interval was placed in the *Olcostephanus* (*O.*) *leanzai* Subzone of the *Holcoptychites neuquensis* Zone by Aguirre-Urreta & Rawson (1997). Now that *O.* (*O.*) *leanzai* is placed in synonymy with *O.* (*O.*) *laticosta* the name of the subzone has to be changed.

The only non-olcostephanid ammonites that we have found within the *O.* (*O.*) *laticosta* Subzone are seven fragments of an indeterminate neocomitid (probably the predecessor of *Hoplitocrioceras*) from the highest part of the subzone, five at Agua de La Mula (Bed MO10, two figured by Aguirre-Urreta & Rawson 2001, fig. 6a, b, e, f) and two from El Salado Sur.

The *O.* (*O.*) *laticosta* fauna is one of the most widespread ammonite faunas that we have found in the Neuquén Basin, extending some 450 km north to south along the axis of the basin.

5. Age of the fauna

The great majority of *Olcostephanus* found in the *O.* (*O.*) *laticosta* Subzone belong to the index species. This form is not known with certainty outside the Neuquén Basin. Correlation with other areas is, therefore, difficult. However, three lines of evidence suggest that the *O.* (*O.*) *laticosta* Subzone is of mid Early Hauterivian age, corresponding approximately with the *Crioceratites loryi* Zone of the Mediterranean Province.

First, the occurrence of the short-lived subgenus *O.* (*Jeannoticeras*) as a minority element of the fauna of the upper half of the *laticosta* Subzone indicates a possible correlation with the *jeannoti* Subzone of south-east France, which lies in the upper part of the *Crioceratites loryi* Zone (Figure 7; Bulot *et al.*, 1993; Hoedemaeker & Rawson, 2000).

Second, the fragment of *O.* (*O.*) *boesei* from the upper part of the *laticosta* Subzone suggests a correlation with a Peruvian level rich in the same species. The Peruvian fauna is currently being revised by Dr Luc Bulot (pers. comm., 2001), who considers that *O.* (*O.*) *boesei* is very close to *O.* (*O.*) *sayni* (Kilian). In south-east France *O.* (*O.*) *sayni* is limited to the *Crioceratites loryi* Zone and is most common in the *jeannoti* Subzone (Bulot *et al.*, 1993, table 10).

Finally, the occurrence of *O.* (*O.*) *variegatus* in the upper part of the *Hoplitocrioceras giovinei* Subzone, just above the *O.* (*O.*) *laticosta* Subzone, suggests a correlation of at least part of the *giovinei* Subzone with the *variegatus* horizon of south-east France, which lies immediately above the *jeannoti* Subzone (Figure 7).

The correlations now suggested are different from those in an earlier scheme (Aguirre-Urreta & Rawson, 1997), where the *O.* (*O.*) *leanzai* (now *laticosta*) Subzone was correlated provisionally with the top

part of the *Acanthodiscus radiatus* Zone of the West Mediterranean Province. That initial correlation was a 'best-fit' model as at that time the only firm evidence for correlating the Argentine and West Mediterranean successions came from horizons well below and above the *laticosta* Subzone. The discovery of *Jeannoticeras* in the upper part of the *laticosta* Subzone and of *O.* (*O.*) *variegatus* just above provides a crucial intervening link between the two regions.

Acknowledgements

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