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Abstract

We analyze the Late Triassic extinction and Early Jurassic recovery of bivalve faunas within marine environments in the Atuel river area of the Neuquén Basin, Argentina. Data were collected from a hundred samples with invertebrates in a well-exposed latest Triassic to early Jurassic section in the Neuquén Basin (southern Mendoza Province, Argentina) and allow a high-resolution reconstruction of the local diversity dynamics. The nearly continuous presence of marine estenohaline major taxa such as cnidarians, rhynchonelliform brachiopods, echinoderms and cephalopods indicates normal salinity throughout. All bivalve species were identified, and each occurrence was recorded in meters above the base. To analyze the systematic diversity trends, diversity curves were calculated on the basis of the first and last appearance data for each bivalve species, and both total diversity and boundary crossers diversity were used. As a result, four main phases were identified: a) Triassic equilibrium phase (late Norian?-Rhaetian), with relatively high origination and extinction rates; b) extinction phase (Rhaetian), with high extinction rates and low origination rates; c) recovery phase (late Early to early Late Hettangian), with high origination rates and almost null extinction rates; and d) Jurassic equilibrium phase (Late Hettangian-Sinemurian), again with similar and relatively high origination and extinction rates. The extinction and recovery phases are separated by a gap of about 135 meters without identifiable benthonic invertebrates but with early Hettangian ammonites. On the other hand, bivalve palaeoecologic diversity seems to have been more homogeneous along the section, being dominated by attached epifaunal species before and after the extinction. Slight differences observed include a) shallow burrowers were more diverse during the Rhaetian than during the earliest Jurassic and b) epifaunal free lying and semi-infaunal attached bivalves were more diverse after the Rhaetian extinction.

Keywords	Triassic/Jurassic extinction, Bivalvia, Early Jurassic biotic recovery, Argentina, marine diversity
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La Plata, June 26th, 2017

Editor-in-Chief,
Palaeogeography, Palaeoclimatology, Palaeoecology
Dr. D.J. Bottjer.

Dear Dr. Bottjer

We are pleased to submit the manuscript entitled “*Biotic recovery after the end-Triassic extinction event: evidence from marine bivalves of the Neuquén Basin, Argentina*” to be considered for publication in PALAEOGEOGRAPHY, PALAEOCLIMATOLOGY, PALAEOECOLOGY as a research paper.

The manuscript includes an analysis of the biotic recovery after the end-Triassic extinction event, based on data of bivalve species diversity and ecologic features, carefully collected over a long time from an exceptionally well-exposed section in the Andes of western Argentina.

This is an original manuscript which is not under consideration for publication elsewhere. We feel that our manuscript will have a broad interest among palaeontologists, especially those dealing with extinction/recovery aspects of benthonic faunas, since it provides a new set of data and their analysis of the T/J extinction event and its recovery from the Southern Hemisphere.

We hope you find this a publishable manuscript.

Sincerely,

Dr. Susana E. Damborenea
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BIOTIC RECOVERY AFTER THE END-TRIASSIC EXTINCTION EVENT:
EVIDENCE FROM MARINE BIVALVES OF THE NEUQUÉN BASIN, ARGENTINA

HIGHLIGHTS

- High-resolution reconstruction of bivalve diversity dynamics through the T/J biotic crises in a Southern Hemisphere location.
- Biotic recovery of marine bivalve faunas after Triassic/Jurassic extinction in the Neuquén Basin, Argentina, was relatively fast, within Middle and lowermost Late Hettangian times.
- T/J biotic crisis and recovery happened in four phases, each characterized by relationships between regression lines of cumulative FADs and LADs: Triassic equilibrium, extinction, recovery and Jurassic equilibrium.
- Recovery was mainly triggered by immigration into the basin of widely distributed genera.
- The origination of new taxa was locally restricted.
- Of the main bivalve life-habits categories, epifaunal free-lying and semi-infaunal attached were not recorded from Triassic, but all were present in the recovery phase.

1 **BIOTIC RECOVERY AFTER THE END-TRIASSIC EXTINCTION EVENT:**
2 **EVIDENCE FROM MARINE BIVALVES OF THE NEUQUÉN BASIN,**
3 **ARGENTINA**

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5
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10
11 **Abstract**

12 We analyze the Late Triassic extinction and Early Jurassic recovery of bivalve faunas within
13 marine environments in the Atuel river area of the Neuquén Basin, Argentina. Data were
14 collected from a hundred samples with invertebrates in a well-exposed latest Triassic to
15 early Jurassic section in the Neuquén Basin (southern Mendoza Province, Argentina) and
16 allow a high-resolution reconstruction of the local diversity dynamics. The nearly
17 continuous presence of marine stenohaline major taxa such as cnidarians, rhynchonelliform
18 brachiopods, echinoderms and cephalopods indicates normal salinity throughout. All bivalve
19 species were identified, and each occurrence was recorded in meters above the base. To
20 analyze the systematic diversity trends, diversity curves were calculated on the basis of the
21 first and last appearance data for each bivalve species, and both total diversity and boundary
22 crossers diversity were used. As a result, four main phases were identified: a) Triassic
23 equilibrium phase (late Norian?-Rhaetian), with relatively high origination and extinction
24 rates; b) extinction phase (Rhaetian), with high extinction rates and low origination rates; c)
25 recovery phase (late Early to early Late Hettangian), with high origination rates and almost
26 null extinction rates; and d) Jurassic equilibrium phase (Late Hettangian-Sinemurian), again
27 with similar and relatively high origination and extinction rates. The extinction and recovery
28 phases are separated by a gap of about 135 meters without identifiable benthonic
29 invertebrates but with early Hettangian ammonites. On the other hand, bivalve
30 palaeoecologic diversity seems to have been more homogeneous along the section, being
31 dominated by attached epifaunal species before and after the extinction. Slight differences

32 observed include a) shallow burrowers were more diverse during the Rhaetian than during
33 the earliest Jurassic and b) epifaunal free lying and semi-infaunal attached bivalves were
34 more diverse after the Rhaetian extinction.

35

36 **Keywords:** Triassic/Jurassic extinction, Bivalvia, Early Jurassic, biotic recovery, Argentina,
37 marine diversity

38

39 **1. Introduction**

40 The end Triassic extinction event is one of the “big five” global crisis in the history
41 of life in the marine realm (Raup and Sepkoski, 1982), with a total loss of about 22% of
42 families and a generic loss estimated by different authors between 33% and 73% (Jablonski,
43 1994; Benton, 1995; Bambach et al., 2004; McGhee et al., 2004, 2013). The extinction was,
44 according to some authors, equally or more severe than the end Cretaceous crisis, with a
45 calculated species loss (based on rarefaction techniques) of about 80% (Raup and Sepkoski,
46 1988; Jablonski, 1994). Several studies suggest that the ecologic effect of this extinction on
47 the global biosphere was more significant than the magnitude of taxonomic diversity loss
48 would suggest (McGhee et al., 2004, 2013; Mander et al., 2008; Ros, 2009; Ros and
49 Echevarría, 2011, 2012; Ros et al., 2011).

50 Paradoxically, the end-Triassic extinction and the subsequent biotic recovery are not
51 so well known as others (Hallam and Wignall, 1997, p. 142; Wignall and Bond, 2008), or at
52 least did not attract the same amount of attention (Twitchett, 2006), probably due to the fact
53 that there are few adequate fossiliferous sections worldwide. As a result, most of the
54 published analyses were based on data from the Northern Hemisphere: Europe (Johnson and
55 Simms, 1989; Allasinaz, 1992; Warrington et al., 1994; McRoberts and Newton, 1995;
56 McRoberts et al., 1995; Kiessling et al., 2007; Wignall and Bond, 2008; Mander and
57 Twitchett, 2008; Mander et al., 2008; Clémence et al., 2010), Tibet (Hautmann et al., 2008)
58 and the North American Cordillera (Tanner et al., 2004; Guex et al., 2004; Wignall et al.,
59 2007). This limited picture will be surely enriched (and may even change) as Southern
60 Hemisphere information becomes better known; for instance, sections in the Peruvian Andes

61 have provided good data to quantitatively analyze ammonoid post-extinction recovery and
62 diversification (Guex et al., 2012).

63 When quantified, the known results are diverse: the recovery period after the end
64 Triassic extinction was inferred to be long for reef communities (up to between 5 and 10
65 million years, see Cooper, 1989; Lathuilière and Marchal, 2009; Kiessling, 2010), relatively
66 faster for other benthonic faunas (Hallam, 1987, 1996; Wignall and Bond, 2008), but not
67 necessarily geographically homogeneous (Raup and Jablonski, 1993; Jablonski, 1994), and
68 may have been nearly “instantaneous” locally (Hautmann et al., 2008). For ammonites the
69 diversification was fast, likely less than 100 ky after the extinction (Guex et al., 2012).

70 Bivalves are one of the best studied groups in relation to the recovery after the end-
71 Triassic extinction event. This is due to their abundance and diversity in different marine
72 and marginal marine habitats, and also to the fact that they are relatively well-known. It was
73 even suggested that bivalves may “serve as a proxy for marine invertebrate biodiversity
74 changes as a whole” (McRoberts et al., 1995). Bivalves provided the material of several
75 studies in this context, mainly focused on the extinction itself and on European
76 comprehensive data bases (Hallam, 1981; Hallam and Miller, 1988; Allasinaz, 1992;
77 McRoberts and Newton, 1995; McRoberts et al., 1995; Wignall and Bond, 2008; Mander et
78 al., 2008), or on global comprehensive data (Hallam, 1981; Ros, 2009; Ros and Echevarría,
79 2011, 2012). Likewise, most of what is known about the characteristics of the biotic
80 recovery phase or rebuilding of the marine ecosystem after the extinction event is also based
81 upon European bivalve data (McRoberts and Newton, 1995; Hallam, 1996; Mander et al.,
82 2008). Still, more geographically explicit data are needed to understand the spatial fabric of
83 extinctions and recoveries (Jablonski, 2005; Valentine et al., 2008).

84 The aim of this paper is to analyze the recovery phase in an exceptionally well-
85 exposed latest Triassic-earliest Jurassic section of the Andes at a very well-known South
86 American region, the Neuquén Basin in western Argentina, through a detailed analysis of
87 bivalve species diversity and ecologic features. South American Late Triassic-Early Jurassic
88 bivalve faunas were the subject of recent revisions and ongoing taxonomic research
89 (Damborenea, 1987a, 1987b, 1993, 1998, 2002, 2004; Aberhan, 1994, 2004; Damborenea
90 and Lanés, 2007; Pérez et al., 2008; Damborenea and Manceñido, 2012). This paper is based
91 on data collected over the years in a key area of the Neuquén Basin where the Triassic-

92 Jurassic transition is documented in a fully marine succession (Riccardi et al., 1997a, 1997b,
93 2004; Lanés, 2005). Though this analysis covers the extinction and provides some
94 comparisons for the Triassic data, it is mostly focused on the recovery, for which enough
95 robust data are available. The extinction event itself is poorly known in this particular area,
96 and the scarce data are not adequate to meaningfully recognize detailed timing and pattern.
97 We analyze the Rhaetian-Sinemurian time interval in the area of the upper Atuel river in
98 Mendoza Province (Argentina) with the purpose to characterize and time the recovery and
99 understand its relationships to environmental changes, as a contribution to discriminate
100 between regional and global conditions in the post T/J recovery issue. This new set of local
101 data can be compared with information from other latitudes and contribute to future global
102 analyses.

103

104 **2. Late Triassic-Earliest Jurassic faunas in South America**

105 Latest Triassic - Earliest Jurassic sediments are known from several locations along
106 western South America, but good continuous sections through marine sediments are few and
107 many are still poorly known (see discussion in Riccardi et al., 2004; Damborenea et al.,
108 2009). Nevertheless, when studied in detail some of them have proven to be exceptionally
109 good, and are providing key palaeontologic data to understand the faunal turnover at the T/J
110 boundary (i.e., Schaltegger et al., 2008; Guex et al., 2012).

111 Late Triassic marine faunas were mentioned from Colombia (Geyer, 1973), and are
112 known from several localities in Perú (Jaworski, 1922; Körner, 1937; Steinmann, 1929;
113 Cox, 1949; Nicol and Allen, 1953; Boit, 1966; Rangel, 1978; Maeda et al., 1983; Stanley,
114 1994; Hillebrandt, 1994), and Chile (Fuenzalida-Villegas, 1937; Barthel, 1958; Thiele-
115 Cartagena, 1967; Cecioni and Westermann, 1968; Westermann, 1970; Hayami et al., 1977;
116 Escobar, 1980; Moscoso and Covacevich, 1982; Chong and Hillebrandt, 1985; Fang et al.,
117 1998; Rubilar, 1998; Pérez-Barría, 2004a, 2004b, 2005; Nielsen, 2005). In Argentina marine
118 Triassic-earliest Jurassic deposits were only relatively recently found in the Atuel River area
119 (Riccardi et al., 1988, 1991, 1997a, 1997b, 2004; Riccardi and Iglesia-Llanos, 1999;
120 Damborenea and Manceñido, 2012). References from Bolivia (Beltan et al., 1987; Suárez-
121 Riglos and Dalenz-Farjat, 1993) need revision.

122 Earliest Jurassic (Hettangian-early Sinemurian) marine faunas, with emphasis on
123 ammonites, were described or illustrated from Colombia (Geyer, 1973), Perú (Tilmann,
124 1917; Geyer, 1979; Prinz, 1985; Prinz and Hillebrandt, 1994; Hillebrandt, 1994; Guex et al.,
125 2004; Schaltegger et al., 2008), Chile (Quinzio, 1987; Covacevich et al., 1991; Aberhan,
126 1994, 2004; Hillebrandt, 2000b; Pérez et al., 2008) and Argentina (Riccardi et al., 1988,
127 2004; Damborenea, 2002). A regional biostratigraphic frame based on ammonites is
128 available (Hillebrandt, 2000a, 2000b; Riccardi, 2008a, 2008b).

129

130 **3. Geologic setting**

131 The Neuquén Basin is a back-arc basin of extensional origin developed in the
132 western convergent margin of the South American Plate. Though the marine basin later
133 extended to western San Juan and Neuquén Provinces, marine sediments of Late Triassic-
134 Earliest Jurassic age are limited to one of its northern depocenters in southern Mendoza (see
135 Riccardi et al., 1988, 1991, 1997a), known as the Atuel/Valenciana half-graben (Manceda
136 and Figueroa, 1993) or Atuel depocenter (Figures 1, 2).

137 These deposits have been intensively studied from several points of view:
138 sedimentology and lithofacies (Lanés, 2005), biofacies (Damborenea and Manceñido, 2005),
139 tectosedimentary evolution (Lanés et al., 2008; Giambiagi et al., 2008), and petrofacies
140 (Tunik et al., 2008), and are well-dated by ammonites (Riccardi et al., 1988, 1991, 1997a,
141 1997b, 2004; Riccardi and Iglesia Llanos, 1999).

142 The lithostratigraphic frame used here was established by Riccardi et al. (1997a); we
143 follow Lanés (2005, and Lanés et al., 2008) on the depositional systems and environmental
144 interpretation; and the local biostratigraphy is according to Riccardi (2008a, 2008b; Figure
145 3). All deposits studied here belong to a synrift phase (Lanés 2005) and were interpreted as
146 deposited in a fandeltaic environment.

147 The Arroyo Malo Formation (Riccardi et al., 1997a) crops out in the Arroyo Malo
148 halfgraben (Giambiagi et al., 2008) in the core of an anticline at Arroyo Alumbre, a
149 northern tributary of Arroyo Malo (Figure 2), and it comprises the lower 286 m of marine
150 sediments in our logged section (Figure 4). At its type-locality the base does not crop out,
151 and this unit comprises sediments of late Triassic to early Hettangian age. Lanés et al.
152 (2008) recognized a facial stacking pattern including five facies, with plane-laminated

153 mudstone deposits and low-density turbidites at the base, followed by high and low-density
154 turbidites, slump-derived cohesive debris flows and sedimentary deformation, and ending
155 with channelled hyperconcentrated flow deposits, high and low density turbidites, and
156 traction current deposits in lenses alternating with tabular beds of intraformational breccia
157 and massive mud-supported conglomerates. There is an upwards increasing trend of debris
158 flow, hyperconcentrated flow, and traction current deposits, and an upwards widening of
159 lenses and trough-cross bedded sandstones (Lanés, 2005). Deposits of the Arroyo Malo
160 Formation were interpreted as ranging in palaeoenvironment from basin area far from the
161 delta front to slope-type fan delta upper front below wave base (Lanés et al., 2008). The last
162 30-40 m deposits are large lenses of pebbly sandstones and clast-supported conglomerates
163 which were either referred to the El Freno Formation (Riccardi et al., 1997a; Lanés, 2005) or
164 to the top of the Arroyo Malo Formation (Lanés et al., 2008; Echevarría et al., 2017; here).

165 The upper 600 m of the logged section are referred to the lower section of the Puesto
166 Araya Formation. Facies associations include well-bedded coarsening and thickening
167 upwards low and high-density turbiditic sections, with usual slump folds, alternating with
168 plane laminated mudstones, intraformational breccias and sandstones, and massive pebbly
169 mudstones (Lanés et al., 2008). The Arroyo Alumbre/Malo section ends with tabular beds of
170 tangential cross-bedded sandstones cut by channelled trough-cross bedded sandstones
171 interpreted as mouth bars cut by distributary channels (Lanés, 2005).

172

173 **4. Material and methods**

174 *4.1. Database*

175 The database here analyzed was built up after more than 30 years of sampling along
176 the Arroyo Malo section, resulting in a high sample intensity and homogeneity across the
177 logged section. One hundred samples with invertebrates were gathered from the Rhaetian-
178 early Sinemurian interval (comprising more than 800 m thickness) at two measured sections
179 at Arroyo Alumbre and from other isolated localities of the Atuel river region, southern
180 Mendoza Province, Neuquén Basin (Figure 1). Sections were measured by Riccardi et al.
181 (1988, 1991, 1997a, 1997b, 2004; see also Damborenea, 2002; Damborenea and Manceñido,
182 2012). Some of the specimens were collected from the same sections by Silvia Lanés, who
183 analyzed in detail the sedimentology (Lanés, 2005; Lanés et al., 2008).

184 All bivalve taxa were identified at the species level by SD, and to avoid distortions
185 due to differences in scope in species concept only data from own or personally studied
186 collections were used for this analysis. The late Triassic fauna was recently systematically
187 reviewed (Damborenea and Manceñido, 2012); on the other hand, most of the
188 Hettangian/Sinemurian bivalves are still awaiting systematic revision, and thus many of the
189 recognized species are named using open nomenclature. Specimens related to this study are
190 housed in the Invertebrate Palaeontology collections of the La Plata Natural Sciences
191 Museum (MLP).

192 To perform the ecologic analyses all recognized species were assigned to one of five
193 available categories: epifaunal attached (EA); epifaunal free lying (EF); semi-infaunal
194 attached (SIA); infaunal shallow burrower (ISB); and infaunal deep burrower (IDB).
195 Epifaunal attached bivalves were mostly epibyssate, with only one species fully cemented
196 (*Liostrrea* sp.) and one cemented only during juvenile stages (*Gryphaea* sp.), which was
197 assigned to the free lying category. When required, especially to compare with other basins,
198 cemented [EA(C)] and epibyssate [EA(B)] taxa were discriminated. Among shallow
199 burrowers only one detritus feeding species (*Palaeoneilo* cf. *elliptica*) was identified, hence
200 they were all grouped together in the category ISB, discriminating when necessary between
201 ISB(S) for suspension feeders and ISB(D) for detritus feeders.

202 The location of samples containing bivalve specimens and the actual occurrence of
203 each species in the section recorded in meters above the base of a combined section are
204 shown on Figure 4. Whenever possible, samples were dated according to ammonite
205 occurrences. The relative abundance of taxa was not systematically recorded and thus only
206 presence/absence data are used for this first analysis.

207 As a result most biases can be considered minimized: sampling intensity was even
208 across the section; within the section the main marine biofacies recognized by Damborenea
209 and Manceñido (2005) are well represented, so facies control on the data can be neglected.
210 Environmental conditions at the time of deposition were determined using Lanés' detailed
211 sedimentary analysis of the same sections (Lanés, 2005; Lanés et al., 2008).

212 The main bias to take into account during the analysis is the edge effect, i.e., the
213 apparent declination of diversity as we approach to the edges of analyzed strata due to
214 incompleteness of the fossil record (Raup, 1972; Foote, 2000). This is notorious for the

215 Triassic, since it is a minor proportion of the section extension (about 22%) and is bounded
216 by the base of the section and by the mass extinction at its top. Although the range of the
217 species known to be present in the basin on subsequent stages was extended, there is a
218 regional hiatus in the fossil record affecting the top of the section, so an increase on
219 extinction levels and a reduction on apparent diversity are also expected at this point due to
220 the edge effect.

221

222 4.2. Analytic methods

223 A diversity curve was constructed considering the first and last appearance data for
224 each species (FAD and LAD respectively); for the species known to be present in the basin
225 afterwards, the LAD in the section was not considered. Floated *ex-situ* material was only
226 taken into account when its stratigraphic provenance could be narrowed to short intervals. It
227 was not considered when building the general diversity curve, but it was used during the
228 ecologic analysis and to examine the faunal composition of the gross time bins analyzed
229 (Triassic, Jurassic recovery, Jurassic equilibrium). As a consequence, overall diversity will
230 be underestimated in the general diversity curve (especially for the Triassic), but its main
231 changes will be better represented. The degree of resolution used is one meter (e.g., samples
232 collected at 182.1 and 182.4 meters were considered as a single sample at 182 meters). As a
233 consequence, despite being a continuous section, the analyses can be perceived as performed
234 on one meter bins.

235 Preservation potential across the section seems to be roughly homogeneous. A mean
236 of 2.31 identified species per level could be recognized in Triassic strata, while a mean of
237 2.95 identified species per level were recovered from Jurassic strata. When compared to
238 relative extension within the section these data result in 0.20 identifications per meter for the
239 Triassic and 0.18 identifications per meter for the Jurassic. The term identification refers
240 here to species identified in a sample, so if a species was identified in two samples, it will be
241 counted twice. This suggests that the lower diversity seen in the Triassic is simply the
242 consequence of having less thickness to study. When the *ex-situ* material is included, this
243 difference in diversity strongly decreases.

244 Two diversity metrics were used: total diversity (TD), i.e., for each sample: all
245 species actually present in a sample plus the species present lower and higher in the section,

246 though not in the sample; and boundary crossers (BC) at the top of the sample-bin, i.e., all
247 species present before and after the top of the sample-bin (Foote, 2000). This last
248 measurement avoids singletons (i.e., species present in a single sample), which may
249 represent mostly taphonomic biases or extremely rare species, especially considering that
250 this is the analysis of only one section.

251 In order to analyze instantaneous rates of origination and extinction, the number of
252 FADs and LADs were divided by BC measure from the bottom boundary (i.e., the number
253 of species entering the bin). Since BC measure avoids singletons, these were not counted
254 among the FADs and LADs. The results obtained by this method correspond very well with
255 those obtained using the estimated *per-capita* rates (Foote, 2000), but are easier to visualize.
256 It must also be pointed out that these rates will represent local origination rate (i.e., covering
257 origination and immigration) and local extinction rate (i.e., the species might be found in
258 other basins afterwards).

259 To check for general trends in origination and extinction, cumulative FADs and
260 LADs were compared to meters from the base, this time considering also singletons. When
261 doing this comparisons regression lines were calculated, by ordinary least squares between
262 FAD/LAD and section thickness. The slope of the regression lines of FADs and LADs
263 against thickness will represent the number of species originating or going extinct per meter
264 during the interval considered.

265 Based on the sediment thickness for the Hettangian, the only complete stage within
266 the section, an average sedimentation rate (ASR) can be calculated. According to the
267 International Commission of Stratigraphy (2017) time scale, the Hettangian lasted 2 my, and
268 in the log section is represented by about 400 meters. This results in an ASR of 0.2 m/ky, or
269 one meter of sediment every 5000 years. This value was used to estimate origination and
270 extinction rates relative to time.

271

272 **5. Results**

273 *5.1. Systematic diversity trends*

274 Figure 5 shows the diversity curve for both metrics (TD and BC). The lower
275 diversity shown by the Triassic strata is most probably caused by the edge effect (see

276 Material and Methods). When *ex situ* samples are included, diversity seems closer to that
277 seen for the Hettangian-Sinemurian.

278 Bivalve diversity curve clearly shows a major diversity drop at the end-Triassic
279 (finishing in the lower-most Hettangian) followed by a gap in the bivalve fossil record,
280 roughly encompassing the *Psiloceras primocostatum* to *P. rectocostatum* Zones (\approx Planorbis
281 Z). After that, diversity starts to rise in the *Kammerkarites bayoensis* (\approx early Liasicus)
282 Zone followed by an increase peak in the *Discamphiceras reissi* (\approx late Liasicus) Zone. All
283 these major changes in diversity can also be noticed from the instantaneous rates (Fig. 5).

284 Also probably due to the edge effect, diversity drop at the end-Triassic may appear
285 more gradual than it might have been. Interestingly, diversity rise during the Hettangian is
286 sharper than the extinction. This is most likely a taphonomic bias: the 360 m sample comes
287 from a relatively rich fossiliferous level. When long term trends of origination and
288 extinction are calculated (Fig. 6) this sample can be clearly seen as an outlier in the
289 origination regression line, and the extinction phase appears much shorter than the total
290 recovery phase.

291 When the cumulative FADs and LADs are plotted against section thickness, the
292 difference between both curves represents the diversity changes through time (shaded area
293 in Fig. 6). Four main phases were identified and characterized by their regression lines (see
294 also Table 1): a first one (*Triassic equilibrium phase*) of almost parallel regression lines with
295 relatively high rates (0.044 species/m for origination and 0.046 species/m for extinction); a
296 second one (*extinction phase*) with high extinction rates (0.077 species/m) and low
297 origination rates (0.011 species/m); a third one (*recovery phase*) of high origination rates
298 (0.066 species/m) and almost null extinction rates (0.005 species/m); and a fourth one
299 (*Jurassic equilibrium phase*) of almost parallel regression lines, with moderate rates (0.027
300 species/m for origination and 0.032 species/m for extinction). The extinction and recovery
301 phases are separated by a gap of about 135 meters with almost no identifiable benthonic
302 invertebrates, although ammonites are present and a few beds with shell hash indicate the
303 presence of shelly fauna. The only bivalve species which spans this gap in the region,
304 according to its records in the section just before and after it, is the pectinid *Praechlamys* cf.
305 *valoniensis*, which is then the single detected bivalve survivor through the T/J crisis. Though
306 not considered as a phase *per se* (since there are no data to analyze or characterize it) the gap

307 between extinction and recovery will be here referred to as "survivor phase" in figures and
308 tables.

309 Regarding systematic representation of high rank categories, the Triassic shows a
310 diverse pattern, with the 17 identifiable species recovered belonging to 13 superfamilies and
311 10 orders. During the *recovery phase* the orders Limida and Pectinida (either pectinoids or
312 monotoids) seem to dominate, while pholadomyoids, pinnoids, crassatelloids and ostreoids
313 were represented by a single species each. High rank taxa are more equally represented
314 during the *Jurassic equilibrium phase*; the order Pectinida is still the most diverse, Limida is
315 represented by only one species by the end of the span; and many other orders are again
316 recorded in the basin.

317

318 5.2. Palaeoecologic diversity trends

319 Bivalve palaeoecologic diversity shows some peculiarities. The five main
320 autoecologic categories are present throughout most of the section (Fig. 7), though epifaunal
321 free-lying and semi-infaunal attached bivalves were not recorded from Triassic outcrops.
322 Considering the Triassic sample as a whole (including the *ex-situ* samples), infaunal habits
323 seem to dominate over epifaunal ones. Associated fauna includes brachiopods (free-lying
324 and pedunculate), gastropods, a coral colony and diverse cephalopods (ammonoids,
325 nautiloids, coleoids).

326 Two identifiable taxa surpass the Triassic/Jurassic boundary: *Neoschizodus?* sp. (its
327 last record in the basin being close to the base of the Hettangian) and the long lasting species
328 *Praechlamys cf. valoniensis*. *Sphaeriola?* sp. is represented by a single record in the lower-
329 most Hettangian. The last record of *Neoschizodus?* sp. and *Sphaeriola?* sp. in the earliest
330 Hettangian suggests that in the basin the extinction phase culminated at this stage. The
331 "survivor phase" (190-320 m), encompassing the *Psiloceras primocostatum* and *P.*
332 *rectocostatum* zones (\approx Planorbis), yielded only unidentifiable shell debris (besides
333 ammonites).

334 The recovery phase (319-512 m) shows an increasing trend of absolute diversity,
335 though with a high peak at the beginning (360 m). At this point all autoecologic categories
336 of bivalves are represented, though three of them only by one species and other by two (Fig.
337 7). Nine of fifteen species (60%) are epifaunal attached (all epibyssate), and this ecological

338 category together with the infaunal deep burrower are the only two increasing in diversity
339 during this interval (Fig. 7). Associated fauna is represented by solitary corals, brachiopods,
340 a possible scaphopod, gastropods, ammonites and crinoids.

341 The final Jurassic equilibrium stage shows a somewhat stable diversity, decreasing at
342 the end most likely due to the edge effect. Twenty-nine species have been identified for the
343 interval, though standing diversity never reached the twenty species. Although epifaunal
344 attached bivalves are still dominant (12 species: 41%), they decrease during this time lapse
345 (by the end of the section there are only 5 species out of 15, Fig. 7). Infaunal shallow
346 burrowers diversify a little (5 species: 17%) though they do not reach the diversity levels
347 seen during the Triassic and the maximum standing diversity observed is 3 species. Infaunal
348 deep burrowers continue to diversify, as well as epifaunal free-lying bivalves (species of
349 *Entolium*, *Lywea*, *Kolymonectes*). The associated fauna is still diverse, with mobile epifauna
350 (gastropods, regular echinoids), nektonic and nekto-benthonic cephalopods (ammonoids and
351 nautiloids) and solitary corals. No crinoids were found at this stage and curiously no
352 brachiopods.

353

354 **6. Discussion**

355 *6.1. Diversity pattern*

356 The pattern of diversity variation can be clearly subdivided in four phases and a gap
357 ("survivor phase", Figs. 5, 6 and 7). The parallel regression lines for FADs and LADs vs.
358 thickness clearly point to times of relatively stable diversities (equilibrium phases). The
359 steeper slopes for Triassic equilibrium phase might be related to the edge effect. Despite the
360 diversity underestimation, the recognition of a Triassic equilibrium phase allows for the
361 delimitation of a relatively short (about 325 ky) extinction interval. In comparison, and in
362 spite of the sudden diversity increase given by the 360 m sample bin, recovery lasts at least
363 three times longer (about 965 ky) or even five times if we also consider the "survivor phase"
364 (about 675 ky). This data is similar to that found in Great Britain, where after a fast
365 extinction a relatively slower recovery (though within the Hettangian) was observed
366 (Wignall and Bond, 2008). Though a "survivor phase" can be recognized on Wignall and
367 Bond (2008) data, it shows higher diversity than in the section analyzed on this paper. This
368 suggests a particularly severe end-Triassic extinction in the Neuquén Basin, with only two

369 of eighteen species surviving the boundary, and one of them disappearing shortly after.
370 Nevertheless, the extinction proportion (about 89%) is in accordance with other species-
371 level analyses (McRoberts and Newton, 1995).

372 According to Hallam (1996) the bivalve diversification trend during the recovery
373 seems to continue until the lowermost Sinemurian in Great Britain. On the other hand the
374 known example from Tibet shows an almost instantaneous recovery instead (Hautmann et
375 al., 2008), though data are not recorded on a section-thickness base in that case. Broad
376 bivalve species diversity in the Tibetan section is similar to our data (14 taxa for the
377 uppermost Triassic and 24 for the lowermost Jurassic), but extinction proportion is much
378 lower (57%). All this suggests a general diversity pattern for our region more similar to
379 Europe than to the Tibet examples, but this is just a limited statement and should not be read
380 as a generalization, since these are the few known examples with enough comparable data.

381

382 *6.2. Ecologic pattern*

383 The high ecologic diversity in Tibet somewhat matches the early diversity in
384 Argentinian section (Fig. 8), though in the South American basin species diversification
385 probably lasted longer and the ecological categories represented, together with their relative
386 abundance, differed markedly.

387 During the Triassic the proportion infaunal/epifaunal in the Neuquén Basin (Fig. 8)
388 was slightly dominated by infaunal habits (53% vs. 47%). In the Southern Alps and
389 Northwest Europe (McRoberts and Newton 1995) proportions were similar (46%
390 infaunal/44% epifaunal and 50% infaunal/46% epifaunal respectively), while in the
391 Northern Alps (McRoberts and Newton, 1995) and Tibet (Hautmann et al., 2008) epifaunal
392 habits clearly dominated (32% infaunal/60% epifaunal and 36% infaunal/64% epifaunal
393 respectively). Given the low diversity recorded, the absence of semi-infaunal attached and
394 free-lying habits might be a sampling bias (they are not very frequent and the Triassic
395 portion of the section is highly affected by the edge effect). Otherwise, general proportions
396 for the different life habits are similar to those found in Europe (McRoberts and Newton,
397 1995). Comparison is again restricted to the few regions with available data. Yet, dominance
398 of infaunal habits coincides with global studies which show that infaunal bivalves surpassed
399 in diversity epifaunal ones during the Late Triassic (Stanley, 1968; Ros and Echevarría,

400 2011). At the very end of this phase, three bivalve species are recorded: a) a very doubtful
401 *Neoschizodus?* sp., with its record range ending there; b) *Praechlamys* cf. *valoniensis*
402 (Defrance), which is clearly a survivor into Hettangian and even Sinemurian times; and c)
403 one specimen of doubtful affinities, referred to *Sphaeriola?* sp.

404 After the end-Triassic extinction a long “survivor phase” was identified (135 m,
405 about 675 ky). During this phase, spanning the *P. primocostatum* to *P. rectocostatum* Zones
406 (\approx Planorbis), no benthonic fauna was recorded. It might be considered as the survival
407 interval (*sensu* Kauffman and Erwin, 1995; Kauffman and Harries, 1996), though it must be
408 pointed out that no disaster or opportunistic species were detected in this section.

409 Despite the fact that only one species can be considered as survivor from the end-
410 Triassic extinction event, the posterior scarcity of infaunal habits (38% vs 55% for epifaunal
411 ones) suggests a similar pattern (favouring epifaunal life habits) to that found by McRoberts
412 and Newton (1995) for Europe. Based on that pattern they suggested a drop in primary
413 productivity as potential killing mechanism, since epifaunal bivalves are more efficient
414 filter-feeders than infaunal ones. This pattern is even more evident in the Tibet section (13%
415 infaunal habits vs. 75% epifaunal ones in the Jurassic, Hautmann et al., 2008). One main
416 difference is the strong abundance of bivalves with cementing habits in Tibet, which are
417 almost absent in the Neuquén Basin for the Hettangian-Sinemurian (only juveniles of
418 *Gryphaea* sp. can be regarded as cemented). This may simply reflect availability of suitable
419 substrates in Tibet.

420 The recovery phase can be compared to the recovery interval (*sensu* Kauffman and
421 Erwin, 1995; Kauffman and Harries, 1996), though neither Lilliput effect or beds dominated
422 by opportunistic taxa were recorded among bivalves from this region. The earliest
423 Hettangian benthonic fauna recorded here after the long barren interval occurs within the *K.*
424 *bayoensis* (\approx early Liasicus) Zone, has low bivalve diversity (2 epifaunal species), and is
425 accompanied by few gastropod and isolated crinoid remains. This might be referred to a
426 recovery stage 1 (*sensu* Twitchett, 2006), though the presence of crinoids would indicate
427 some tiering differentiation. At 360 m (within the *D. reissi* (\approx late Liasicus Zone) there was
428 a relatively rich fossiliferous shell bed with more diverse bivalves (the same 2 species
429 recorded earlier plus at least 6 other species, including epifaunal and infaunal ecologic
430 types); the first brachiopods (2 species) and solitary corals (Echevarría et al., 2017) recorded

431 after the extinction appear also at this level. Tiering is fully recovered at this point (recovery
432 stage 4 *sensu* Twitchett, 2006), since there are deep burrowers (pholadomyids, see Fig. 7),
433 shallow burrowers (venerids), semi-infaunal molluscs [*Pinna (Pinna)* sp.], low epifaunal tier
434 (limids, pectinids, brachiopods) and high epifaunal tier (crinoids, solitary corals?). Mobile
435 epifauna (gastropods) and nektonic fauna are also represented. If we consider the
436 sedimentary thickness between the beginning of the “survivor stage” (about 184m) and the
437 360m sample, a time lapse of 880 ky can be estimated. This clearly points to a relatively fast
438 ecologic recovery, though the ongoing increasing diversity suggests that this recovery had
439 not yet been fulfilled at this point. It must be also pointed out that the epifaunal attached
440 byssate life habit dominated the ecologic diversity, accounting for the preeminence of the
441 Pectinida and Limida at this phase. Only *Palmoxytoma cf. cygnipes* and *Antiquilima?* sp. are
442 characteristic of this phase, all other bivalves being long-lived elements common in the
443 following Jurassic equilibrium phase.

444 During the Jurassic equilibrium phase, marked by the relatively stable diversity of 16
445 to 18 bivalve species, the change in proportions between the different ecologic categories
446 was remarkable. The lack of two highly stenohaline groups like crinoids and particularly
447 brachiopods (a widespread group in the Jurassic of the basin), is suggestive of some sort of
448 salinity anomaly during this last phase. This agrees with the prograding interpretation within
449 a deltaic environment made by Lanés (2005), though the presence of other stenohaline
450 groups, like corals and ammonoids, indicates that any salinity variation should have been
451 subtle. On the other hand, this potential environmental alteration is insufficient to explain
452 the ecologic changes in bivalve associations, marked by the reduction of epifaunal habits
453 and slight diversification of infaunal ones (especially deep burrowers), though epifaunal
454 habits still dominate. Consequently, the ecological changes observed for bivalves during the
455 Sinemurian in the analyzed section might result from ecologic successions in an
456 environment more favorable for epifaunal habits, rather than the consequence of particular
457 facial/ environmental variations along it. This dominance (with both attached and free lying
458 habits well represented) is a common feature of Pliensbachian bivalve faunas in Neuquén
459 Basin. At that stage the basin expanded extensively towards the south (Fig. 1), at the same
460 time increasing its facial diversification, which may have favored epifaunal diversity.

461

462 6.3. *Taxonomic composition through time*

463 From the palaeobiogeographic point of view, there was a high proportion of
464 endemism in Late Triassic faunas here discussed, but the local diversity trends at species
465 level for the recovery phase cannot be discussed because the systematic revision is still
466 underway. Instead, it is possible to analyze the generic composition of the bivalve faunas
467 through time. Genera were assigned to one of six evolutionary/biogeographic categories
468 according to their known previous records of local and global occurrences: A) genera
469 globally extinct in the Rhaetian, B) genera surviving the T/J boundary in this section, C)
470 genera surviving the T/J boundary in the basin but not recorded in the Jurassic of this
471 particular section, D) genera known from the Triassic elsewhere but immigrant into de
472 Neuquén basin in the Jurassic; E) genera originated in the Jurassic elsewhere and immigrant
473 into the Neuquén basin; and F) genera originated in the Jurassic in the Andean region, i.e.
474 regionally endemic genera (Table 2).

475 It is interesting to point out that at the generic level the number of taxa recorded in
476 this section before and after the extinction are similar: 18 genera were recorded in the
477 Triassic and 20 in Hettangian-early Sinemurian.

478 From the 18 bivalve genera present in the late Triassic of the studied section, only
479 four became globally extinct before the end of the Triassic (A in Table 2): *Palaeocardita*,
480 *Septocardia*, *Cassianella*, and *Minetrigonia*. Small doubtful specimens from the earliest
481 Jurassic were very doubtfully referred to *Neoschizodus?* sp. Three genera appeared in the
482 Jurassic: *Palmoxytoma*, *Ceratomya* and *Lywea* (E and F in Table 2). All other genera are
483 also known (here or elsewhere) to have persisted into the Jurassic. Of these, only five genera
484 survived in the study area (B in Table 2), three of them being represented after the extinction
485 event by a different species (*Pseudolimea*, *Otapiria* and *Pholadomya*), whilst *Praechlamys*
486 cf. *valoniensis* is the only species that spanned the boundary. Nevertheless, it is evident that
487 some of the genera present in the Triassic of this section did survive elsewhere in the region,
488 as they are known from later Early Jurassic beds of the Neuquén Basin (C in Table 2), these
489 include *Palaeoneilo*, *Asoella*, *Cultrioipsis*, *Liostrea* and *Nicaniella*.

490 Although known from the Triassic around the world, the following genera have not
491 yet been recorded in Triassic beds of the Neuquén Basin, but are present in the early
492 Jurassic, thus they may be regarded locally as early Jurassic immigrants (D in Table 2):

493 during the Hettangian *Camptonectes*, *Entolium*, *Agerchlamys*, *Plagiostoma*, and *Kalentera*
494 are locally recorded. To these, *Pinna*, *Eopecten*, *Antiquilima*, *Gryphaea* and *Pleuromya* may
495 be added, although they are known from late Triassic of northern Chile (Hayami et al., 1977;
496 Chong and Hillebrandt, 1985; Rubilar, 1998). There is also a small group of early
497 Sinemurian immigrants, which includes *Inoperna*, *Kolymonectes*, *Frenguelliella* and
498 *Prosogyrotrigonia*. *Lywea* is the only genus originated in the Andean region during the
499 early Jurassic (F in Table 2). All these genera (categories B to F) are ubiquitous elements of
500 later Early Jurassic South American faunas.

501

502 **7. Conclusions**

503 Four phases of biotic recovery after the end-Triassic extinction event can be clearly
504 distinguished in the Neuquén Basin on the basis of the analysis of marine bivalve diversity
505 through time (from Rhaetian to Early Sinemurian), each characterized by the relative
506 relationships between regression lines of cumulative FADs and LADs: Triassic equilibrium,
507 extinction, recovery and Jurassic equilibrium.

508 After a barren interval with no benthonic fauna, spanning most of the Planorbis
509 Zone, bivalve fauna recovery was relatively rapid, within the Middle and lowermost Late
510 Hettangian (*K. bayoensis* to *S. peruvianus* local ammonite Zones, equivalent to Liasicus to
511 early Angulata Zones).

512 The taxonomic composition analysis through time (at the generic level) suggests that
513 the recovery was mainly triggered by immigration into the basin of widely distributed
514 genera, and the origination of new taxa was restricted.

515 Of the five main autoecologic categories (epifaunal attached, epifaunal free lying,
516 semi-infaunal attached, infaunal shallow burrower, and infaunal deep burrower), two
517 (epifaunal free-lying and semi-infaunal attached) were not recorded from Triassic outcrops.
518 Considering the Triassic sample as a whole, infaunal habits seem to dominate over epifaunal
519 ones. At the recovery phase all autoecologic categories of bivalves are represented.

520 This new set of local data provides an important addition to the knowledge of Early
521 Jurassic biotic recovery in the Southern Hemisphere, and can be compared with information
522 from other latitudes to contribute to future global analyses.

523

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530

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768 **Figure 1.** Location map. **A.** General palaeogeographic situation (modified from Legarreta and Uliana, 2000).
769 **B.** Geologic sketch of the river Atuel area in southern Mendoza province (simplified from Giambiagi
770 et al., 2008), with location of main measured section at Arroyo Alumbre/Malo.

771

772 **Figure 2.** **A:** General view of the Arroyo Alumbre/Malo section from the south, late Triassic sediments crop
773 out at the anticlinal nucleus at the photograph center. **B:** Base of the measured section and outcrops of
774 the Arroyo Malo Formation seen from Arroyo Alumbre.

775

776 **Figure 3:** Biostratigraphic framework for the Early Jurassic of west-central Argentina showing the range of
777 local ammonite and bivalve zones (local ammonite zonation from Riccardi, 2008a, 2008b; bivalve
778 zonation updated from Damborenea, 2002). To the right, inferred distribution and relationships of
779 lithostratigraphic units in the Atuel river region modified from Lanés et al. (2008). Black bar shows
780 extent of Arroyo Alumbre/Malo logged section.

781

782 **Figure 4.** Bivalve species ranges against log in the Arroyo Alumbre/Malo section in the Atuel river region (see
783 location on Figure 1). To the left of section the location of each palaeontologic sample containing
784 bivalves is indicated, shaded bar indicates Triassic/Jurassic boundary zone. Boundaries of ammonite
785 local zones are shown as broken lines. The presence of other macroinvertebrate groups is indicated to
786 the right of the section.

787

788 **Figure 5.** Total diversity against section thickness. (TD) and boundary crossers (BC) along the section.
789 Origination/migration rate and local extinction rate are also shown.

790

791 **Figure 6.** Cumulative FADs and LADs against section thickness and their regression lines (F_1 to F_4 and L_1 to
792 L_4 respectively). Shaded area represents changes in diversity through time.

793

794 **Figure 7.** Ecologic diversity against section thickness. **EA:** epifaunal attached, **ISB:** infaunal shallow
795 burrowers, **IDB:** infaunal deep burrowers, **EF:** epifaunal free lying, **SIA:** semi-infaunal attached.

796

797 **Figure 8.** Life habit percentage composition of some Triassic and earliest Jurassic bivalve assemblages.

798 *Ecologic categories:* **EA(B):** epifaunal attached (byssate); **EA(C):** epifaunal attached (cemented); **EL:**
799 epifaunal free lying; **SIA:** semi-infaunal attached **ISB(S):** infaunal shallow burrower
800 (suspensivorous); **ISB(D):** infaunal shallow burrower (detritivorous); **IDB:** infaunal deep burrower.
801 Tibetan data from Hautmann et al. (2008), European data from McRoberts and Newton (1995).

802

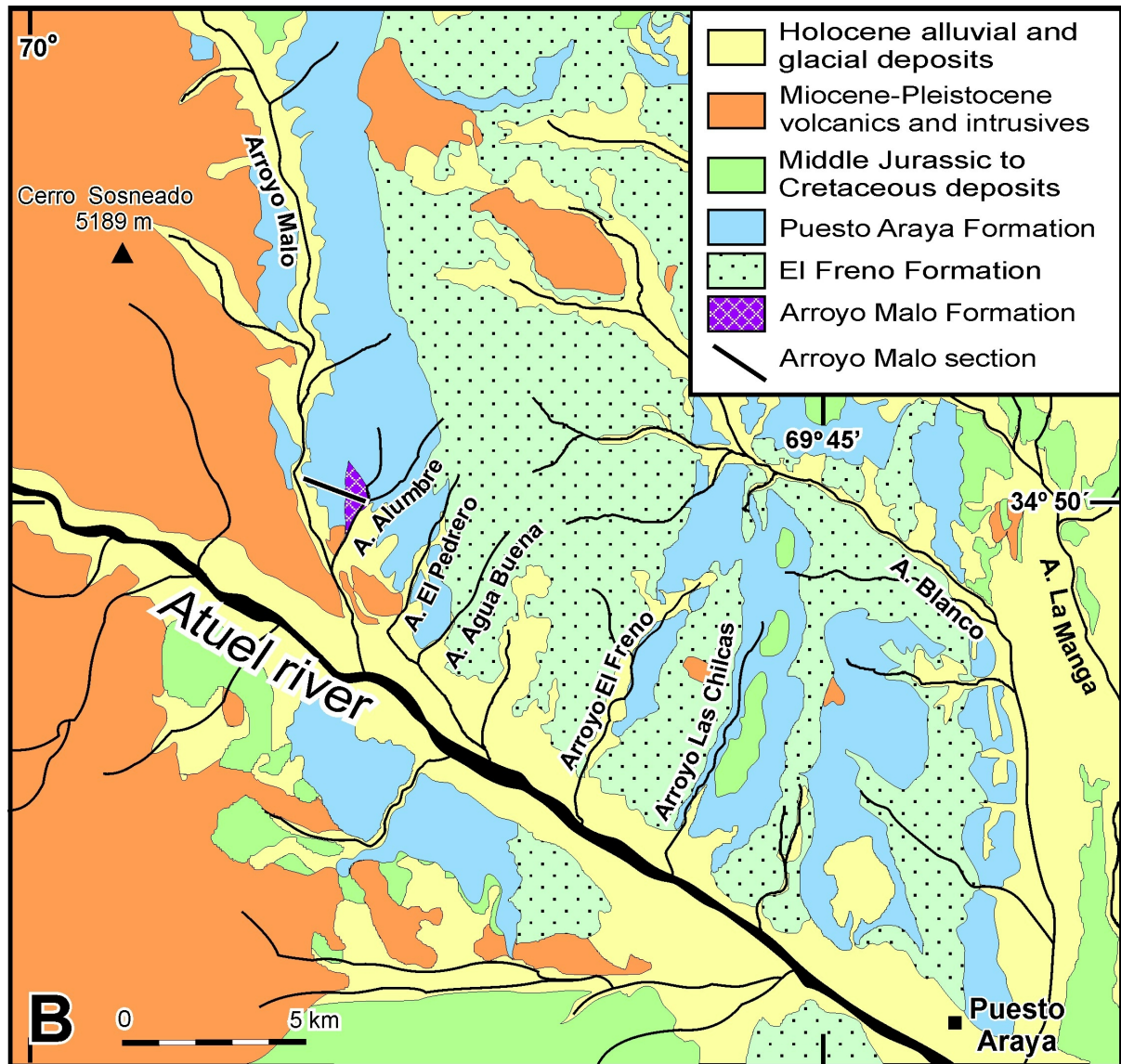
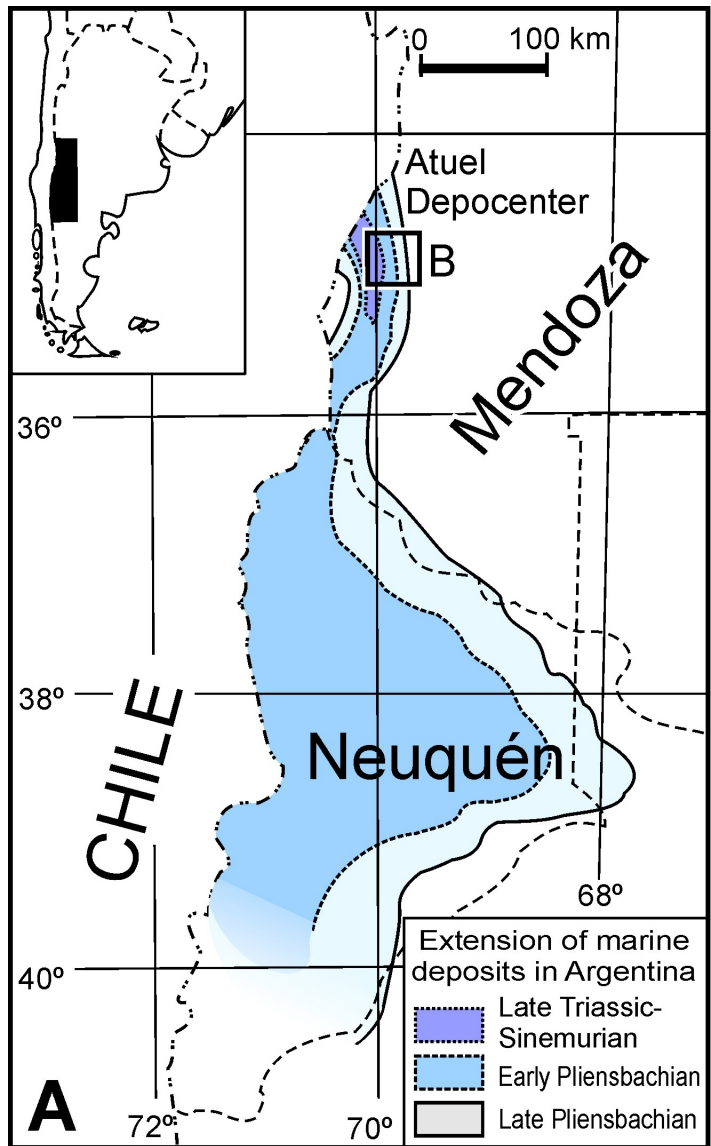
803

804 **Table 1.** Extension and characterization of the recognized phases at the Alumbre/Malo Triassic/Jurassic
805 section. Estimated time in years is included merely for rough comparative reference, since it was based on
806 average sedimentation rates.


807

808

809 **Table 2.** Summary of data from the Alumbre/Malo section analyzed in this paper. *Extinction categories:* **A:**
810 genus globally extinct in the Rhaetian; **B:** genus surviving the T/J boundary in the Alumbre/Malo
811 section; **C:** genus surviving the T/J boundary in the basin but not recorded in the Jurassic of the
812 Alumbre/Malo section; **D:** genus known from the Triassic elsewhere but immigrant into the Neuquén
813 basin in the Jurassic; **E:** genus originated in the Jurassic elsewhere and immigrant into the Neuquén
814 basin; **F:** genus originated in the Jurassic of the Andean region. *Ecologic categories:* **EA(B):** epifaunal
815 attached (byssate); **EA(C):** epifaunal attached (cemented); **EL:** epifaunal free lying; **SIA:** semi-
816 infaunal attached **ISB(S):** infaunal shallow burrower (suspensivore); **ISB(D):** infaunal shallow
817 burrower (detritivore); **IDB:** infaunal deep burrower. *Biogeographic categories* according to Ros et al.
818 (2014)

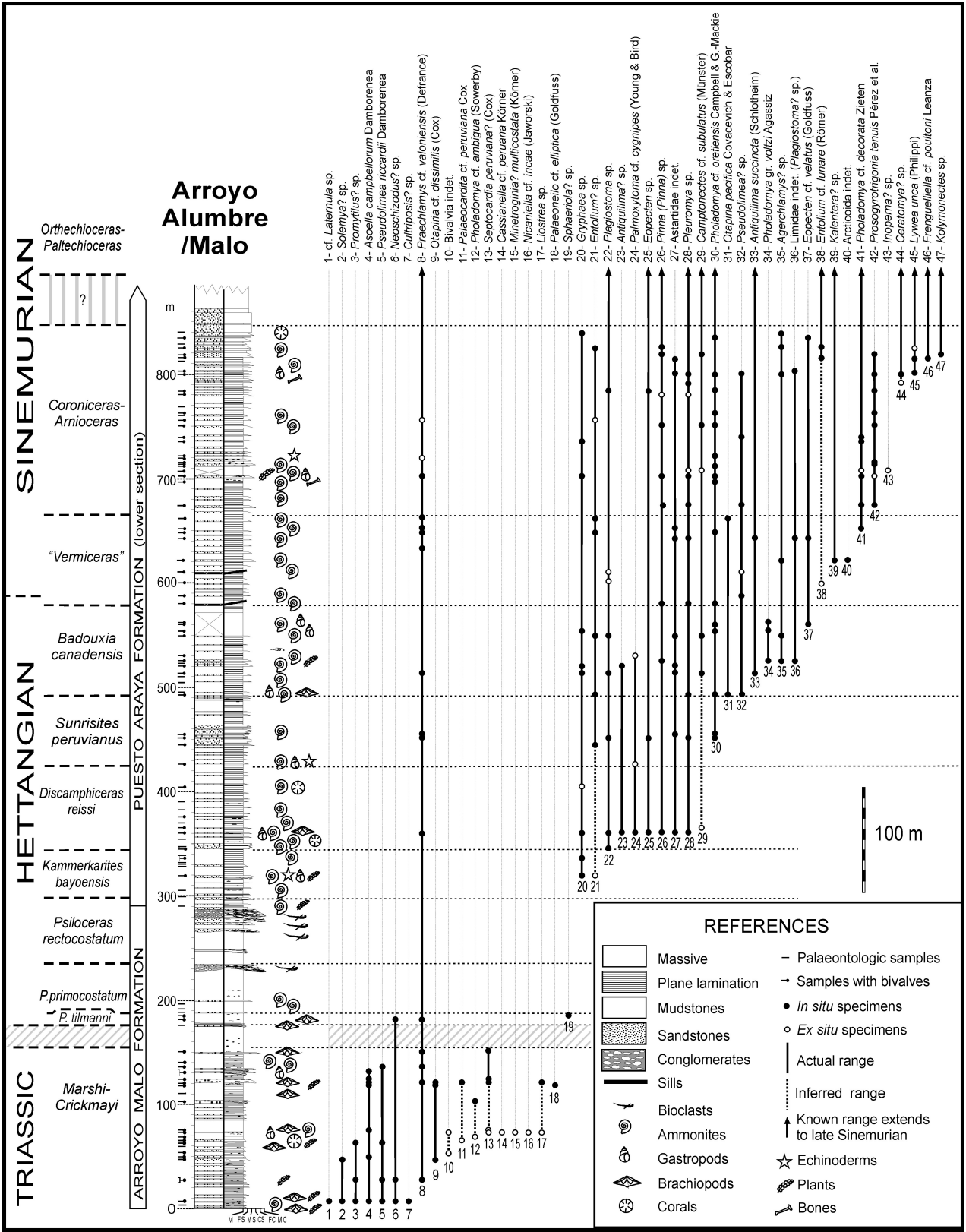


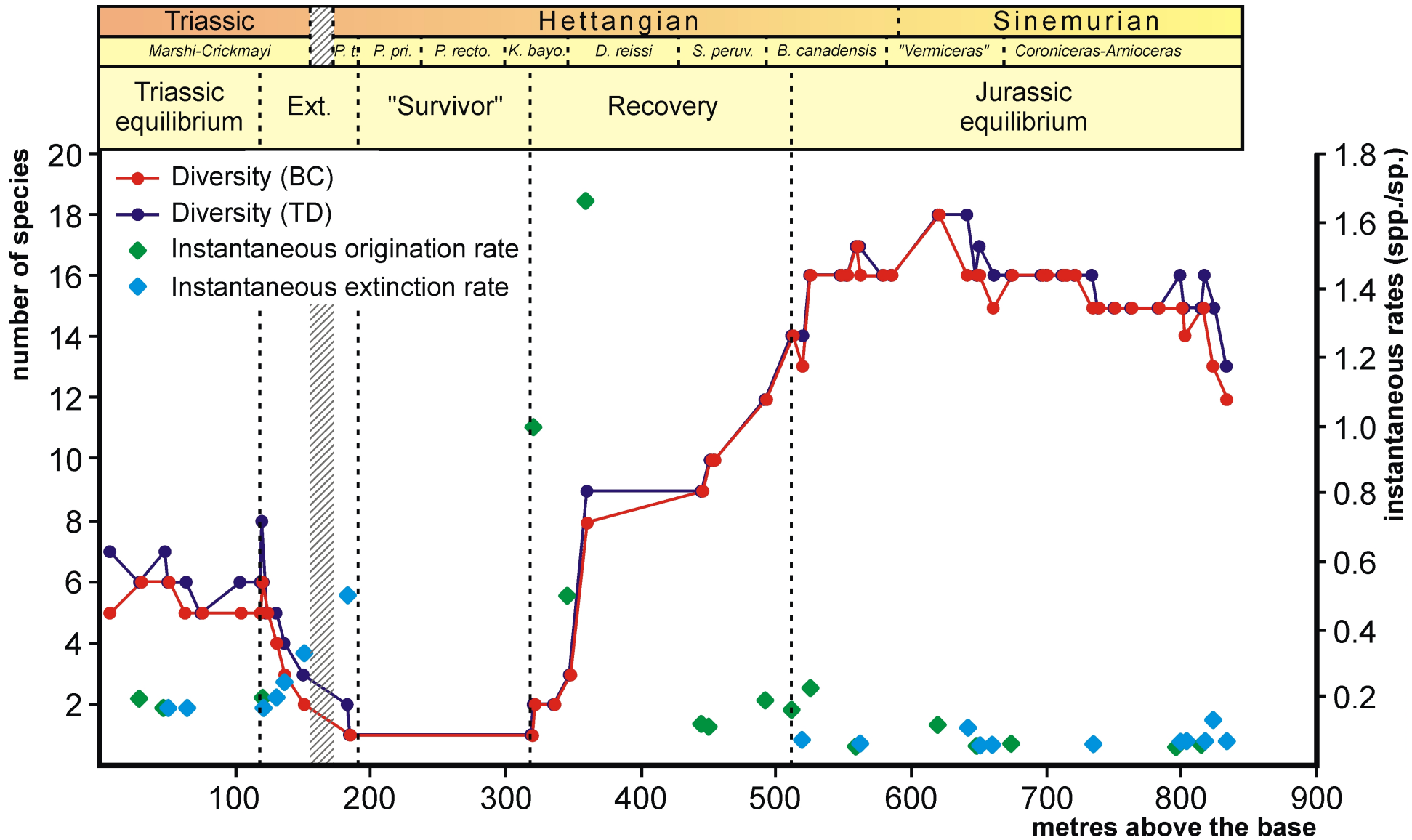


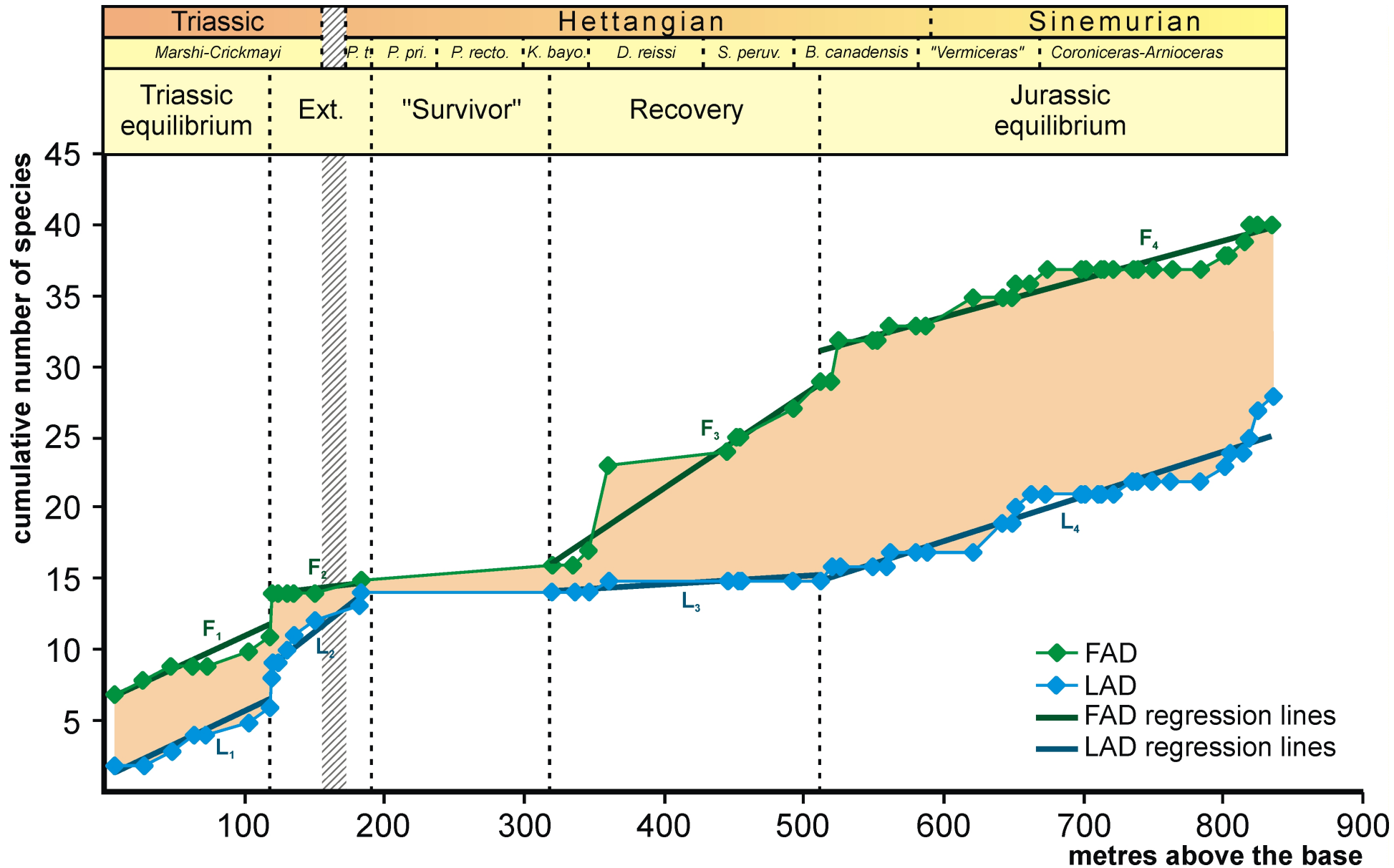
STAGE	AMMONITES		BIVALVES	Western area	Eastern area	
TOARCIAN	AALENSIS	Dumortiera	Meleagrinea 	Tres Esquinas Fm.		
	PSEUDORADIOSA	P. tenuicostatum				
	DISPANSUM					
	THOUARSENSE	Phymatoceras	Parvamussium cf. pumilum			
	VARIABILIS	Collina chilensis				
	BIFRONS	Peronoceras pacificum				
		Peronoceras largaense				
	SERPENTINUM	Dactylioceras hoelderi				
TENUICOSTATUM	TENUICOSTATUM	Posidonotis cancellata				
PLIENSBACHIAN	SPINATUM	Fanninoceras disciforme	Radulonecites sosneadoensis	Puesto Araya Fm.		
	MARGARITATUS	Fanninoceras fannini				
	DAVOEI	A. behrendseni				
	IBEX	Eoamaltheus meridianus	Otapiria neuquensis			
		Meridiceras externum				
JAMESONI	Miltoceras chilcaense					
SINEMURIAN	RARICOSTATUM	Orthechioceras- Paltechioceras	Cardinia cf. listeri	El Freno Fm.		
	OXYNOTUM OBTUSUM TURNERI	?	?			
	SEMICOSTATUM	Coroniceras-Arnioceras	Otapiria pacifica			
	BUCKLANDI	"Vermiceras"				
HETTANGIAN	ANGULATA	Badouxia canadensis	Palmoxytoma cf. cygnipes	Arroyo Malo Fm.		
		Sunrisites peruvianus				
	LIASICUS	Discamphiceras reissi				
		Kammerkarites bayoensis				
	PLANORBIS	Psiloceras rectocostatum				
		Psiloceras primocostatum				
Psiloceras tilmanni						
RHAET.		Marshi-Crickmayi	Septocardia cf. peruviana			

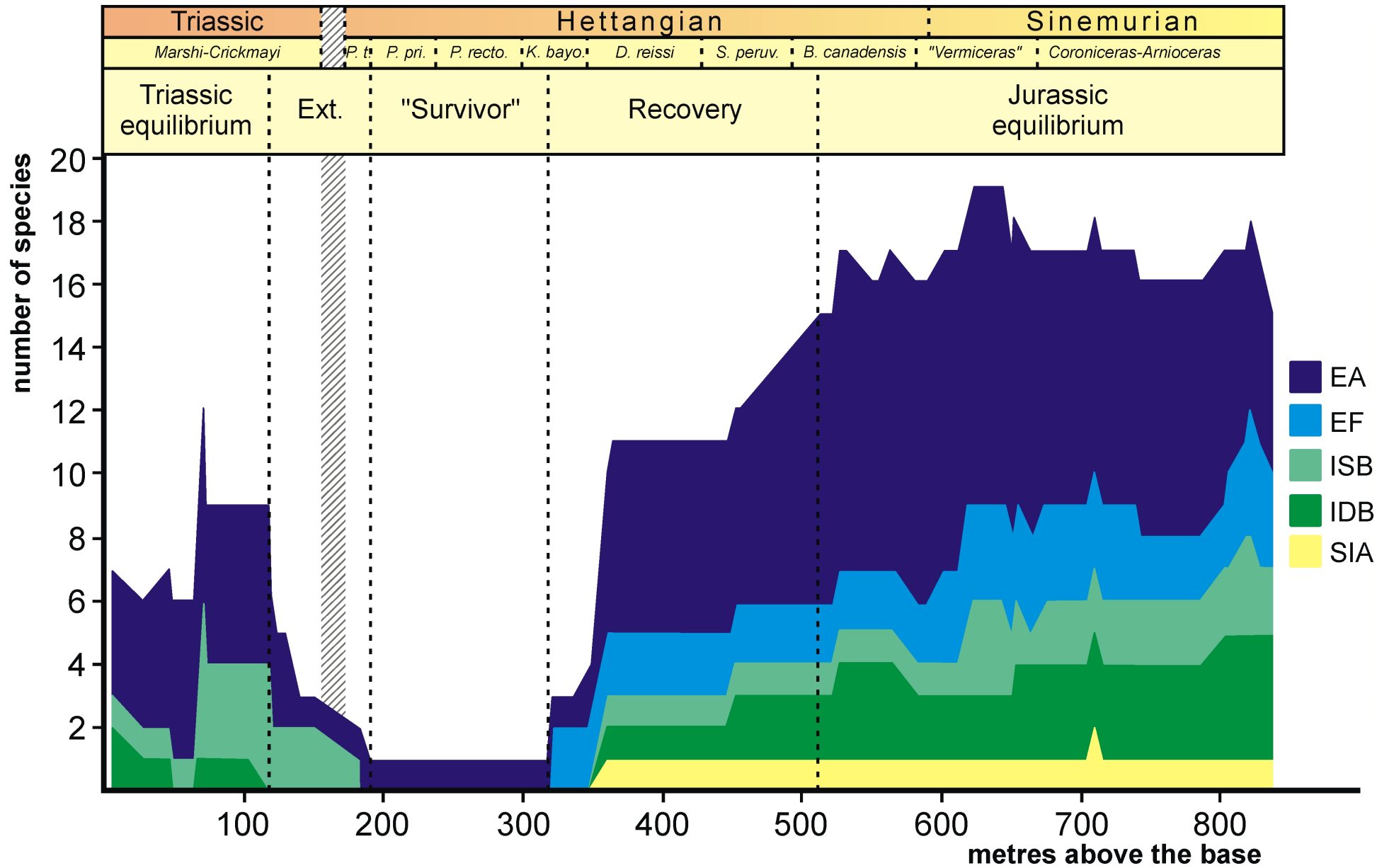
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Neuquén Basin

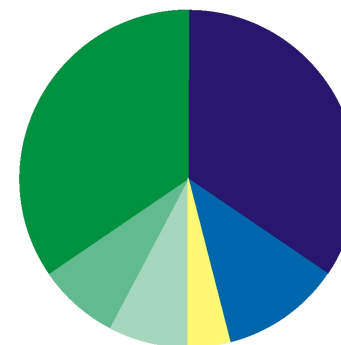
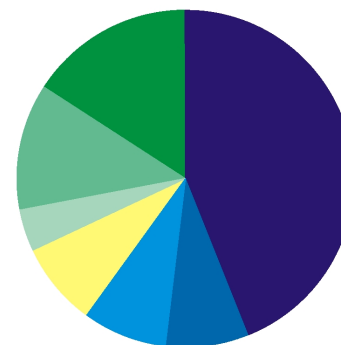
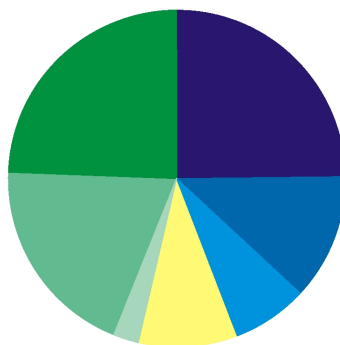
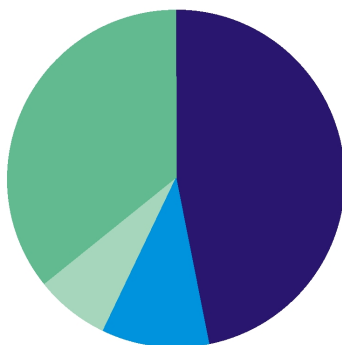
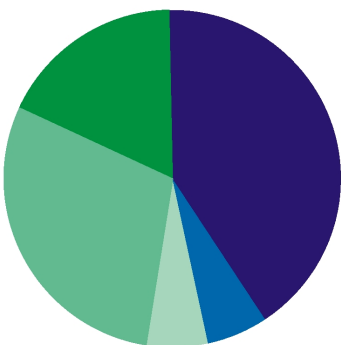
Tibet

Southern Alps

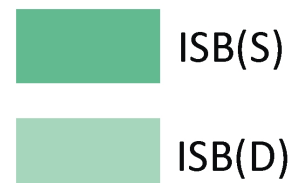
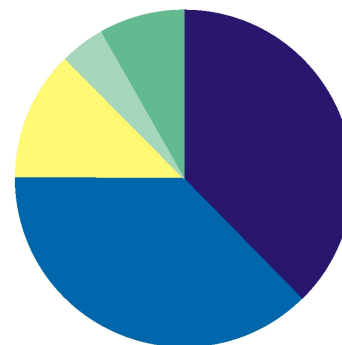
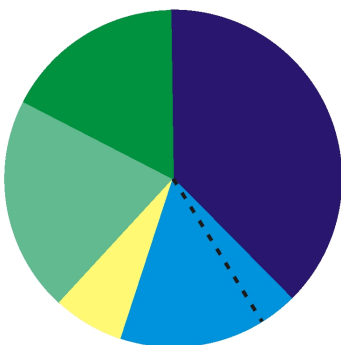
Northern Alps

Northwest Europe

Triassic



Jurassic



Recognized phases	m above base	Time involved (aprox. Zones, see fig. 4 for detail)	Estimated time (ky)	Estimated rates		Regression	
				species/m	species/100,000 years	R2	
Triassic equilibrium	7 to 119	<i>Marshi-Crickmayi</i> to <i>P. tilmanni</i>	560	FAD	0.044	0.88	0.764
				LAD	0.046	0.92	0,876
Extinction	119 to 184		325	FAD	0.011	0,22	0.523
				LAD	0.077	1.54	0.932
"Survivor"	184 to 319	<i>P. tilmanni</i> to <i>P. rectocostatum</i>	675				
Recovery	319 to 512	<i>K. bayoensis</i> to <i>S. peruvianus</i>	965	FAD	0.066	1.32	0.911
				LAD	0.005	0.10	0.716
Jurassic equilibrium	512 to 834	<i>B. canadensis</i> to <i>Coroniceras-Arnioceras</i>	1.610	FAD	0.027	0.54	0.907
				LAD	0.032	0.64	0.927

Genus	species	Range in section		Extinct. cat.	Ecologic cat.	Biogeography category at this age
		m above base	biozones			
" <i>Laternula</i> "	sp.	7	Marshi-Crickmayi	?	IDB	?
<i>Solemya?</i>	sp.	7 to 47	Marshi-Crickmayi	C?	IDB	Tethys-Circumpacific
<i>Promytilus?</i>	sp.	7 to 63	Marshi-Crickmayi	C?	EA(B)	Bipolar?
<i>Asoella</i>	<i>campbellorum</i> Damborenea	7 to 130	Marshi-Crickmayi	C	EA(B)	Tethys, Circumpacific, Austral
<i>Pseudolimea</i>	<i>riccardii</i> Damborenea	7 to 135	Marshi-Crickmayi	B	EA(B)	Cosmopolitan
	? sp.	492 to 800	B. canadensis to Cor-Arnioc		EA(B)	
<i>Neoschizodus?</i>	sp.	7 to 182	Marshi-Crickmayi to tilmanni	B?	ISB(S)	Cosmopolitan
<i>Cultriopsis?</i>	sp.	7	Marshi-Crickmayi	C	EA(B)	Cosmopolitan
<i>Praechlamys</i>	cf. <i>valoniensis</i> (Defrance)	28 to 756	Marshi-Crickmayi to Cor-Arnioc.	B	EA(B)	Cosmopolitan
<i>Otapiria</i>	cf. <i>dissimilis</i> (S. Cox)	47 to 120	Marshi-Crickmayi	B	EA(B)	Circumpacific, Austral, Boreal
	<i>pacifica</i> Covacevich & Escobar	492 to 661	B. canadensis to Vermiceras		EA(B)	
<i>Palaeocardita</i>	cf. <i>peruviana</i> L. Cox	65 to 119	Marshi-Crickmayi	A	ISB(S)	Tethys, Circumpacific, Austral
<i>Pholadomya</i>	cf. <i>ambigua</i> (J. Sowerby)	67 to 103	Marshi-Crickmayi	B	IDB	Cosmopolitan
	cf. <i>oretiensis</i> Campbell & G.Mackie	451 to 834	S. peruvianus to Cor-Arnioc		IDB	
	gr. <i>voltzi</i> Agassiz	525 to 562	B. canadensis		IDB	
	cf. <i>decorata</i>	651 to 739	Vermiceras to Cor-Arnioc		IDB	
<i>Septocardia</i>	<i>peruviana?</i> (L. Cox)	72 to 150	Marshi-Crickmayi	A	ISB(S)	Tethys, Circumpacific, Austral
<i>Cassianella</i>	cf. <i>peruana</i> Körner	72	Marshi-Crickmayi	A	EA(B)	Cosmopolitan
<i>Minetrigonia?</i>	<i>multicostata</i> (Körner)	72	Marshi-Crickmayi	A	ISB(S)	Circumpacific, Austral, Boreal
<i>Nicaniella</i>	cf. <i>incae</i> (Jaworski)	72	Marshi-Crickmayi	C	ISB(S)	Eastern Tethys, Austral?
<i>Liostrea</i>	sp.	72 to 119	Marshi-Crickmayi	C	EA©	Cosmopolitan
<i>Palaeoneilo</i>	cf. <i>elliptica</i> (Goldfuss)	118	Marshi-Crickmayi	C	ISB(D)	Cosmopolitan
<i>Sphaeriola?</i>	sp.	184	P. tilmanni	C	ISB(S)	Cosmopolitan
<i>Gryphaea</i>	sp.	320 to 735	K. bayoensis to Cor-Arnioc	D	EA©	J Cosmopolitan
<i>Entolium</i>	sp.	320 to 824	K. bayoensis to Cor-Arnioc	D	EL	Cosmopolitan
	cf. <i>lunare</i> (Römer)	600 to 824	Vermiceras to Cor-Arnioc		EL	
<i>Plagiostoma</i>	sp.	346 to 783	D. reissi to Cor-Arnioceras	D	EA(B)	Trias:Tethys & boreal; J: cosmopolitan
	? sp.	525 to 803	B. canadensis to Cor-Arnioc		EA(B)	
<i>Antiquilima</i>	sp.	360 to 520	D. reissi to B. canadensis	D	EA(B)	Cosmopolitan
	<i>succincta</i>	512 to 642	B. canadensis-Vermiceras		EA(B)	
<i>Palmoxytoma</i>	cf. <i>cygnipes</i> (Young & Bird)	360 to 530	D. reissi to B. canadensis	E	EA(B)	Cosmopolitan
<i>Eopecten</i>	sp.	360 to 783	D. reissi to Cor-Arnioceras	D	EA(B)	Tethys, Circumpacific, Austral
	cf. <i>velatus</i> (Goldfuss)	560 to 834	B. canadensis to Cor-Arnioc		EA(B)	
<i>Pinna</i>	sp.	360 to 824	D. reissi to Cor-Arnioceras	D	SIA	Cosmopolitan
<i>Pleuromya</i>	sp.	360 to 800	D. reissi to Cor-Arnioceras	D	IDB	Cosmopolitan
<i>Camptonectes</i>	cf. <i>subulatus</i> (Münster)	364 to 818	D. reissi to Cor-Arnioceras	D	EA(B)	Cosmopolitan
<i>Agerchlamys</i>	sp.	525 to 824	B. canadensis to Cor-Arnioc	D	EA(B)	Circumpacific, bipolar
<i>Kalentera?</i>	sp.	621	Vermiceras	D	ISB(S)	Circumpacific, bipolar
<i>Prosogyrotrigonia</i>	<i>tenuis</i> Pérez et al.	674 to 818	Coroniceras-Arnioceras	D	ISB(S)	Tethys, Circumpacific
<i>Inoperna?</i>	sp.	707	Coroniceras-Arnioceras	D	EA(B)	Tethys, Austral
<i>Ceratomya?</i>	sp.	763 to 800	Coroniceras-Arnioceras	E	IDB	?
<i>Lywea</i>	<i>unca</i> (Philippi)	783 to 834	Coroniceras-Arnioceras	F	EL	Eastern Pacific
<i>Frenguelliella</i>	cf. <i>poultoni</i> Leanza	803	Coroniceras-Arnioceras	D	ISB(S)	Circumpacific
<i>Kolymonectes</i>	sp.	818	Coroniceras-Arnioceras	D	EL	Circumpacific, bipolar