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Heterochrony in Middle Jurassic species of *Gryphaea* (Ostreoidea, Gryphaeidae) from southern South America

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┤ **ABSTRACT** ├

Morphological changes along ontogeny, based on size, are analysed in five species of *Gryphaea* from the Middle Jurassic of southern South America. Three of these taxa are new: *G. apiculata* n. sp., *G. varillasensis* n. sp. and *G. euteicha* n. sp. All five species have thin radial striae on the left valve. They are regarded as closely related on the basis of the similar configuration of the main part of the left valve (especially during the first ontogenetic stages), the associated development of the posterior flange (and sulcus), the comparable variability and/or recurrent morphology of these and other structures, and their relative stratigraphic position or age. They show differences in the relative appearance time and development of several characters, and similar changes probably have also occurred stratigraphically, at least, in *G. oxytropis* PHILIPPI and *G. euteicha* n. sp. All these features allow the recognition of size (morphology)-based heterochronic processes (peramorphic and paedomorphic), either in the origin of most of these taxa or in morphologic changes which developed along time in some of them. This work provides preliminary evidence of the most remarkable iterative occurrence of heterochrony known to date in oysters.

KEYWORDS │ Heterochrony. Systematics. Oysters. Middle Jurassic. South America.

INTRODUCTION

The oysters are abundant in the diverse and well-preserved macrobenthic fauna from the marine Jurassic in northern Chile and mid-western Argentina. They have been mentioned and analysed mainly from the middle of the XIXth to the beginning of the XXth centuries, based on specimens collected during geological surveys (Forbes, 1846; Hupé, 1854; Burmeister and Giebel, 1861; Gottsche, 1878, 1925; Möricke, 1894; Tornquist, 1898; Jaworski, 1915, 1925, 1926a, 1926b). The identified taxa, generally not illustrated, were mainly related with European species. Further

detailed systematic studies were carried out by Gottsche (1878, 1925), Philippi (1899) and Jaworski (1915, 1925, 1926a, 1926b), whose taxonomic conclusions influenced later authors' identifications of these oysters. Hayami (1961), Hallam and Gould (1975) and Hallam (1982) included some of the southern South American taxa in their analysis of the probable interrelations of the Jurassic species of *Gryphaea*. Aberhan (1994) figured and characterized new Early Jurassic specimens collected in northern Chile.

The Jurassic (and Triassic) oysters of southern South America were recently studied in detail by Rubilar

(1998), and the main results were summarized in a preliminary paper (Rubilar, 2000). In this study, a group of five Middle Jurassic (and probably early Upper Jurassic) *Gryphaea* species was recognized. These species not only have close morphological relationships (further than the presence of thin radial striae on the left valve; see below), but also show clear anatomical differences when their ontogeny is compared. These differences also occurred along the stratigraphical succession in some of them.

The aim of this contribution is to assess the ontogenetic affinities and differences among these species in the light of several heterochronic processes, based on material from five main localities in Chile and Argentina (Fig. 1).

Heterochrony in oysters: examples and criteria for its recognition

The most-known example of heterochrony in oysters of the family Gryphaeidae involves three species of Lower Jurassic *Gryphaea* from England, in which a paedomorphic process has been recognized (Hallam, 1982; Johnson, 1993, 1994; Jones and Gould, 1999; Gould, 2000). Another case corresponds to the probable paedomorphic origin of Middle Jurassic '*Catinula*' from *Gryphaea* in Europe (Stenzel, 1971; Hallam and Gould, 1975; Sylvester-Bradley, 1977), although the gradualist pattern involved has been emphasized (Johnson and Lennon, 1990; Johnson, 1993, 1999). Furthermore, new and diverse examples have been found in some Tithonian and Neocomian oysters from the mid-western Argentina (Rubilar et al., 2000).

The evidences advocated here to regard species related to each other in a phylogenetic sense, crucial in determining heterochronic changes among taxa, are descriptive: the degree of morphological (ontogenetic) affinities (Fig. 2; Table 1) and relative stratigraphical position. Nevertheless, the lack of phylogenetic reconstruction (e.g. using cladistic methods) is not a limitation to obtain significant heterochronic information (McKinney and McNamara, 1991, p. 31).

The heterochronic processes were inferred from relative changes in size and shape of the specimens and their characters in a morphological sense (Table 1; Fig. 3), and the terms of this size (morphology)-based heterochrony ('allometric heterochrony') follow McNamara (1986), McKinney (1988), and McKinney and McNamara (1991).

These results are preliminary, because they should be tested considering the ontogenetic age of specimens, necessary to confidently discuss the types of heterochrony ('true' heterochrony) involved in changes among species (Alberch et al., 1979; McKinney and

McNamara, 1991; Jones and Gould, 1999). Nevertheless, classical studies of heterochrony are not comparisons of shifts on developmental timing but allometric or morphological studies instead, and in several cases size seems to be a suitable proxy for age (McKinney and McNamara, 1991; Smith, 2001). Furthermore, a recent approach re-focuses heterochrony as the change in the sequence of events, suggesting comparisons across taxa independently of external criteria (age, stage or size; Smith, 2001).

SYSTEMATICS, MATERIAL AND LOCALITIES

Of the five species here discussed, only *Gryphaea oxytropis* PHILIPPI (1899, Lám. 5, fig. 1a, b) was previously described. The holotype is housed in the Museo Nacional de Historia Natural of Santiago, Chile (MNHN, SGO PI. 5015). Three other supposedly different taxa named by Philippi (1899) can be included in this taxon: *G. carinata* PHILIPPI, *G. tricarinata* PHILIPPI and *G. schultzei* PHILIPPI. They have a moderate to large size, a nearly narrow main convexity zone (generally named 'keel'), and a variable development of the anterior margin or flange in the main part of the shell (Fig. 2; Rubilar, 1998). In the context of this paper, they are regarded as morphotypes in a probable anagenetic evolutionary series.

Three of the studied species are new (*G. apiculata* n. sp., *G. varillasensis* n. sp. and *G. euteicha* n. sp.). Due to the mainly paleobiological appeal of this contribution, their systematic treatment is restricted to the diagnosis and a general comparison among them (see APPENDIX). Another taxon (*Gryphaea* n. sp. A) is left in open nomenclature considering the scarce material available.

The thin radial striae on the left valve are also present in other undescribed late Middle Jurassic oyster species from South America, generally assigned to the European *Gryphaea calceola* QUENSTEDT, following Gottsche (1878, 1925). Nevertheless, they are characterized especially by the development of, at least, three equivalent morphotypes in the left valve (Rubilar, 1998), and probably branched from an ancestral stock represented by the earliest *G. euteicha* n. sp. The taxonomic significance of this ornamentation is under evaluation.

Philippi (1860) described '*Ostrea striata*' referring to the type of ornamentation mentioned above. The geographic and stratigraphic provenance of the type specimen, lost in the MNHN, is uncertain in the north of Chile. It is only known from an external view of a left valve in an early growth-stage (Philippi, 1860, Lám. 1, Fig. 10; 1899, Lám. 6, Fig. 3), which can be
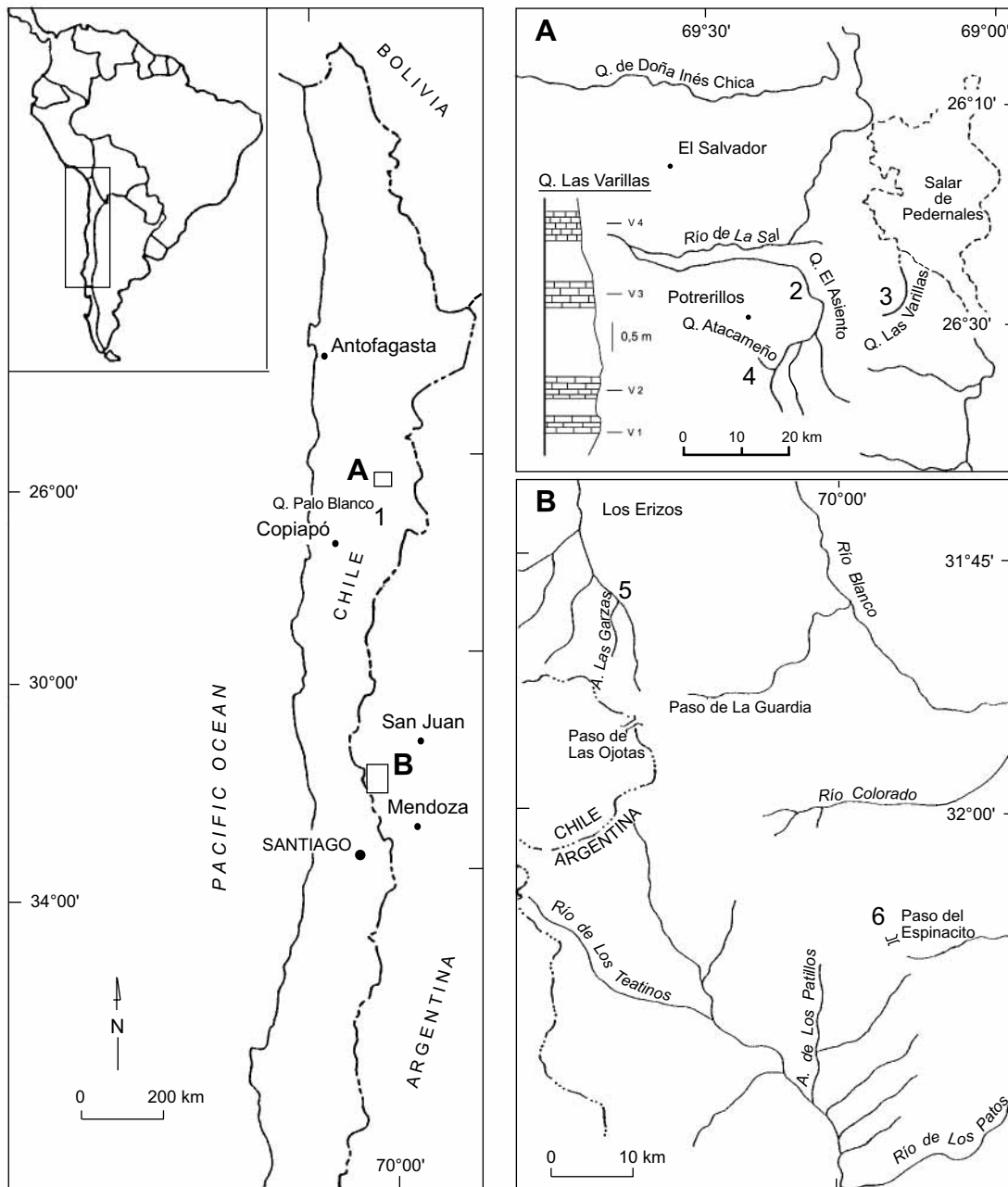
FIGURE 1 | **Sketch showing localities mentioned in text, which are concentrated especially in two areas: A) northeastern Copiapó, Chile (the synthetic stratigraphic log was measured in Quebrada Las Varillas). B) southwestern San Juan, Argentina. 1: Quebrada Palo Blanco; 2: Quebrada El Asiento; 3: Quebrada Las Varillas; 4: Quebrada Atacameño; 5: Arroyo Las Garzas; 6: Paso del Espinacito.**

related with *G. oxytropis* and *G. varillasensis* n. sp. Nevertheless, its certain affinities with one or another species cannot be established at this stage, based on the ontogenetic changes described here. Then, 'Ostrea striata' is considered a *nomen dubium*.

The new data obtained from southern South American oysters lead to question the validity of the subgenus '*Bilobissa*' STENZEL (1971), which is therefore not adopted here and so the species dealt with are referred only to *Gryphaea* in its wide sense.

Material

The taxonomical analysis was based on the following material, mostly left valves: 25 specimens of *G. apiculata* n. sp. (SNGM 8581-8605); 106 specimens of *G. oxytropis* PHILIPPI (SNGM 8364-8386, 8388-8434, 8437-8439, 8441-8464, 8466, 8475-8476, CPBA 18113, 18146-18150); 7 specimens of *G. varillasensis* n. sp. (SNGM 8467-8473); 118 specimens of *G. euteicha* n. sp. (SNGM 8435-8436, 8440, 8606-8721); and 4 specimens of *Gryphaea* n. sp. A (SNGM 8722-8723; DNGM 7888, 7943).

The material described, illustrated or mentioned in this paper is housed in the following institutions: Servicio Nacional de Geología y Minería (SNGM, Chile), Museo Nacional de Historia Natural (MNHN, SGO PI, Chile), Instituto de Geología y Recursos Minerales (DNGM, Argentina), and Universidad de Buenos Aires (CPBA, Argentina).

Localities and age

Gryphaea apiculata n. sp. is recorded only from Quebrada El Asiento (Fig. 1A, locality 1), a locality described by Pérez (1982, p. 43, fossil locality 11). It was collected from Middle Bajocian beds, associated with a species of *Stephanoceras* ammonoid.

The here analysed specimens of *G. varillasensis* n. sp. and most of those of the *G. oxytropis* and *G. euteicha* n. sp. come from a short stratigraphical sequence located in Quebrada Las Varillas (Fig. 1A, locality 3).

In general, *G. oxytropis* is recorded from several localities in Chile and Argentina (Rubilar, 1998), usually associated with Reineckeiidae ammonites ranging from Late Bathonian to Early Callovian in age (e.g. Riccardi and Westermann, 1991; Riccardi et al., 1999). However, some specimens have been collected from certain Middle Callovian outcrops in Argentina (P. Álvarez, oral comm., 2003).

In Quebrada Las Varillas, the first representatives of *G. oxytropis* and *G. varillasensis* n. sp. are associated with the ammonites *Chondroceras* cf. *allani* (MCLEARN), *Iniskinites* (?) sp. and an indeterminate Perisphinctidae (Fig. 1A, level V1), which indicate a Late Early Bajocian – Late Bathonian age (A. Riccardi, oral comm., 1997). *G. oxytropis* is also present in other three probably Late Bathonian levels of this succession (see below), whereas *G. varillasensis* n. sp. is absent from the last one (Fig. 1A, levels V1 to V3).

G. euteicha n. sp. was recovered especially from the upper level of the Quebrada Las Varillas section (Fig. 1A, level V4), associated with Late Bathonian *Iniskinites* and *Cadomites* ammonoids. Nevertheless, it is also present lower (Fig. 1A, level V3). On the other hand, in Quebrada El Asiento (Fig. 1A) this species appears in stratigraphical levels with Callovian *Macrocephalites* and *Oxycerites* ammonites (west of Estación Montandón; Pérez, 1982, p. 59-60).

The biggest ('giant') Lower Callovian specimen of *G. oxytropis* ever known, collected by Álvarez (1996) in Arroyo Las Garzas (Fig. 1B, locality 5), is mentioned in the text. Two Callovian representatives, one recovered from Quebrada El Asiento (Pérez, 1982, p. 60; fossil locality 10) and the other from Quebrada Palo Blanco

(east of Sierra Agua Amarga; Cornejo et al., 1993; Fig. 1, locality 1) are included in a sketch for comparison (Fig. 4).

Only few specimens of an undescribed species, here named *Gryphaea* n. sp. A, are known from Callovian beds in Paso del Espinacito (Gottsche, 1878, 1925, Lám. 4, fig. 12; Fig. 1B, locality 6). Other two probably co-specific representatives were collected in Quebrada Atacameño (Rubilar, 1998; Fig. 1A, locality 4), where Oppeliidae, Macrocephalitidae, Reineckeiidae and Aspidoceratidae ammonites are present (Callovian to Tithonian). Intensive tectonic activity makes dating these oysters difficult. In this paper, the general description of *Gryphaea* n. sp. A is based exclusively on the material collected by Gottsche (1878).

HETEROCHRONY IN A GROUP OF FIVE SOUTH AMERICAN MIDDLE JURASSIC *GRYPHAEA* SPECIES

The five species of *Gryphaea* here studied are regarded as a group of closely related oysters in a phylogenetic sense, because they share the following characters: 1, the general configuration of the main part of the left valve (Fig. 2), especially in the first ontogenetic stages (prejuvenile); 2, the comparable variability and/or recurrent presence of similar structures (e.g. long subvertical and almost flat anterior tilted surface; anterior flange and sulcus; tubercle-like structures on some or all of the most prominent zones of the shell; Table 1 and Figure 3); 3, the relatively low convexity and general integration of the posterior flange to the ventro-anterior growth of the main part of the shell (resulting in a more or less symmetric left valve in external view; Fig. 4); 4, the usual very small attachment area; and 5, the presence of thin radial striae on its external surface. This ornamentation (present in other taxa of Middle Jurassic oysters) seemingly spreads up to a similar height of the shell in the studied species.

Furthermore, most of the studied species were found in one locality (Quebrada Las Varillas; Fig. 1A), in the same level or in different levels of a relatively short stratigraphical succession. Finally, they can be distinguished from each other mainly by changes in size-shape relations (morphological development) of similar characters, expressed along the ontogeny (Table 1; Figs. 3 and 4).

All these factors, including the most relevant morphological variability observed in the studied samples, enable the recognition of the five species mentioned below (three new species among them) and the establishment of both a likely ancestor–descendant relationship and the probable size (morphology)–based heterochronic process involved in the ontogenetic change recorded among them (Fig. 4, see below).
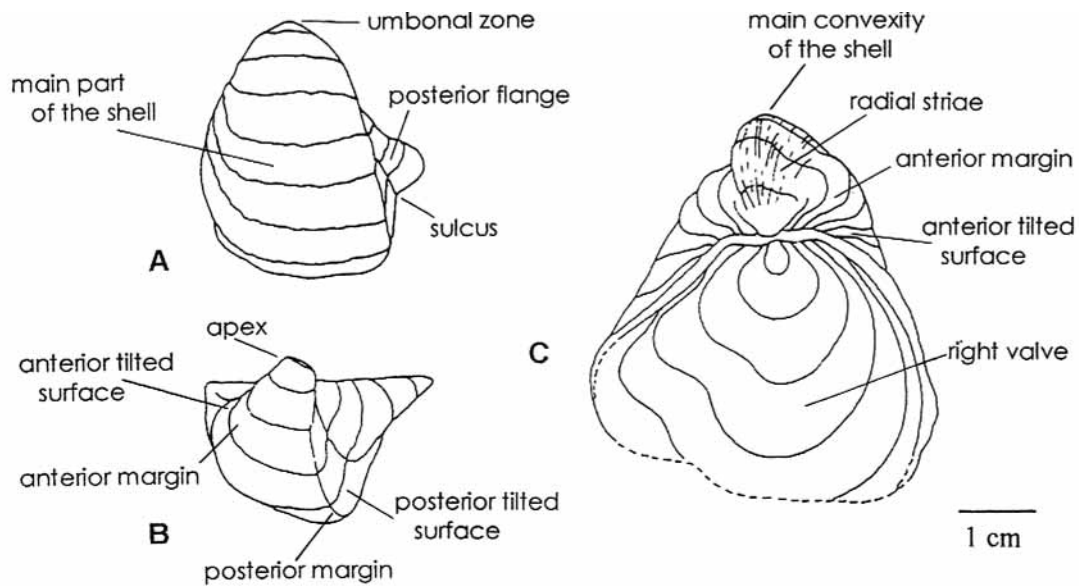
FIGURE 2 | **Shell morphology of the genus *Gryphaea* and terminology of the left valve used throughout the text. A) and B) *G. apiculata* n. sp., left valve, external and dorsal views respectively (based on SNGM 8586). C) *G. oxytropis* PHILIPPI, specimen with both valves together, right valve in external view (based on SNGM 8395).**

Main morphological features of the left valve

In the first ontogenetic stages of the studied species, the main part of the shell (Fig. 2) is prominent and generally has marked changes in its antero-posterior convexity expressed by a posterior and (especially) an anterior margins (Fig. 2B), which are also the boundaries of the external surface of this zone (generally convex and symmetric). These margins are accompanied by a posterior and (especially) an anterior almost flat tilted surfaces, subverticals to the commissural plane (Figs. 2B and C).

In the following growth-stages, the anterior zone of the valve (near the commissural border) exhibits the most remarkable variability among the studied species (and in some of their representatives), where the anterior tilted surface and margin (of the main part of the shell) can be either absent or continue their growth in several ontogenetic pathways. In the last case, the morphological changes involve especially smoothing or tilting (in the anterior tilted surface) and widening or increasing convexity (in the anterior margin). These ontogenetic replacements usually begin around the height where the valve has a marked antero-ventral curvature (in external view). Contrary, in *G. euteicha* n. sp. this curvature is not correlated with a change in the development of the mentioned structures.

In most of the studied species, the earliest (or primary) narrow anterior margin is replaced by a wide and/or strong surface. In two taxa (stratigraphically younger *G. oxytropis* and *G. euteicha* n. sp.), it can be developed as an anterior flange, which tends to be emphasized generally both by locally prominent growth lines and by a more or less deep anterior sulcus (located on the external surface of the main part of the valve; Fig. 4, specimens 4a, 5a, 7a, 8a; Figs. 5.7A, 5.7C and 5.7D, 5.8C, 5.9B and 5.10).

Similarly, in the juvenile and towards the adult growth-stages, the earliest (or primary) small anterior tilted surface is replaced by a generally wider, slightly concave or convex and then not well defined surface. Nevertheless, it tends to be smooth and more or less subvertical to the commissure where the anterior flange is prominent or even tuberculated (Figs. 4, specimens 4d, 7b, 8b, 9a and 9b; 5.7A and 5.7C, 5.8B, 5.9A, 5.11A and 5.11B). In the adult shell of some specimens (especially in *G. euteicha* n. sp.) the anterior and/or posterior tilted surfaces are named 'walls' where they are more or less flat and placed at nearly right angles to the mentioned plane (Figs. 5.7A, 5.8A and 5.9A). In the shells where the posterior flange lacks a well-defined convexity (and is visible only in posterior view), the posterior tilted surface (or wall) can reach the posterior commissural border (Figs. 5.7B and 5.7D, 5.8C and 5.8D).

In an extreme variant, the earliest anterior margin is followed by a faintly convex and slightly tuberculated surface, and the anterior tilted structure is absent (Fig. 4, specimen 11b and 11e).

The posterior margin of the main part of the shell tends to be the most convex (and narrow) zone of the valve in the adult growth-stage (Figs. 2B and 2C), generally named as 'keel'.

TABLE 1 | **Main developmental events and range of variability detected in the left valve, measured in its middle zone (A) or recognized next to the anterior commissure (B). Figure 3 shows the sequence of these ontogenetic events in each species.**

A

Developmental events measured in the middle zone of the left valve			Occurrence or comments
a	Posterior flange in external view	In the earliest growth stage	a1. Not visible	*G. apiculata* n. sp.
			a2. Few or not apparent	*G. euteicha* n. sp.
			a3. Progressively evident with growth	*G. oxytropis* , *G. varillasensis* n. sp. and *Gryphaea* n. sp. A
		In later growth stages	a4. Strong posterior expansion	*G. apiculata* n. sp., *G. euteicha* n. sp. and in some *G. oxytropis*
b	Main convexity of the shell		b1. Relatively narrow and progressively prominent ('keel')	It is located in the posterior half of the valve in *G. apiculata* n. sp. and *G. euteicha* n. sp., in the middle of the shell in *G. oxytropis* and in the middle zone of the main part of the valve in *Gryphaea* n. sp. A
			b2. Wide and low	It is higher in the middle zone of the valve in *G. varillasensis* n. sp.
			b3. Abrupt replacement of the narrow main convexity by a wider surface	This morphological change occurs especially in *Gryphaea* n. sp. A. It is also present in some specimens of *G. oxytropis*
c	Last recognition of thin radial striae			Seemingly with similar spread in the studied species
d	Anterior margin replaced by a flange			*G. oxytropis* (especially younger representatives), *G. euteicha* n. sp
e	Locally prominent structure on the main convexity of the shell		e1. Tubercle-like structure	*G. apiculata* n. sp. (some specimens), *G. oxytropis* (older representatives) and *G. euteicha* n. sp
			e2. Well defined tubercle	*G. oxytropis* (younger representatives) and *Gryphaea* n. sp. A
f	Very curved, angular, ventral commissure			Probably well defined in all the studied species

B

Developmental events recognized in the anterior commissure of the left valve			Occurrence or comments
g	Last development of the anterior tilted surface			It generally undergoes strong changes along the ontogeny
h	Antero-ventral curvature of the valve		h1. Low to moderate	*G. apiculata* n. sp., *G. oxytropis* and *G. varillasensis* n. sp.
			h2. Very pronounced (or angular)	*G. euteicha* n. sp. and *Gryphaea* n. sp. A
i	Last development of the anterior convex margin (or flange)			Structure very reduced in *Gryphaea* n. sp. A

The umbonal curvature (in anterior or posterior view) can be either (1) absent (the apex points to some area located over the hinge plane; Fig. 5.1C), (2) gentle (the apex points to a direction that is subparallel to the hinge plane; Figs. 5.2C and 5.4D), (3) moderate (the apex points to some area located between the hinge and commissural planes; Figs. 5.8B and 5.11D), or (4) strong (the apex points to the commissural plane or beyond this, and the umbo has a curved profile; Fig. 4, specimen 5d).

Height and length of the left valve were measured perpendicular and parallel to the hinge axis, respectively. The size, based on the height of the left valve, can be small (less than 30 mm), medium (between 30 and 60 mm) or large (more than 60 mm)

Developmental events in the left valve

The sequence of appearance/disappearance of six main characters or ontogenetic events (Table 1A), as function of size, was determined and measured from the apex to the ventral commissure along the most convex zone of the left valve (= peripheric growth/size; Fig. 3). This procedure is a lineal analysis because does not consider the different umbonal curvature or bending among the specimens and/or species. The most extreme differences are present in *G. apiculata* (absent or gentle umbonal curvature; Fig. 4, specimens 1c and 2c) and in some Upper Bathonian – Lower Callovian *G. oxytropis* (strong umbonal curvature; Fig. 4, specimen 5d). Nevertheless, most of the measured specimens have a moderate umbonal curvature.
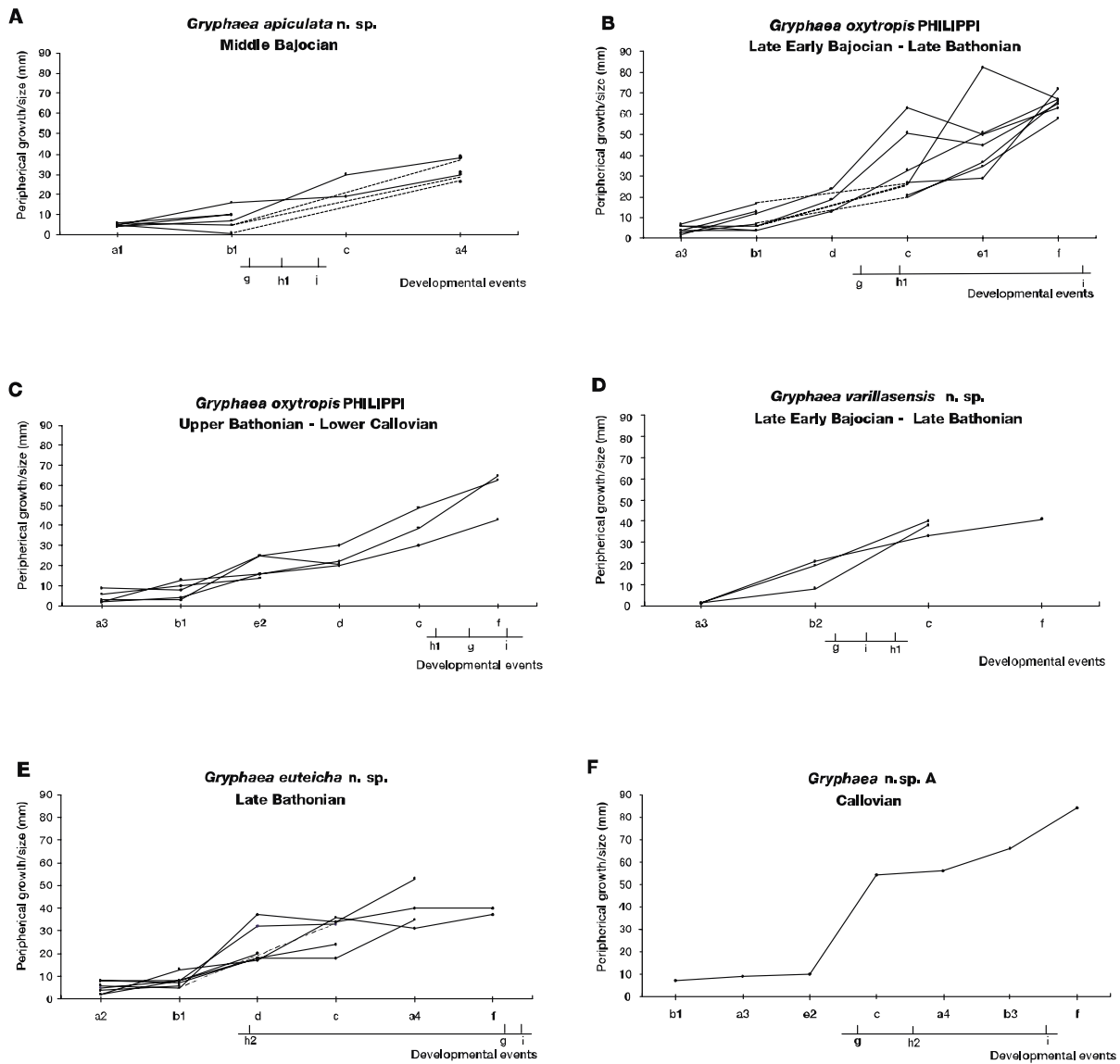
FIGURE 3 | **Comparative developmental events in five species of Middle Jurassic oysters as a funtion of size, measured in the periphery of the left valve. In the horizontal axis the appearance/disappearance of the events are indicated, evaluated along the middle zone of the valve (main convexity of the shell). Below them the relative co-occurrence of other three events observed next to the anterior commissure are indicated, based on the growth lines. The ontogenetic sequence of the older and younger representatives of *Gryphaea oxytropis* PHILIPPI is shown separately. Symbols refer to Table 1. Dotted lines connect the occurrence of two developmental events where the middle is not recorded. Plotted specimens are indicated in the text.**

The recognition of one character or event in each species is only a comparative parameter (= point of reference), because it does not imply that the character or event has the same degree of development in all these taxa, at the respective ontogenetic stage (see Table 1).

The appearance/disappearance of other three characters or events, present next to the anterior commissural margin of the left valve (Table 1B), was correlated with the sequence measured along the most convex zone based on the growth lines (Fig. 3).

The developmental events are graphically exemplified by the following and representative specimens: 6 of G. *apiculata* n. sp. (SNGM 8581, 8587, 8591, 8595); 7 of Late Early Bajocian – Late Bathonian G. *oxytropis* PHILIPPI (SNGM 8389, 8395, 8404, 8406, 8409 - 8410, 8896) and 5 of Late Bathonian – Lower Callovian G. *oxytropis* PHILIPPI (SNGM 8367, 8371, 8377, 8382 – 8383); 3 of G. *varillasensis* n. sp. (SNGM 8467 – 8468, 8470); 7 of G. *euteicha* n. sp. (SNGM 8438, 8512, 8607, 8615, 8622, 8633, 8636); and 1 of *Gryphaea* n. sp. A (DNGM 7943).

Morphology of the species and heterochronic relationships

Gryphaea apiculata n. sp.
Figures 2A and 2B; 4, specimens 1 and 2; 5.1 to 5.3
(see diagnosis in APPENDIX)

This species is of medium to small size (maximum height *ca*. 39 mm). It was recorded from Middle Bajocian beds at Quebrada El Asiento (Pérez, 1982, p. 43; Rubilar, 1998; Fig. 1A), and is considered as the probable ancestral stock to the group of oysters here analysed (Fig. 4).

Gryphaea apiculata n. sp. shows the following most relevant developmental events (Table 1; Fig. 3A): 1, appearance of the posterior flange, not visible in external view (a1); 2, appearance of the relatively narrow and progressively prominent main convexity of the shell, located in the posterior half of the valve from the earliest growth-stage (b1); 3, last development of the anterior tilted surface (g); 4, low to moderate antero-ventral curvature of the left valve (h1); 5, last development of the anterior convex margin (i); 6, probable last recognition of thin radial striae (c; there is a tubercle-like structure at this ontogenetic stage in some specimens); 7, strong posterior expansion of the posterior flange, in external view (a4). In some specimens, as the holotype, events 3 and 5 occur later in the ontogeny.

In the first growth-stages, the main part of the shell has anteriorly both a margin and a tilted surface extended to the commissure (Figs. 2B and 5.1D). Generally, these structures are restricted to a very early stage, and end around the height where the shell has a low to moderate antero-ventral curvature in external view (Figs. 3A and 5.3B). The posterior margin of this area (and the related posterior tilted surface) is more conspicuous as the shell grows up, and constitutes the main convexity of the valve, located in its posterior half (Figs. 2B, 3A, 5.1D and 5.3B).

In the pre-juvenile and juvenile growth-stages, the posterior flange (and sulcus) can be recognized only in posterior view, while it is well defined and visible in external view later in the ontogeny (Figs. 2A, 2B, 3A, 5.1B and 5.1C).

The umbo is opisthogyrous to orthogyrous, short, with a low convexity and gentle or absent curvature or bending, projected very little above the commissural plane (Figs. 5.1C, 5.1D, 5.2B and 5.2C). The thin radial striae are not well preserved; they probably cover most of the external surface of the valve. The ventral commissure is probably very curved.

In some specimens of *G. apiculata* n. sp. the sulcus and posterior flange are visible in external view from the earliest growth-stage. In addition, the main convexity is

narrow, located in the middle part of the shell and bears tubercle-like structures (Figs. 4, specimen 2a and 2b; 5.2A and 5.2B). This overall morphology precedes the anatomical development found in the adult specimens of *G. oxytropis* (compare Fig. 4, specimen 2 with 3 and 4), indicating the phylogenetic relationships between both taxa.

Gryphaea oxytropis PHILIPPI, 1899
Figures 2C; 4, specimens 3 to 6

Gryphaea oxytropis (Holotype: MNHN, SGO PI. 5015) is generally of medium to large size (maximum height *ca*. 72 mm). It has been recorded from Late Early Bajocian to Middle Callovian beds in several localities in Chile and Argentina (Rubilar, 1998; this paper). The ontogenetic changes that occur in the older (Late Early Bajocian – Late Bathonian) and some of the younger (Lower Callovian) representatives of this species are analysed here, based on material collected especially at Quebrada Las Varillas (Fig. 1A) and Quebrada Asientos (Pérez, 1982, p. 60), respectively.

The Late Early Bajocian – Late Bathonian specimens of *G. oxytropis* show the following most relevant developmental events (Table 1; Fig. 3B): 1, appearance of the posterior flange, progressively more evident with growth (a3); 2, appearance of the relatively narrow and progressively prominent main convexity of the shell, with a continuous change of its position from the posterior half to the middle zone of the valve (b1); 3, the anterior margin is generally replaced by an anterior flange (d); 4, last development of the anterior tilted surface (g); 5, low to moderate antero-ventral curvature of the valve (h1); 6, last recognition of thin radial striae (c); 7, first tubercle-like structure on the main convexity of the shell (e1); 8, very curved, angular, ventral commissure (f); 9, last development of the anterior convex margin or flange (i).

On the other hand, in the Upper Bathonian – Lower Callovian specimens of *G. oxytropis* the most relevant developmental events are (Table 1; Fig. 3C): 1, appearance of the posterior flange, progressively more evident with growth (a3); 2, appearance of the relatively narrow and progressively prominent main convexity of the shell, with a continuous change of its position from the posterior half to the middle zone of the valve (b1); 3, first well-defined tubercle on the main convexity of the shell (e2); 4, the anterior margin is replaced by an anterior flange (d); 5, last recognition of thin radial striae (c); 6, low to moderate antero-ventral curvature of the valve (h1); 7, last development of the anterior tilted surface (g); 8, very curved, angular, ventral commissure (f; at this ontogenetic stage, in some specimens there is an abrupt replacement of the narrow main convexity of the shell by a wider surface; Fig. 4, specimen 4a); 9, last development of the anterior convex margin or flange (i).
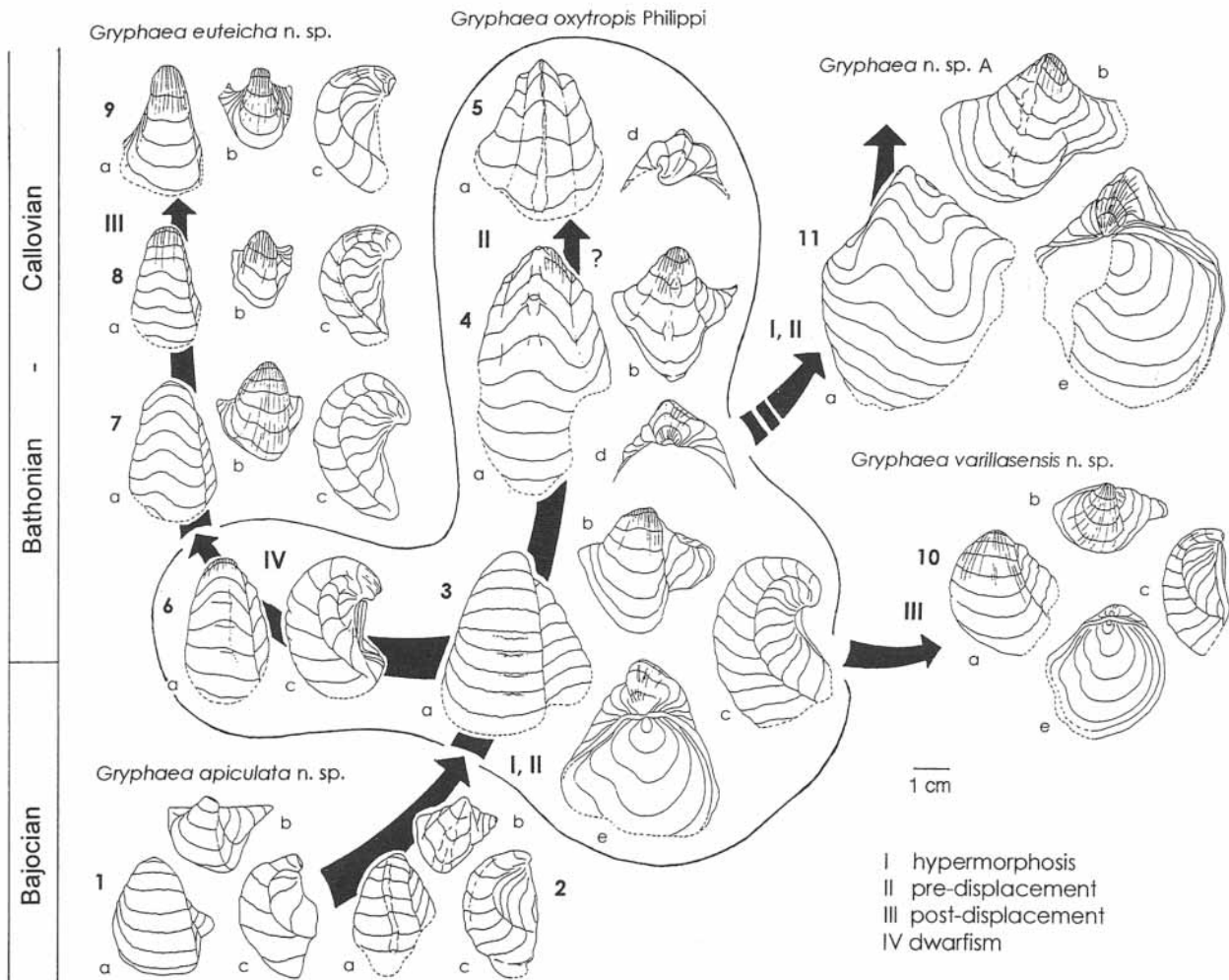
FIGURE 4 | **Size (morphology)-based heterochrony in five species of *Gryphaea* from Middle Jurassic of southern South America, exemplified by specimens (1 to 11) representative of the most important variability observed. The relative position of specimens 3 and 6 to 10 is based on the stratigraphical succession in Quebrada Las Varillas; 5 (Quebrada Palo Blanco), 11 (Paso del Espinacito) and especially 1 and 4 (Quebrada El Asiento) are situated according to their age. Left valve, a: external view; b: dorsal view; c: posterior view; d: internal view. Right valve, e: external view. The figures are based on the following specimens: 1, SNGM 8586; 2, SNGM 8587; 3, SNGM 8395; 4, SNGM 8377; 5, SNGM 8458; 6, SNGM 8434; 7, SNGM 8606; 8, SNGM 8673; 9, SNGM 8607; 10, SNGM 8468; 11, DNGM 7943.**

In the first ontogenetic stages, the left valve of *G. oxytropis* is similar to the adult morphology of *G. apiculata* n. sp., considering especially the form and extension of the anterior margin of the main part of the shell and the earliest position of its posterior margin (Figs. 2B and 2C; 3A to 3C). On the other hand, in *G. oxytropis* the early and intermediate stages of growth are maintained longer, as shown by the larger adults of the later species (Figs. 3B and 3C; 4, specimens 3 to 5) in comparison with *G. apiculata* n. sp. (Figs. 3A; 4, specimens 1 and 2).

This probable extension of the growth period in *G. oxytropis*, or hypermorphosis, results in several morphological characteristics quite different from those of the ancestral adult of *G. apiculata* n. sp. For example, the posterior margin of the main part of the valve (which constitutes its main convexity) is now located in the middle zone of the shell (compare Fig. 4, specimens 1b with 3b and 4b); the earliest anterior margin (of the main part of the shell) not only is maintained and strengthened into the adult growth-stage (Fig. 3B, event i), but also is replaced by a well defined (and somewhere tuberculated) anterior flange in stratigraphically younger (Late Bathonian – Early Callovian) specimens, generally accompanied both by an anterior tilted surface (which tends to be better defined in all growth-stages, along the geologic time; Fig. 3C, events g and i) and a sulcus (Fig. 4, specimens 4 and 5); and the umbo is generally strongly curved (Fig. 4, specimens 3c and 5d). Furthermore, the ventral commissural margin is more angular or very curved (e.g. Alvarez, 1996, Fig. 36b) in comparison with *G. apiculata* n. sp.

The ontogenetically later antero-ventral curvature of the shell in *G. oxytropis* than in *G. apiculata* n. sp. (Fig. 3A to 3C, event h) may be correlated with the greater extension and strength of the anterior margin.

The older (Late Early Bajocian – Late Bathonian) representatives of *G. oxytropis*, found in Quebrada Las Varillas, show the strongest resemblance with *G. apiculata* n. sp. in the first stages of growth (e.g. the form and extension of the anterior and posterior margins of the main part of the shell; Figs. 2B and 2C). On the contrary, the posterior flange (and sulcus) is generally convex (and visible in external view) earlier in *G. oxytropis* than in *G. apiculata* n. sp. (Fig. 3A to 3C, event a; compare Fig. 4, specimens 1a and 3b), showing a probable pre-displacement process associated with the hypermorphosis in the origin of the first taxon.

Gryphaea oxytropis can be interpreted as a polymorphic species on account of its wide range of variability, especially in the dorso-ventral extension and convexity of the anterior margin/flange of the main part of the left valve, the related extension and width of the anterior tilted surface (Fig. 3B and 3C, events g and i), and in the general convexity of this anterior zone of the shell (Fig. 4, specimens 3 to 6). In this context, '*Gryphaea tricarinata* PHILIPPI (1899, p. 12 - 13, Lám. 5, fig. 1a - c), regarded as a synonym of *G. oxytropis* (Rubilar, 1998), represents a morphotype with a well-developed anterior flange and sulcus.

These morphological differences during growth, observed in specimens collected at several localities, seem to be related with their stratigraphical positions, and hence they could represent an anagenetic change caused by a persistent pre-displacement heterochronic process. This is evidenced especially by the growth and position of the tubercles in the main convexity zone ('keel'), in addition to the mentioned basic pre-displacement development of the sulcus and posterior flange.

Well-defined tubercles are absent in Late Early Bajocian - Late Bathonian specimens, although the ventral half of the valve generally tends to have localized elevations in the main convexity zone (Fig. 3B, event e1 and Fig. 4, specimens 3a and 6a). On the contrary, most of Late Bathonian and Early Callovian specimens have moderate to large tubercles from the first growth-stages (Figs. 3C, event e2 and Fig. 4, specimens 4 and 5), and these may also be present on the anterior and posterior flanges. The Callovian representatives also seem to have a narrower and earlier developed main convexity zone (Fig. 4, specimen 5) than Bathonian - Callovian specimens.

The size differences in mature representatives of *G. oxytropis* suggest tendencies to gigantism and dwarfism. The biggest known specimen of this species (height *ca*. 128 mm) was collected by Alvarez (1997; CPBA 18146) in Lower Callovian beds of Arroyo las Garzas (San Juan Province, Argentina; Fig. 1B). On the other hand, the smallest mature specimens (maximum height *ca*. 40 mm; Fig. 4, specimen 6) come from Quebrada Las Varillas

(Fig. 1A), among others with a 'normal' height (*ca*. 70 mm). They are regarded as adults because of the early development of a strongly curved ventral commissure and the growth of the valves focused subvertical to the commissural plane in this zone (Fig. 4, specimen 6c). In these specimens the posterior flange is very narrow relative to the common development in *G. oxytropis* (Fig. 4, specimens 3 to 5). This can be regarded as a 'morphofunctional limitation'. These dwarf specimens are considered to be the direct predecessors of *G. euteicha* n. sp., with which they share the maximum size (compare Figure 4, specimens 6 with 7 to 9), among other characters.

Gryphaea varillasensis n. sp.
Figures 4, specimen 10; 5.4 and 5.5
(see diagnosis in APPENDIX)

This species has a medium sized shell (maximum height *ca*. 47 mm). It was recovered from Late Early Bajocian - Late Bathonian units in Quebrada Las Varillas (Fig. 1A, levels V1 to V3).

Gryphaea varillasensis n. sp. shows the following most relevant developmental events (Table 1; Fig. 3D): 1, appearance of the posterior flange, progressively more evident with growth (a3); 2, development of a wide and low main convexity of the shell, located in the middle zone of the valve (b2); 3, last development of the anterior tilted surface (g); 4, last development of the anterior convex margin (i); 5, low antero-ventral curvature of the valve (h1); 6, last recognition of thin radial striae (c); 7, very curved (more or less angular) ventral commissure (f).

Gryphaea varillasensis n. sp. and *G. oxytropis* have a very similar early development of the left valve in terms of the structure, width and almost symmetric convexity of the main part of the shell, the early appearance (in external view) of the posterior flange, the gentle or absent umbonal bending, and the type of thin radial striae (Figs. 3B, 3D and 4, specimens 3e and 10b). Nevertheless, in *G. varillasensis* n. sp. this early development of the left valve is maintained until the mature stage of growth, where the most convex surface remains low, the external surface of the main part of the shell is very wide and almost symmetric (without an anterior flange), the sulcus (narrow and relatively shallow) and posterior flange (low convex) tend to have a low development or to be integral with the antero-posterior convexity of the valve, the umbo maintains gentle (or absent) curvature (with a very reduced convexity; Fig. 4, specimen 10c and 10e), and the ventral commissural margin may be only slightly curved.

Then, in comparison with the older (Late Early Bajocian – Late Bathonian) representatives of *G. oxytropis*, *G. varillasensis* n. sp. shows a marked ontogenetic delay in

the appearance of high shell convexity (e.g. absence of a narrow main convexity zone, an anterior convex margin or even a flange), whereas other characters tend to have the same rate of development as in the mentioned representatives of *G. oxytropis* (especially the depth of the sulcus and width of the posterior flange, the spread of the thin radial striae, and probably the length of the anterior margin of the main part of the shell; compare Fig. 4, specimens 3 and 10).

These differences in the rate of development of certain structures, which are relatively retarded in *G. varillasensis* n. sp. with respect to its probable ancestor (*G. oxytropis*), would represent a heterochronic process of post-displacement. Moreover, some characters in *G. varillasensis* n. sp. are more comparable with *G. apiculata* n. sp., as is the case with the lowest umbonal convexity and curvature (compare Fig. 4, specimens 2c and 10c). This apparent 'regression' of *G. varillasensis* n. sp. to an ancestral morphology (showed by *G. apiculata* n. sp.; see Fig. 4) can be interpreted as another evidence of the mentioned post-displacement process and, at least indirectly, supports the origin of *G. oxytropis* (probably the direct ancestor of *G. varillasensis* n. sp.) from *G. apiculata* n. sp.

Nevertheless, the small size of *G. varillasensis* n. sp. relative to *G. oxytropis* can be interpreted as a partial operative concurrence with progenesis, where the adult descendant is smaller and retarded relative to the ancestor (although in progenesis the morphological change affects the whole organism).

Excluding the holotype (Figs. 5.5A to 5.5C), some specimens have a shorter extension of the anterior tilted surface, followed by a low to moderate antero-ventral curvature of the shell (Fig. 3D, events g and h1), and the anterior margin of the valve may have a convex outline (Figs. 4, specimen 10; 5.4B and 5.4C). This morphology is probably related with the absence of a prominent anterior margin or flange (of the main part of the shell) in the juvenile and adult growth-stages. Then, it would represent an emphasized tendence to the mentioned delay in the appearance of a high shell convexity, in comparisson with the Late Early Bajocian – Late Bathonian representatives of *G. oxytropis*.

Gryphaea euteicha n. sp.
Figures. 4, specimens 7 to 9; 5.6 to 5.11
(see diagnosis in APPENDIX)

This species has small to medium size (maximum height *ca*. 43 mm; generally less than 35 mm). It has been recorded from Late Bathonian and Callovian strata in Quebrada Las Varillas (Fig. 1A, levels V3 and V4) and Quebrada El Asiento (Pérez, 1982, p. 59-60; Fig. 1A; Rubilar, 1998), respectively. The ontogenetic changes that

occur in the older (Late Bathonian) representatives of this species are analysed here.

In Quebrada Las Varillas, the upper levels with *G. oxytropis* (maximum height *ca*. 70 mm; Fig. 4, specimen 3) also bear smaller shells, which belong either to *G. oxytropis* (with a tendency to dwarfism; Fig. 4, specimen 6) or to the earliest *G. euteicha* n. sp. (Fig. 1A, levels V3 and V4).

Some of the last mentioned specimens are considered morphologically 'precursors' (Figs. 4, specimen 7; 5.11), with a transitional morphology between *G. oxytropis* and the most common representatives of *G. euteicha* n. sp. (Fig. 4, specimens 8 and 9). On the other hand, this earliest evolutionary stage of *G. euteicha* n. sp. probably represents the ancestral stock of other South (and North) American late Middle Jurassic species, which share the general pattern of *G. euteicha* n. sp. left valve although their variability includes, at least, three different morphotypes.

Typical representatives of *G. euteicha* n. sp. show the following most relevant developmental events (Table 1; Fig. 3E): 1, appearance of the posterior flange, little or not visible in external view (a2); 2, origin of the relatively narrow and progressively prominent main convexity of the shell, located in the posterior half of the valve (b1); 3, very pronounced (angular) antero-ventral curvature of the valve (h2); 4, the anterior margin is replaced by an anterior flange (d); 5, last recognition of thin radial striae (c); 6, strong posterior expansion of the posterior flange (a4); 7, very curved, angular, ventral commissure (f); 8, last development of the anterior tilted surface or wall (g); 9, last development of the anterior convex margin or flange (i).

In the first ('precursor') specimens of *G. euteicha* n. sp., the posterior flange has a low and uniform convexity, at least, in a young growth-stage (dorsal and middle part of the shell), resembling dwarf specimens of *G. oxytropis* (Fig. 4, specimen 6), where it is generally very narrow in external view (in some specimens it may be wider just at maturity, near the ventro-posterior margin). In the mentioned specimens of *G. oxytropis* the posterior flange generally is, however, wider throughout the ontogeny, and is usually well defined in external view from its origin.

Gryphaea euteicha n. sp. and *G. oxytropis* have a very similar early development of the left valve in width and convexity (at first almost symmetric and then asymmetric) of the main part of the left valve, the early origin of the posterior flange (Figs. 3B and 3E, events a and b1) and the gentle or absent umbonal curvature (compare Fig. 4, specimens 3b and e with 7b and 8b).

Stratigraphically, the mentioned low development of the posterior flange in *G. euteicha* n. sp. is very marked, and in the younger specimens this structure is very expand-

ed only in the adult growth-stage (Fig. 3E, event a4) or even just visible in posterior view (Figs. 4, specimens 8 and 9; 5.6A and 5.6B, 5.7B to 5.7D, 5.8C and 5.8D), similar to some extent to *G. apiculata* n. sp. (Fig. 4, specimen 1a to c). According to this trend, the posterior flange has a retarded growth relative to *G. oxytropis* (Fig. 4, specimens 3a and 6a), exhibiting a post-displacement process.

In the earliest and most of the later (typical) representatives of *G. euteicha* n. sp., the main convexity of the shell is located near the posterior margin of the left valve (Figs. 4, specimens 7b and 8b; 5.6B, 5.7A and 5.11A), as in *G. apiculata* n. sp. (Fig. 4, specimen 1b) and in the first growth-stages of *G. oxytropis* (Fig. 4, specimen 3e), whereas it is placed in the middle part of the adult shell in the last species (Fig. 4, specimens 3b, 4b, 5a and 6a). In other words, *G. euteicha* n. sp. has morphological characters of maturity (the position of the main convexity of the shell) similar to those present only in the first growth-stages in *G. oxytropis*.

On the contrary, other structures of the left valve have an equivalent development throughout the ontogeny in both species (e.g. the general prominent and narrow main convexity of the shell, the presence of the anterior margin or flange and a tilted surface in the first stages of growth or along the ontogeny, the extension of the thin radial striae, the moderate to strong umbonal curvature, and the curvature of the ventral commissural margin; Fig. 3B and 3E, events b1, f to i), as it is a characteristic in the post-displacement heterochronic process here proposed.

The specimens of *G. euteicha* n. sp. from the upper levels in Quebrada Las Varillas have new and remarkable characters, especially in the antero-ventral zone of the shell. The left valve tends to have a pronounced antero-ventral expansion, originated from an early curvature in the commissural margin (Figs. 4, specimen 9; 5.6B and 5.8A to 5.8C), the anterior tilted surface (long and generally high = anterior wall; Figs. 5.7A and 5.7C, 5.8B and 5.8C, 5.9A and 5.9B) and the anterior margin (or flange) are well developed along the growth, and the antero-posterior convexity of the shell (Fig. 5.8E) tends to be evenly

symmetric (Figs. 4, specimen 9a, b; 5.8A and 5.8C). These characters suggest a very accentuated anagenetic post-displacement process.

***Gryphaea* n. sp. A**
Figure 4, specimen 11

The following description of the ontogenetic changes that occur in this taxon is based on the material collected by Gottsche (1878, 1925, Lám. 4, Fig. 12; DNGM 7943) from Callovian levels at Paso del Espinacito (Fig. 1B). They are of medium to large size (maximum height *ca*. 71 mm). Other two large specimens (maximum height *ca*. 113 mm), not well preserved and collected in Quebrada Atacameño (Rubilar, 1998; Fig. 1A), are also assigned to this species.

The best-preserved specimen (Gottsche, 1878, Lám. 4, fig. 12; fig. 4, specimen 11) shows the following most relevant developmental events (Table 1; Fig. 3F): 1, appearance of the relatively narrow and progressively prominent main convexity of the shell, located in the middle zone of the main part of the valve (b1); 2, appearance of the posterior flange, progressively more evident with growth (a3); 3, first tubercle on the main convexity of the shell (e2); 4, last development of the anterior tilted surface (g); 5, last recognition of thin radial striae (c); 6, very pronounced (angular) antero-ventral curvature of the valve (h2); 7, strong posterior expansion of the posterior flange (a4); 8, abrupt replacement of the narrow main convexity of the shell by a wider surface (b3); 9, last development of the anterior margin (i); 10, very curved, angular, ventral commissure (f).

Gottsche's specimen could be considered morphologically close to older and younger representatives of *G. oxytropis*, here described. Despite the few available specimens and limited biostratigraphic information on *Gryphaea* n. sp. A (and the presence of a slightly tuberculated 'anterior margin' of the main part of the shell, in the analysed specimen; see below), the development of the anterior commissural zone and especially the absence of an anterior flange allow to consider the mentioned specimen as closely related to the older (Late Lower Bajocian – Upper Bathonian) representatives of *G. oxytropis*.

FIGURE 5 | **1 to 3. *Gryphaea apiculata* n. sp. Quebrada El Asiento, Middle Bajocian. 1) Holotype, SNGM 8586, left valve. 1A: anterior view; 1B: external view; 1C: posterior view; 1D: dorsal view. 2) Paratype, SNGM 8587, left valve. 2A: external view; 2B: dorsal view; 2C: posterior view. 3) Paratype, SNGM 8589, left valve. 3A: external view; 3B: dorsal view; 3C: posterior view.**

4 and 5. *Gryphaea varillasensis* n. sp. Quebrada Las Varillas, Late Early Bajocian - Late Bathonian. 4) Paratype, SNGM 8468, specimen with both valves. 4A: left valve, dorsal view; 4B: left valve, external view; 4C: right valve, external view; 4D: left valve, posterior view. 5) Holotype, SNGM 8467, specimen with both valves. 5A: left valve, dorsal view; 5B: left valve, external view; 5C: right valve, external view.

6 to 11. *Gryphaea euteicha* n. sp. Quebrada Las Varillas, Late Bathonian. 6) Paratype, SNGM 8633, left valve. 6A: posterior view; 6B: external view. 7) Paratype, SNGM 8622, specimen with both valves. 7A: left valve, dorsal view; 7B: left valve, posterior view; 7C: left valve, anterior view; 7D: left valve, external view. 8) Holotype, SNGM 8607, left valve. 8A: dorsal view; 8B: anterior view; 8C: external view; 8D: posterior view; 8E: internal view. 9) Paratype, SNGM 8615, left valve. 9A: anterior view; 9B: external view. 10) Paratype, SNGM 8636, left valve, external view. 11) SNGM 8606, left valve. 11A: dorsal view; 11B: anterior view; 11C: external view; 11D: posterior view.

1 cm
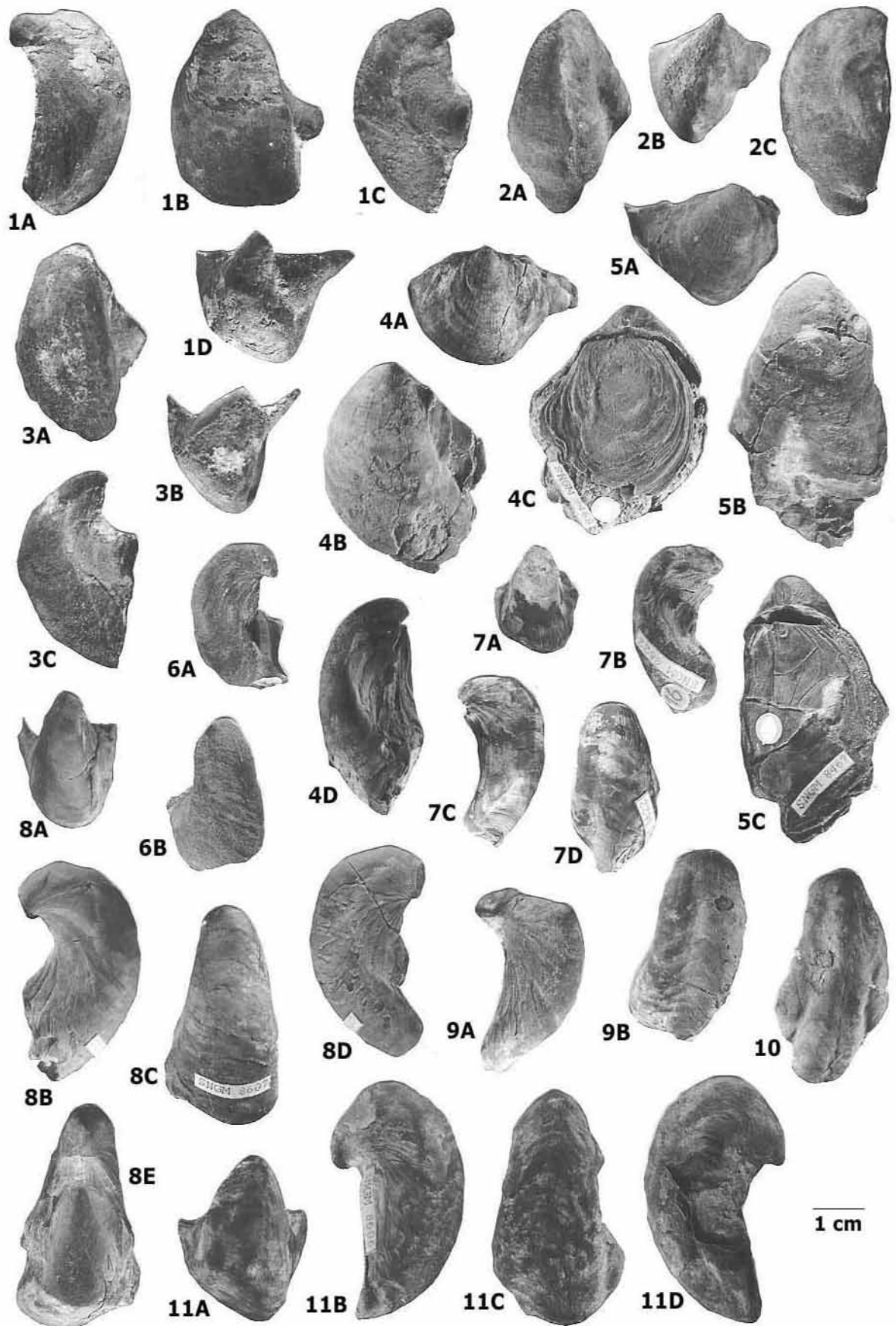
The mentioned specimen shares with the older *G. oxytropis* the general morphology of the main part of the left valve (e.g. the form of its anterior margin and especially the short ontogenetic extension of the anterior tilted surface) and the early appearance of the posterior flange (and sulcus) in the first growth-stages (Figs. 3B and 3F, events a, g, i).

Nevertheless, in Gottsche's specimen the prominent and narrow main convexity of the valve occurs earlier and has well defined tubercles (Figs. 3F, event e2 and 4, specimen 11b). In addition, the almost flat and slightly tuberculated surface or zone, present in a pre-juvenile growth-stage, that replaces the earliest anterior convex margin of the main part of the shell (Fig. 4, specimen 11e), seems to be equivalent to the strong margin generally present towards the adult stage in the mentioned *G. oxytropis* (Fig. 4, specimen 3a and 3e). It is remarkable that both structures constitute the anterior commissural border of the shell, in absence of the anterior tilted surface at these growth-stages.

This appearance of structures at an earlier growth-stage in *Gryphaea* n. sp. A relative to late Lower Bajocian – Upper Bathonian *G. oxytropis*, resulting in a morphologically more advanced (and larger) left valve, can be related with a pre-displacement heterochronic process.

On the other hand, in the specimen of *Gryphaea* n. sp. A, the ontogenetic events towards the adult growth-stage include a very pronounced antero-ventral (and posterior) curvature (and expansion) of the shell (Fig. 3F, event h2). In addition, the narrow main convexity of the shell (located in the middle portion of the main part of the valve from the first growth-stages) is replaced by a wider convex surface (Fig. 3F, event b3), the sulcus is broad, and in the adult stage the valve has almost subparallel margins (Fig. 4, specimen 11). On the contrary, in late Lower Bajocian – Upper Bathonian *G. oxytropis* the antero-ventral curvature of the shell is low to moderate, the main convexity of the shell is generally narrow and is always located in the middle part of the left valve (as a whole), the sulcus is deeper than wide (Fig. 4, specimens 3 to 6), and the shell has a subtriangular outline.

These morphological differences in the adult shell of *Gryphaea* n. sp. A and *G. oxytropis*, and the greater size of the valve in the first taxon (considering especially the probable cospecific specimens collected in Quebrada Atacameño), show a partial operative concurrence with hypermorphosis, where the adult descendant (*Gryphaea* n. sp. A) is larger and differs from the ancestor (although in hypermorphosis the morphological change affects the whole organism).

DISCUSSION AND CONCLUSION

The significance of *G. apiculata* n. sp. as the ancestor of the group of South American Middle Jurassic oysters here studied is supported by its stratigraphical position and because most of its external left valve anatomy and morphological development can be more or less recognized in all the other species here described (Fig. 4): 1, the earliest configuration of the main part of the shell (especially the presence of an anterior tilted surface and margin), including the form of the umbonal apex and the generally very small attachment area; 2, the general symmetric outline of the valve; 3, the presence of an antero-ventral curvature; 4, the relatively low convexity and adult expansion of the posterior flange, approximately at the height where the antero-ventral curvature occurs; 5, the tendency to have an asymmetric ventral commissure; and 6, probably the nature and extension of the thin radial striae.

Excepting *G. varillasensis* n. sp., all the studied species have, at least, a tendency to develop tubercle-like structures on some (or all) the most prominent zones of the valve (main convexity and flanges). This is regarded as another evidence for the mentioned close morphological relationships, because its absence in any ontogenic stages in *G. varillasensis* supports the supposedly 'retarded' development of this species in comparison with *G. oxytropis*.

Gryphaea oxytropis and *G. euteicha* n. sp. have the strongest morphological affinities with *G. apiculata* n. sp., based especially on the tendency to have a prominent anterior commissural border in the adult shell, as a result of the co-occurrence of a well defined anterior tilted surface and margin.

In *G. oxytropis* and *G. euteicha* n. sp. this anterior tilted surface tends to be particularly well defined along ontogeny and the related margin can be reinforced by an anterior flange, showing that they are closely related. In fact, *G. euteicha* n. sp. probably descends from dwarf representatives of *G. oxytropis*, along a progressive anagenetic process (Fig. 4). The mentioned similar development in the anterior commissural border, particularly best expressed along time in both species, could be interpreted as a parallelism, although this growth actually indicates their common ancestor. On the other hand, the origin of *G. oxytropis* from *G. apiculata* n. sp. is also evidenced because in the Middle Bajocian population of the late species a morphotype strongly similar to the first Late Early Bajocian – Late Bathonian *G. oxytropis* is present (compare Fig. 4, specimens 2, 3 and 4).

Gryphaea euteicha n. sp. is the descendant species morphologically most similar to *G. apiculata* n. sp., resembling its main ontogenetic development. They share especially the tendency to have a wide and almost flat

external surface of the left valve, the delayed emergence of the posterior flange and the posterior position of the main convexity of the shell (which concurred to the development of a more or less defined posterior tilted surface or wall in the valve), and probably its size. In the context of this work, this affinity reflects a post-displacement heterochronic process that explains this apparent 'regression' to an ancestral morphology and, at least indirectly, supports the origin of *G. oxytropis* (probably the direct ancestor of *G. euteicha* n. sp.) from *G. apiculata* n. sp. (Fig. 4).

This origin of *G. oxytropis* from *G. apiculata* n. sp., and the significance of the last species as the ancestor of the taxa here studied, is also indirectly supported by the resemblance between *G. varillasensis* n. sp. (probably originated from *G. oxytropis*) and *G. apiculata* n. sp., considering the lowest umbonal convexity and curvature (Fig. 4, specimens 2c and 10c).

Gryphaea oxytropis shows the highest morphological variability, which seems to be closely related to several heterochronic processes. It is evidenced by the probable anagenetic change involved in its evolutionary history, and especially by the fact that the older specimens are related to the origin of, at least, two sympatric species in a relatively short period of time (Fig. 4). The apparent anagenetic tendency here mentioned, based, for example, on variations of the convexity of both main part of the shell and anterior margin (and flange), must be studied in detail with a more accurate biostratigraphic record.

In summary, all these strong morphological affinities, as well as the ontogenetic differences in relative time apparition and development of several characters (e.g. margins, sloped surfaces, antero-ventral curvature and convexity of the main part of left valve; main convexity of shell and tubercle-like structures; posterior and anterior flanges and sulcus; curvature of the umbo; size change of the shell), are interpreted as the products of heterochronic processes, involving the cladogenetic origin of the older *G. oxytropis* (Late Early Bajocian – Late Bathonian) from *G. apiculata* n. sp. (Middle Bajocian), and *G. varillasensis* n. sp. (Late Early Bajocian – Late Bathonian), *G. euteicha* n. sp. (Late Bathonian – Callovian) and *Gryphaea* n. sp. A (Callovian) from the earliest representatives of *G. oxytropis* (Fig. 4). On the other hand, these heterochronic processes involves anagenetic variations in *G. euteicha* n. sp. and probable *G. oxytropis*.

These size (morphology)-based heterochronies may be considered misleading, because changes in rate and timing of ontogenetic events can, by definition, only be determined where the ontogenetic age of compared specimens is known (e.g. McKinney and McNamara, 1991; Jones and Gould, 1999). Nevertheless, their detection and evident correspondence with schemes based on allometric

manifestations (size-based heterochronies), described by several authors (see McKinney and McNamara, 1991, figs. 2-6), are valid and informative results at this descriptive level of analysis. They show the high importance of heterochrony as the paleobiological mechanism involved in the origin and variability of these oysters, and provide hypotheses to be tested including the ontogenetic age of each compared specimen. If the rate of change in body size results similar between compared (closely related) species, as is suggested by the seemingly similar spread of radial striae, the processes here recognized may reflect the 'true' heterochronies involved.

The group of five species analysed represents the most remarkable example of iterative heterochrony known to date in oysters, where several characters and morphologically well-defined ontogenetic variations support the ancestor-descendant relationships among them. The most-known and discussed example involving three species of *Gryphaea* from Hettangian to Pliensbachian in England has been classically considered an example of phyletic size increase with a paedomorphic (neotenic) relationship (see Jones and Gould, 1999, and references there). Although this heterochronic process was recently assessed by comparing standardized specimens of common age (Jones and Gould, 1999), they may not represent a unique lineage considering unpublished data from South America (Rubilar, 1998).

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APPENDIX

Diagnosis of new species

SYSTEMATIC PALEONTOLOGY

Superfamily: Ostreoidea RAFINESQUE, 1815
Family: Gryphaeidae VYALOV, 1936

GENUS *Gryphaea* LAMARCK, 1801

Gryphaea apiculata n. sp.
Figures 2A and 2B; 4, specimens 1 and 2; 5.1 to 5.3

Etymology: *apiculus* (Latin): pointed, sharp, refering to the apex form.

Material: Holotype: SNGM 8586 (Fig. 5.1).
Paratypes: SNGM 8581 - 8582, 8587, 8589, 8591, 8595.

Type locality and age: Quebrada El Asiento (26º23'S; 69º23'W), Chile (fossil locality No. 11 *in* Pérez, 1982, p. 43). Middle Bajocian.

Diagnosis: Medium to small (maximum height *ca*. 39 mm) and subtriangular to subtrapezoidal (in some cases subovoidal) *Gryphaea*. In the dorsal third, the main part of the shell has an anterior margin and a tilted surface (extended to commissure). The posterior margin of this zone (and the associated posterior tilted surface) is oriented in a ventroposterior direction along growth, and constitutes the most convex surface of the shell, generally located in the posterior half of the valve. The posterior flange is visible in external view only in the ventral portion of the shell and has a low convexity. The umbo is opisthogyrous to orthogyrous, with a low convexity, a gentle or absent curvature and a short and sharp apex. External thin radial striae are not well defined. The shell has a medium thickness.

Discussion: *G. apiculata* n. sp. shares with *G. varillasensis* n. sp. and *G. euteicha* n. sp. the earliest (primary) conformation of the main part of the shell, with a posterior and specially an anterior margins and a more or less convex (symmetric) external surface. Moreover, in *G. varillasensis* n. sp. the umbo has a low convexity and a gentle or absent curvature, as in *G. apiculata* n. sp.

Nevertheless, this species has close morphological affinities with *G. euteicha* n. sp., considering the generally wide and almost flat external surface of the left valve, the delayed emergence of the posterior flange and the posterior position of the main convexity of the shell. On the contrary, *G. apiculata* n. sp. differs from *G. euteicha* n. sp. because in the last species the anterior tilted surface is usually well defined and high (= anterior wall) along the ontogeny, the antero-ventral curvature (and the related expansion of the shell) is more pronounced (and does not affect the development of the anterior wall), the anterior

margin of the main part of the shell tends to be replaced by an anterior flange with the growth, and the umbo is generally more curved.

Gryphaea apiculata n. sp. differs from *G. varillasensis* n. sp. because in the latter the antero-ventral curvature of the shell is generally lower (and the anterior margin of the valve can be uniformly convex), the anterior tilted surface and margin (of the main part of the shell) are restricted to the earliest growth-stage, the main convexity of the left valve is lower, symmetric, and located in the middle part of the shell, and the posterior flange becomes progressively more evident with growth.

Gryphaea varillasensis n. sp.
Figures 4, specimen 10; 5.4 and 5.5

Etymology: It refers to the type locality.

Material: Holotype: SNGM 8467 (Fig. 5.5).
Paratypes: SNGM 8468 - 8470.

Type locality and age: Quebrada Las Varillas (26°26'S; 69°11'W), Chile. Late Early Bajocian - Late Bathonian.

Diagnosis: Medium (maximum height *ca*. 47 mm) and subovoidal to subcircular *Gryphaea*. The main part of the left valve is delimited by rounded anterior and posterior margins only near the apex of the umbonal zone. The general convexity of the shell is low and wide, also reduced near the anterior commissure, and higher in the middle part of the valve. The posterior flange is as wide as long during growth, and has a low convexity. The umbo is opisthogyrous to orthogyrous, few convex, with a gentle (or absent) curvature and a short apex. External thin radial striae are well defined in the dorsal and middle third of the shell. The ventral commissure is gently or very curved in the adult growth-stage. The shell has a medium to low thickness.

Discussion: *G. varillasensis* n. sp. shares with *G. apiculata* n. sp. and *G. euteicha* n. sp. the earliest (primary) conformation of the main part of the shell, with a posterior and specially an anterior margins and a more or less convex (symmetric) external surface. Moreover, in *G. apiculata* n. sp. the umbo has a low convexity and a gentle or absent curvature, as in *G. varillasensis* n. sp.

This species differs from *G. apiculata* n. sp. because in the latter the antero-ventral curvature of the shell is low to moderate, the anterior tilted surface and margin (of the main part of the shell) can be well defined in the adult growth-stage, the main convexity of the shell is high, narrower and located in the posterior half of the valve, and the posterior flange is visible in external view later in the ontogeny.

Gryphaea varillasensis n. sp. differs from *G. euteicha* n. sp. because in the latter the left valve is generally narrow, the antero-ventral curvature of the shell is very pronounced, the anterior tilted surface and margin (or flange) of the main part of the shell are well developed along the ontogeny, the main convexity of the shell is higher (and narrow) from the first growth-stages and usually is located in the posterior half of the valve, the posterior flange is visible or well recognized in external view only in later growth-stages, and the umbo is more convex and curved.

Gryphaea euteicha n. sp.
Figures 4, specimens 7 to 9; 5.6 to 5.11

Etymology: *eu* (Greek): well; *teichos* (Greek): wall, refering to the well defined anterior and posterior tilted surfaces (or walls) of the main part of the shell.

Material: Holotype: SNGM 8607 (Fig. 5.8).
Paratypes: SNGM 8435, 8440, 8612, 8615 - 8616, 8622, 8626, 8633, 8636, 8641 - 8642, 8665, 8670, 8673, 8720 - 8721.

Type locality and age: Quebrada Las Varillas (26°26'S; 69°11'W), Chile. Late Bathonian. Other locality: Quebrada El Asiento, *ca*. 6.1 km to west of Estación Montandon; Pérez, 1982, p. 59-60), Chile. Callovian.

Diagnosis: Small to medium (maximum height *ca*. 43 mm) and subovoidal - subrectangular to subtrigonal *Gryphaea*, with a tendency to have a concave anterior margin. The main part of the left valve is very prominent, delimited by narrow anterior and posterior margins, accompanied by anterior and posterior subvertical and flat surfaces (or walls) extended to the commissure. The anterior margin tends to be replaced by an anterior flange along the ontogeny, emphasized by an anterior sulcus (located on the external surface of the valve). The main convexity of the shell is located on its posterior half. The posterior flange tends to be not visible in external view, integrated to the posterior surface (or wall) of the valve. The umbo is orthogyrous to gently opisthogyrous or prosogyrous, with a moderate to low convexity, generally with a gentle or absent curvature (in some cases moderate to high) and a long apex. The thin radial striae are well defined in the dorsal third of the shell. The anterior commissure is more curved than the posterior one. The umbonal cavity is deep. The shell is generally thick to very thick.

Discussion: *G. euteicha* n. sp. shares with *G. apiculata* n. sp. and *G. varillasensis* n. sp. the earliest (primary) conformation of the main part of the shell, with a posterior and specially an anterior margins and a more or less convex (symmetric) external surface.

This species has close morphological affinities with *G. apiculata* n. sp., considering the generally wide and almost flat external surface of the left valve, the delayed emergence of the posterior flange and the posterior position of the main convexity of the shell. On the contrary, *G. euteicha* n. sp. differs from *G. apiculata* n. sp. because in the latter the anterior tilted surface has a lower degree of development and generally is restricted to the first growth-stages, the antero-ventral curvature is low to moderate and usually is present at the same height where the anterior tilted surface and margin (of the main part of the shell) have their last occurrence, the mentioned anterior margin never is replaced by an anterior flange, and the umbo generally has a lower curvature.

Gryphaea euteicha n. sp. differs from *G. varillasensis* n. sp. because in the latter the left valve is generally wider along the growth, the antero-ventral curvature of the shell usually is very reduced (and the anterior margin of the valve may have a convex outline), the anterior tilted surface and margin (of the main part of the shell) are not well developed because they are restricted to the earliest growth-stage, the main convexity of the shell is low, wider and is located in the middle part of the valve, the posterior flange is progressively evident with growth, and the umbo has a lower convexity and curvature.