ONTOGENY AND SEXUAL DIMORPHISM OF *EURYCEPHALITES GOTTSCHEI* (TORNQUIST) (AMMONOIDEA) OF THE ANDEAN LOWER CALLOVIAN (ARGENTINE-CHILE)

HORACIO PARENT

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ABSTRACT - A comparative ontogenetic-biometric analysis applied to a newly-collected, stratigraphically homogeneous samples of *Eurycephalites vergarensis* [M] and *Xenocephalites gottschei* [m] shows they are the macro- and microconch dimorphs of a single bio-species. Both dimorphs are identical up 18mm in diameter ("critical diameter"). Strong morpho-ornamental differentiation of the [m] relative to the [M] developed beyond the critical diameter, as a consequence of: a) an heterochronic process, progenesis; b) a late modification probably linked to sexual maturity, a trend to body chamber uncoiling; and c) epigenetic outgrowths combined with acceleration in mature costulation. These two last modifications are hard to explain in terms of heterochrony. The previously known material of the species shares the same morpho-ornamental patterns and dimorphic relationships. Both dimorphs must be given the same, single specific name: *Eurycephalites gottschei* (TORNQUIST, 1898) [M&m]. A detailed systematic description is given for this species.

KEYWORDS: CALLOVIAN, AMMONITINA, EURYCEPHALITINAE, ONTOGENY, SEXUAL DIMORPHISM, COMPLEX PROGENESIS.

RÉSUMÉ - Une analyse biométrique comparative prenant en compte l'ontogénése est appliquée à un échantillon stratigraphiquement homogène comportant *Eurycephalites vergarensis* et *Xenocephalites gottschei*. Elle montre que ces deux formes sont les dimorphes, respectivement macroconque [M] et microconque [m], d'une unique espèce biologique. Les deux dimorphes sont identiques jusqu'à un diamètre de 18mm (=diamétre critique). Au delà de cette taille on note, chez le microconque et par comparaison avec le macroconque, de fortes différenciations dans la géométrie et l'ornementation des coquilles; celles-ci seraient la résultante: a) d'un processus hétérochronique, la progénèse; b) d'une modification tardive probablement liée à l'acquisition de la maturité sexuelle, la tendance au déroulement de la loge d'habitation; et c) des modifications épigénétiques associées à une accélération mature de la costulation. Ces deux dernières modifications restent difficiles à interpréter en termes d'hétérochronie. L'analyse d'un matériel complémentaire se rapportant au même groupe d'ammonites montre un dimorphisme identique et des caractéristiques morpho-ornementales équivalentes. Il convient, en conséquence, d'accorder une dénomination spécifique unique aux deux dimorphes: *Eurycephalites gottschei* (TORNQUIST, 1898) [M&m]. Une description systématique détaillée de l'espèce est donnée en complément de l'analyse.

MOTS-CLÉS: CALLOVIEN, AMMONITINA, EURYCEPHALITINAE, ONTOGENÈSE, DIMORPHISME SEXUEL, PROGENÈSE COMPLEXE.

INTRODUCTION

A large proportion of the Jurassic Ammonitina develops a sexual intraspecific polymorphism expressed as morphologic dimorphs, differing in adult size: the macroconch [M] and the microconch [m], thought the female and the male respectively. This dimorphism may be described as a morphogenetic and/or ornamental divergence (generally concurrent) beyond a given size up to which both juvenile dimorphs are identical at the morphological, ornamental and sutural levels. This size, expressed as the conch diameter, may be conveniently called the critical size or diameter (DC) and may be taken as the growth step at which the [m] may have reached its sexual maturity, with subsequent terminal morphologic changes linked to terminal germinal development.

In order to explain the differential size and the morpho-ornamental divergences between macro- and microconchs in several Lower and Middle Jurassic ammonites, Tintant (1963 *teste* Guex 1970: 3) has suggested, then Guex (1981) has proposed the occurrence of neoteny -reduced rate of somatic development- and progenesis -onset of maturity at an early stage of development- in the microconchs relative to the corresponding macroconchs. At an intraspecific level these heterochronic processes produce paedomorphic patterns of retention of macroconch juvenile characters in the adult microconch.

Detection of dimorphism, as well as the establishment of dimorphic correspondence between two forms, may be done from complete adult individuals (Callomon 1981) and/or from complete "growth series" of stratigraphically homogeneous samples, because what are thought to be the conchological, secondary sexual characters are developed only after the DC. Signs of maturity in ammonites have been analyzed by many authors (see Callomon 1981 and references therein): modification of the body chamber through change of coiling and variocostation, crowding and simplification of the last septal sutures, and modification of the final peristome.

Eurycephalites vergarensis (BURCKHARDT, 1903) [M] and *Xenocephalites gottschei* (TORNQUIST, 1898) [m] (both of the Eurycephalitinae Thierry 1978) share almost the same biostratigraphic distribution all along the Vergarensis Zone of the Lower Callovian at the Argentine-Chilean Andes (Riccardi et al. 1988, 1989). Moreover *E. vergarensis* (BURCKHARDT) is the only recorded species of the genus for this Zone. Recently Riccardi & Westermann (1991) have revised all the known material of these two morpho-species, suggesting a possible dimorphic correspondence. But lack of adult individuals with preserved inner whorls prevented those authors from testing such hypothesis.

The Vergarensis Zone in Chacay Melehué (locus typicus) comprises some 30m of dark-grey to black shales with several beds with abundant fossiliferous nodules and concretions belonging to the Los Molles Formation. At this locality, in the basal levels of that Zone, probably the equivalents of beds M267-8 of Riccardi et al. (1989: fig. 2), it has been collected a sample of three sideritic nodules and five concretions containing several well preserved juvenile and adult specimens of *E. vergarensis* (BURDKHARDT) [M] and *X. gottschei* (TORNQUIST) [m]. This material has allowed the study of the inner whorls, including the protoconch in some of the specimens, showing, after dissection, identical nuclei up to about 18mm in mean diameter, onwards from which the characteristic adult morphologies may be discriminated. This fact agrees well with the hypothesis of dimorphic correspondence between those two morpho-species.

The present work has three objectives: 1) to demonstrate and characterize the sexual dimorphic correspondence between *E. vergarensis* (BURCKHARDT) [M] and *X. gottshei* (TORNQUIST) [m] by means of a comparative ontogenetic-biometric analysis applied to the new material, as a sample of a single biospecies, and to the previously known material; 2) to propose the nomenclatural changes that seem the most appropriate ones to take in account the biospecific identity between these two morpho-species; 3) to give a detailed systematic description of the whole development of the dimorphic species.

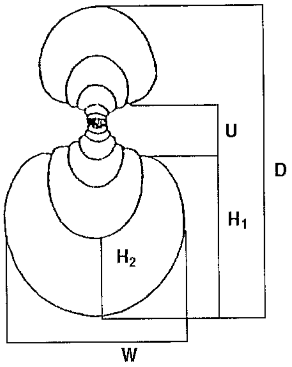
The material was collected in Chacay Melehué, northern Neuquén, 33Km northwest of Chos Malal on National Road 43 towards Andacollo. This collection is housed at the Laboratorio de Paleontología y Biocronología (LPB) of the Instituto de Fisiografía y Geología (Universidad Nacional de Rosario).

MATERIAL AND METHOD

The material, which we will call standard sample (MS), comprises 28 juvenile and adult macroconchs, 19 adult microconchs and 12 undifferenciated juveniles (D<18mm) which may belong to either of these two suspected dimorphs. Almost all these specimens are complete, with phragmacone and body chamber; only 3 undifferentiated juveniles lack body chamber. This assemblage comes from a single fossiliferous level and is clustered into a few nodules and concretions, ensuring the isochronous nature of the MS and consequently the exclusion of temporal and geographic components from the whole intraspecific variation. Taking the MS as reference, all the available material of that studied by Riccardi & Westermann (1991) was introduced as complementary material (MC) in order to cover the whole stratigraphic range of the two morpho-species.

Classical conchological measurements which cover the greatest part (>90%) of the variation of growth and morphology in ammonites (see Reyment & Sandberg 1963; Thierry 1976) were used (Fig. 1): shell diameter (D), umbilical width (U), whorl width (W), and whorl height (H_1). Additionally, the following measurements were used: whorl ventral height (H_2), and numbers of primary and ventral ribs along the last half whorl at the measured diameter (P and V respectively).

FIGURE 1 - Measurements used as biometric data. See explanation in text. *Dimensions mesurées. Explication dans le texte.*



All specimens of the MS were measured at several successive diameters, approximately every 0.5 whorl back from the peristome. These data were subdivided into several subsamples corresponding to successive developmental stages (ED): ED_1, $D<DC=18$mm; ED_2, $DC<D<60$mm; and ED_3, $D>60$mm, attained only by macroconchs. This makes possible a comparative study of preadult (limit at DC) and adult growth rates and relative morphology separately, in both juveniles and adults simultaneously. All measurements were made on inner moulds and are given in millimeters (mm). Any sample and subsample with a bell-shaped frequency distribution was taken to be adequate for t-Student inferential techniques. Significance of random variable values are noted as: (°): $P>0.05$, not-significant; (*): $0.05>P>0.01$, significant; and (**): $P<0.01$, highly-significant.

The ontogenetic-biometric analysis is applied to each character individually through a series of comparisons between [M] and [m] for ED_1 and ED_2 separately.

Growth - The growth curves were obtained by means of least-squares regressions on size, taking as usual diameter D as biological age indicator, and adopting a curve of growth model $Y = aD^m$ which gave the best fit (max r^2). Curve-fitting and growth rates comparisons were made through natural-log-transformed data ($\ln Y = \ln a + m \ln D$). In this form, all samples tended to be normally distributed. t-Student comparisons of growth rates were made following Hald (1952) but using, in case of heterosedasticity, a corrected t-percentile (Snedecor & Cochran, 1967). When growth rates differed insignificantly, a single common equation was calculated for all the compared subsamples; when not, a polyphased model was used. In order to compare the growth patterns of complementary material with those of the standard sample, we calculated the fraction of the former included between the upper and lower growth curves ($me^{\pm 1.96S}$), which embraces 95% of the theoretical population around the mean curve calculated for the standard sample.

Relative morphology - From the data matrix the following ratios were obtained: U/D, W/D, H_1/D, H_2/D, W/H1, P/D and V/D. These measure the instantaneous state of a character relative to another and are relatively size-independent. The mean values were compared by means of a t-Student test.

Ontogenetic trajectories (sensu Alberch et al. 1979).- Somatic and germinal developments of [M] and [m] were compared throughout their ontogenetic trajectories, trying to explain the observed morphogenetic and ornamental divergences which produce the sexual dimorphism in terms of developmental heterochronies. The ontogenetic concepts here applied have been analyzed extensively by Dommergues (1987), Dommergues et al. (1986), Gould (1977), Mc Namara (1981, 1986, 1993), Raff & Kaufman (1991), Wray & Raff (1990). The construction and interpretation of the graphic representations are based on Alberch et al. (1979), Dommergues (1986), Dommergues & Meister (1986) and Mc Namara (1986).

RESULTS

The size distribution frequency of the MS is polymodal (Fig. 2a) with two modes which closely correspond to the adult diameters of [M] and [m], and a third peak which corresponds to the smaller sized juvenile individuals ($D<6$mm). Macro- and microconch adult size distributions are bell-shaped and they do not overlap, there are no intermediate sized adults. The mean adult macroconch size is more than twice that of the microconch (Tab. 1) with a relatively low CV. When the adults of the complementary material are introduced, the pattern does not change, they lay into the same size ranges (Fig. 2b), and the differences between MS and MC are non-significant (Tab. 1).

The three concretions supplied 24 juvenile [M] ($18<D<60$mm) and 19 adult [m] ($D>18$mm). The macro-microconch ratio, assumed to be the best estimator of "sex-ratio", is [M]:[m]=24:19 revealing non-significant bias relative to 1:1 proportion ($X^2=0.372$, $0.25<P<0.50$, df=1). After inclusion of the 5 adults [M] from nodules, the ratio becomes [M]:[m]=29:19 revealing non-significant bias with the 1:1 proportion ($X^2=1.688$, $0.75<P<0.90$, df=1), thus we may assume equal, or very close numbers of females and males in the original population.

The frequency distribution for the number of measured diameters for each specimen of the MS fits to a log-normal theoretical distribution [Kolmogorov-Smirnoff test of goodness of fit for log-transformed variable: Ho=0.158(°), df=58]. Taking into account that for any subsample used in this study

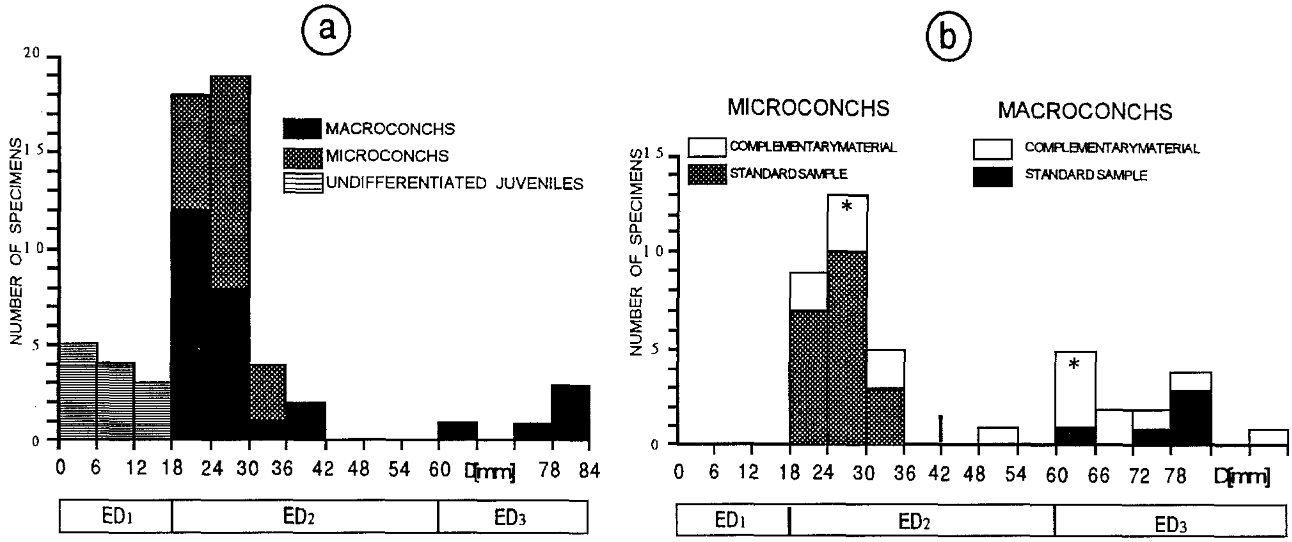


FIGURE 2 - Size-frequency histograms for the reference sample MS (a), and for the adult macro- and microconchs of MS and complementary material MC (b). Developmental stages (ED) indicated following definitions in text. *: types (the lectotype is a microconch, the allotype a macroconch). *Histogrammes de distribution de taille adulte pour l'échantillon de référence MS (a), et pour les adultes du MS et le matériel complémentaire MC (b). Etapes du développements (ED) en référence au texte. *: types (le lectotype est une microconque, l'allotype une macroconque).*

		n	x ± k0.95	RO	CV	Comparison
A)	[M]	5	74.2±9.3mm	62.0-80.3mm	9.0	
	[m]	18	26.1 ±2.0mm	20.5-34.0mm	14.9	F=3.48(*),t=19.6(**)
B)	[M]	11	69.3±6.8mm	45.0-92.3mm	13.9	
	[m]	7	25.9±3.6mm	20.5-30.9mm	14.1	F=6.61(*),t=10.7(**)
C)	[M]			F=1.84(°), t=0.96(°)		
	[m]			F=1.03(°), t=0.11 (°)		

TABLE 1 - Statistical measurements for the adult size of *Eurycephalites gottschei* [M&m] and comparisons between dimorphs of the MS (A), the dimorphs of the MC (B), and the two samples fused of each one of the dimorphs (C). n: sample size, $k_{0.95}$: radius of the confidence-interval of 95% around the mean, RO: sample range, CV: percentual coefficient of variation. *Paramètres statistiques pour la taille adulte de* Eurycephalites gottschei *[M&m] et comparaisons des dimorphes de la MS (A), dimorphes de la MC (B), et les deux échantillons des deux dimorphes (C). n: effectif de l'échantillon, $k_{0.95}$: intervalle de confiance à 95%, RO: étendue totale de la variabilité, CV: coefficient du variation exprimé en pourcentage.*

the frequency distribution was bell-shaped with a single mode, and performing a control of regression residuals in growth analysis, the autocorrelation was neglected.

GROWTH CURVES AND RATES

From a juvenile macroconch (LPB 029/1) the relation between D and whorl number (NV) was estimated by fitting an exponential regression model in the range $0.77<D<21.00$mm; results are: $D= 0.36e^{0.78(NV)}$, $n=8$, $r=0.9996(**)$, $S_{(y.x)}=0.026$. Moreover the partial analysis of several other macro- and microconch specimens shows that the equation obtained represents well the MS (extrapolated for $D>21$mm). Thus from this close correspondence in the relation D-NV in [M] and [m], we may assume that D is a good (but non-linear) estimator of age, for comparisons between dimorphs of the species at least.

Growth rates are indicated by the exponent M of the independent variable D. A t-test performed to U, W, H_1 and H_2 growth rates onto the MS yields non-significant differences between [M], [m], and juveniles at ED_1. Differences between [M] and [m] at ED_2 are non-significant in W and H_1 but significant for U and H_2. Following these results, definitive single simple curves were fitted for W and H_1 (Fig. 3) for both dimorphs throughout development (table 2). Polyphased curves were fitted for U and H_2 (Fig. 3) with a common branch for both dimorphs at ED_1 and a branch for each one of both dimorphs after DC (Tab. 2). This modality does

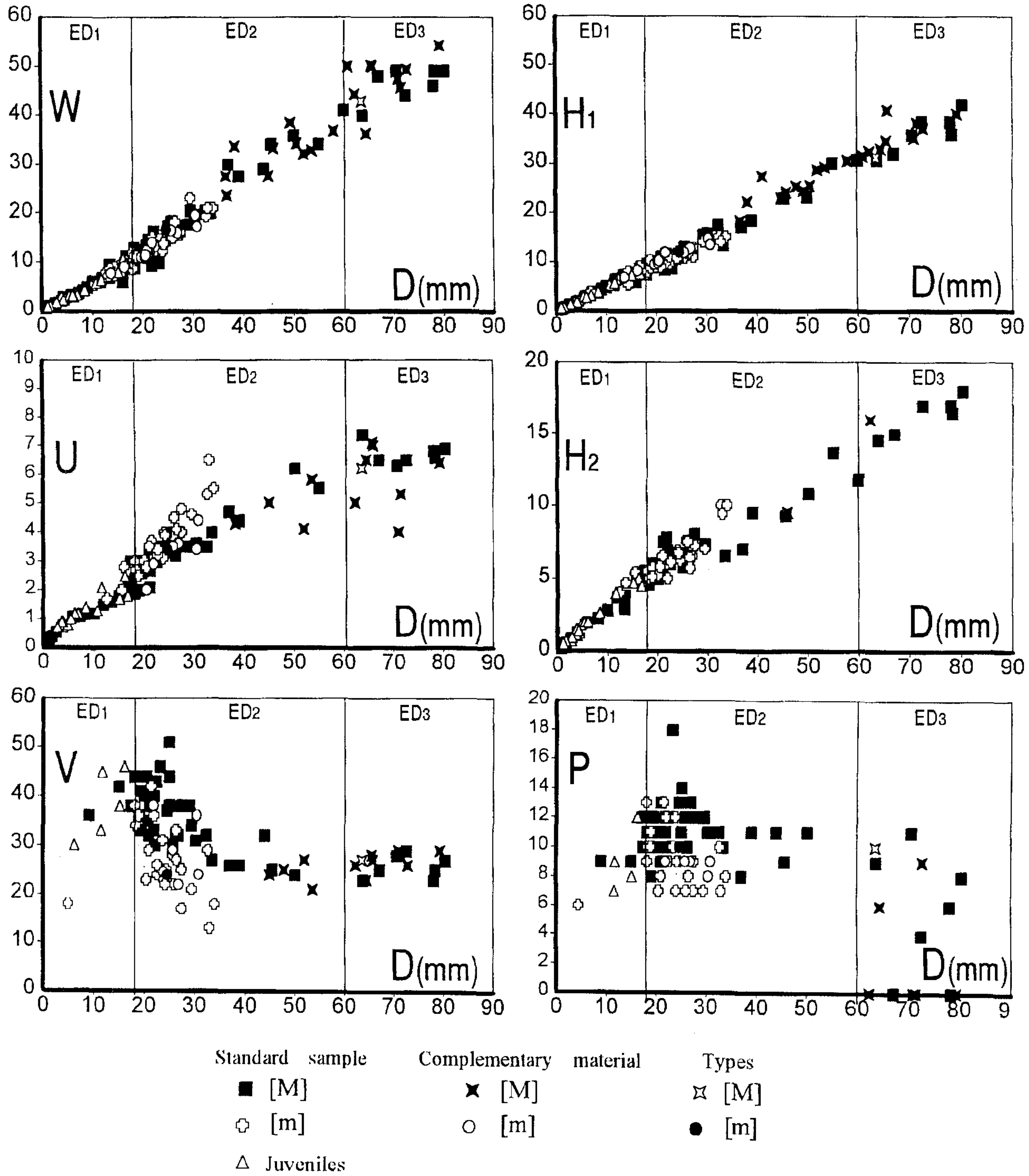


FIGURE 3 - Scatter diagrams of W, H1, U, H_2, V and P versus D for all the studied specimens. Developmental stages (ED) indicated following definitions in text. Regression parameters for the MS in table 2. Types: the lectotype is a microconch, the allotype a macroconch. *Diagrammes de dispersion W, H1, U, H_2, V et P versus D pour tous les échantillons. Etapes du développement (EI) en référence au texte. Paramètres de la régression pour MS dans la table 2. *: types le lectotype est une microconque, l'allotype une macroconque.*

not take in account some doubtfully significant differences between consecutive ED for H_2 in the [M]. The development of ventral and primary ribs is presented through scatter diagrams only (Fig. 3) because no satisfactory simple regression model was found. However these scatters show a

TABLE 2 - Growth curves parameters for the the MS of *Eurycephalites gottschei* [M&m]. n: sample size, N: number of measured specimens, r: correlation coefficient, S: standard regression error in ln-units. *Paramètres de croissance pour la MS* Eurycephalites gottschei *[M&m]. n: effectif de l'échantillon, N: nombre de spécimens, r: coefficient de corrélation, S: erreur standard de la régression exprimée en ln-unités.*

	ED	Dimorph	$Y=aD^m$	n(N)	r	$e=^{+1.96S}$
W	1-3	[M&m]	$0.64D^{0.98}$	148(59)	0.99(**)	1.29;0.78
H1	1-3	[M&m]	$0.46D^{1.01}$	135(59)	0.99(**)	1.22;0.82
U	1	[M&m]	$0.27D^{0.76}$	38(22)	0.97(**)	1.35;0.74
	2,3	[M]	$0.34D^{0.70}$	39(24)	0.94(**)	1.28;0.78
	2	[m]	$0.06D^{1.27}$	27(18)	0.92(**)	1.22;0.82
H2	1	[M&m]	$0.32D^{0.97}$	38(19)	0.98(**)	1.39;0.72
	2, 3	(M]	$0.52D^{0.79}$	29(20)	0.96(**)	1.28;0.78
	2	[m]	$0.37D^{0.90}$	25(17)	0.86(**)	1.20;0.83

very well-defined tendency with a common pattern shared by [M], [m] and juveniles for D<DC, and then for D>DC each dimorph has its proper and decreasing tendency. Comparisons of P and V between [M] and [m] at ED_2 yield significant differences for both cases. The subsamples of P and V for [m] and juveniles at ED_1 are too small to perform a t-test, but they are included into the 95% confidence intervals around the means of the [M]. These results explain the origin of the observed morphological relationships detected with preliminar dissection and described by the ratios of relative morphology, morphological identity until DC followed by strong differentiation for D>DC between [M] and [m] due to differential adult and preadult growth rates.

The proportions of measurements on the MC included between the MS upper and lower growth curves, in accord with the assumption of conspecifity between the two samples were, for all the characters, very high (88-100%) both in the case of the microconchs and the macroconchs. The numbers of P and V for those samples follow similar patterns throughout the development (Fig. 3).

RELATIVE MORPHOLOGY

The comparison between [M], [m] and juveniles of the MS at ED_1 yields non-significant differences for all the relative morphology ratios. Analogous comparisons at ED_2 between [M] and [m] yield significant differences in U/D, H_2/D, P/D and V/D, but differences are not-significant in W/D, H_1/D and W/H_1. These relationships in relative morphology are in agreement with those obtained from growth analysis.

Comparisons of relative morphology between the MS and the MC are made character-by-character, evaluating the proportion of measurements of the last sample included into the 95% confidence intervals around the means of the ratios of the MS. These results show a very high proportion included (89-100%) in those intervals, and once again great consistency between these patterns and those of growth throughout ED_2 and ED_3.

DEVELOPMENTAL HETEROCHRONIES.

The comparative analysis of allometric growth transformed into relative morphological variations (ontogenetic trajectories) of one of the dimorphs relative to the other, may show which are the processes that produce the heterochronic patterns between dimorphs. The evaluation of heterochronies is here constrained by the previous results, since the ontogenetic trajectories were assumed to bifurcate, more or less divergently, only for those characters that show significant differences in growth rates and ratios. The selection of the macroconch as reference may be justified on theoretical palaeobiological grounds and operational stratigraphical arguments (see remarks under genus *Eurycephalites*).

Application of the criteria for maturity in ammonoids to the MS shows that the [m] probably achieved sexual (reproductive) maturity at 18mm in diameter, precociously with respect to the [M] which matures later at approximately 60mm in diameter. This is suggested by the conspicuous and irreversible tendency of the [m] to change in coiling and to assume strong variocostation at adult body chamber. Assuming D is a good direct estimator of biological age, then the [m] is paedomorphic by progenesis (sensu Gould 1977) with respect to the [M]: growth in the former is arrested at 30-35mm in diameter, 0.5-0.8 whorl after DC where germinal development onset occurs, omiting part of ED_2 and ED_3. Although progenesis is a process that may affect the whole organism (Mc Namara 1986: 8), explaining in this case the observed size relationships between the [M] and the [m], the trajectories of U/D, H_2/D, P/D and V/D show a more complex pattern since they are divergently dissociated from DC up to the end of development (Fig. 4). Adult [m] exhibits a strong uncoiling of the body chamber: increased U/D and H_2/D whereas H_1/D remains

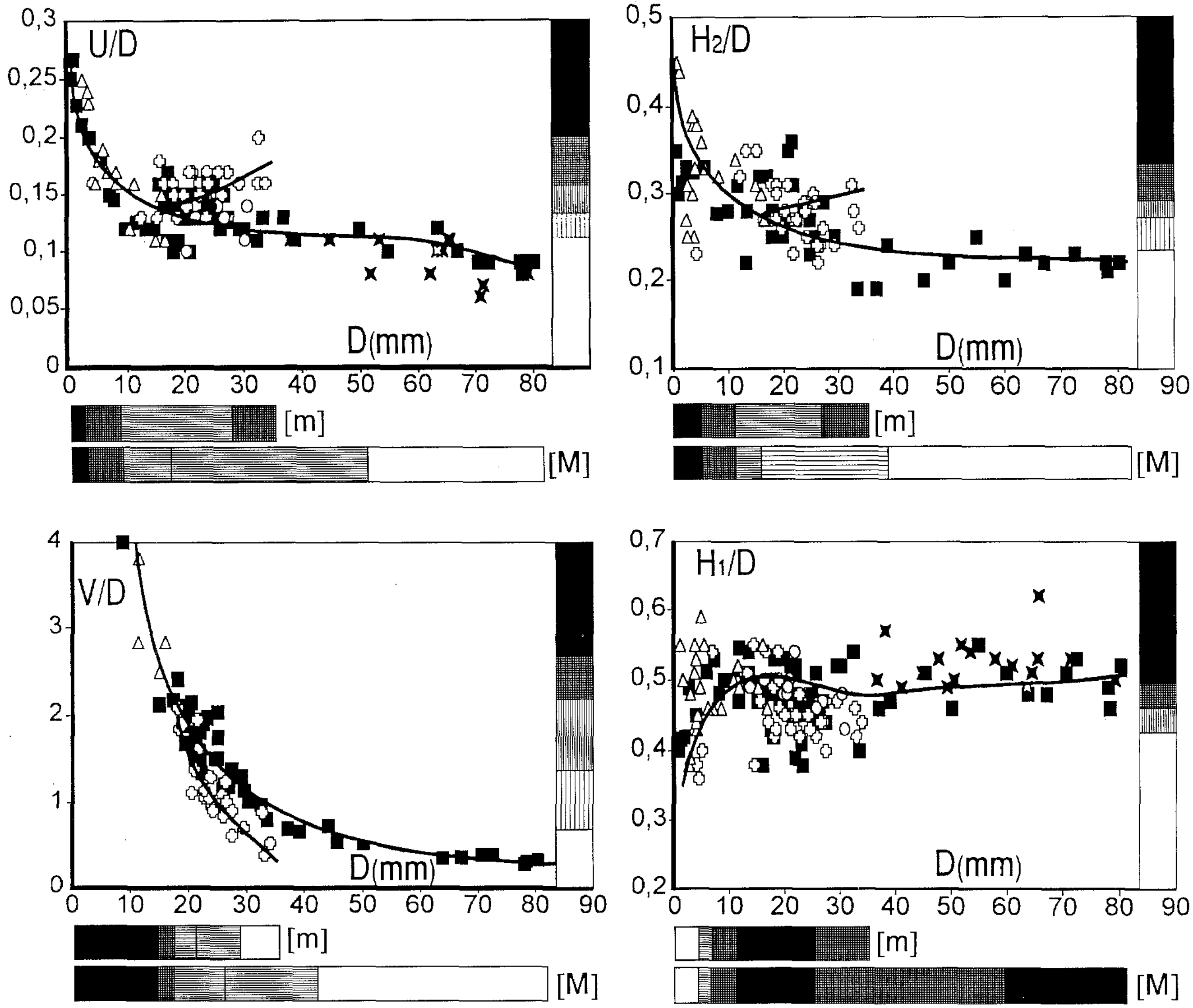


FIGURE 4 - Scatter diagrams of U/D, H_2/D, V/D and H_1/D versus D for all the studied specimens. Ontogenetic trajectories and cartridges for the MS only. Types: the lectotype is a microconch, the allotype a macroconch. *Diagrammes de dispersions U/D, H_2/D, V/D et H_1/D versus D pour tous les échantillons. Itinéraires et cartouches ontogénétiques pour MS exclusivement. *: types (le lectotype est une microconque, l'allotype une macroconque).*

almost constant and undifferenciated with respect to the [M]. This uncoiling morphogenetic pattern of the adult body chamber in the [m] is the opposite to that of tightening developped up to D<12-15mm (Fig. 4). In this way the adult [m] shows analogous (non-homologous) coiling with juvenile whorls; however it may be thought as a feature associated with sexual maturation (Landman et al. 1991). Another dimorphic feature is the ornamentation since the [m] shows, along the adult body chamber, lower numbers of stronger primary and ventral ribs than the [M]. The development of relative numbers of primary and ventral ribs (P/D and V/D) seems to be accelerated (peramorphic mode) respect of the [M] (Fig. 4). The sudden strenghthen of the ventral and, specially, the primary ribs represents epigenetic outgrowths (sensu Landman et al. 1991) of the juvenil costulation. Conversely the macro- and microconch trajectories of W/D and H_1/D are not dissociated throughout the development (Fig. 5), the precocious maturation of [m] is not associated with differential morphological effects on the whorl section.

DISCUSSION AND CONCLUSIONS

The adult size frequency distributions (Fig. 2) show there are no intermediate adult sizes between macro- and microconchs which is in accord

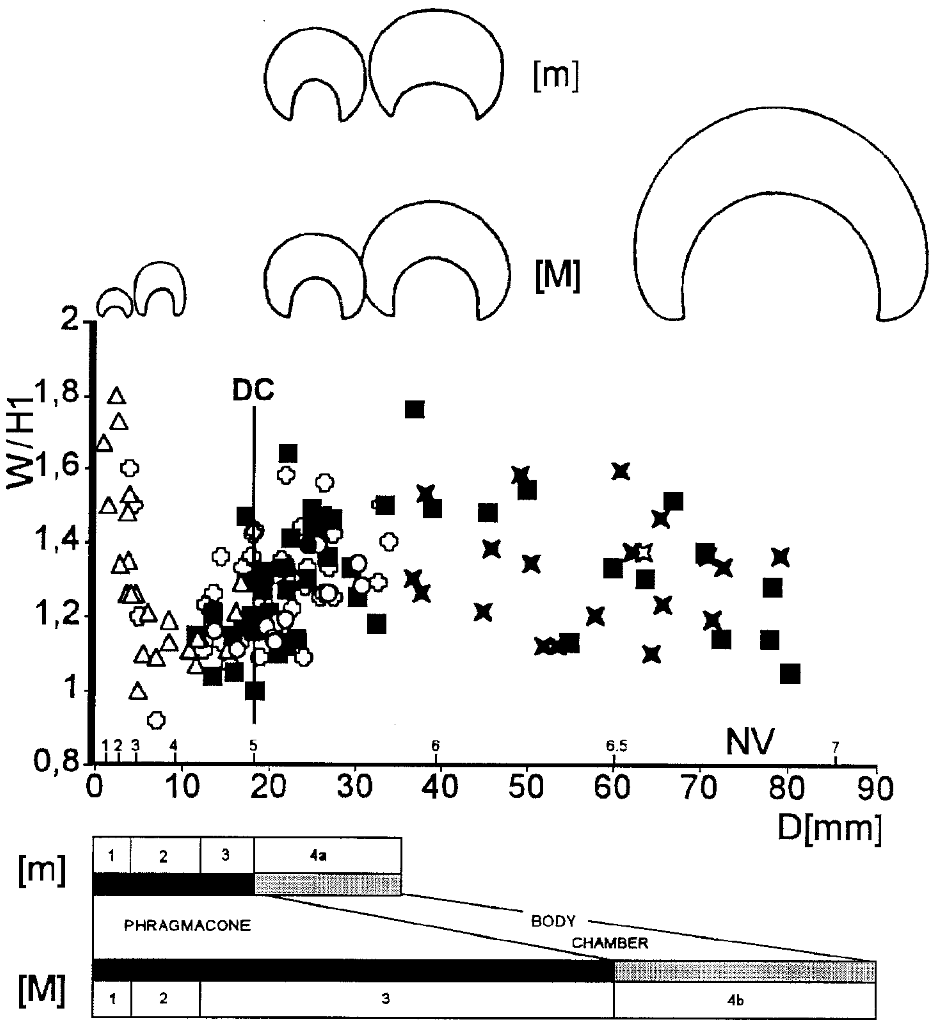


FIGURE 5 - Scatter diagram of W/H_1 versus D and whorl number (NV), mean whorl section (x1) and cartridges showing shell morphological stages throughout the ontogeny of *Eurycephalites gottschei* [M&m]. DC: critical diameter. Shell morphology: 1: smooth, evolute and depressed, 2: involute and compressed with fine, flexuous ribs, 3: involute and depressed with fine, flexuous ribs, 4a: egressive body chamber, coarse and low density ribbing, 4b: narrow umbilicus, smooth flanks and coarse ventral ribbing. Other references in figure 3. *Diagrammes de dispersion W/H_1 versus D et NV, sections axiales moyennes (x 1) et cartouches ontogénétiques illustrant les états morphologiques de* Eurycephalites gottschei *[M&m]. DC: diamètre critique. Etats morphologiques: 1: lisse, évolute et déprimée, 2: involute et comprimée avec côtes faibles et flexueuses, 3: involute et déprimée avec côtes faibles et flexueuses, 4a: loge d'habitation déroulée avec côtes épaisses, 4b: ombilic fermé, flancs lisses et côtes ventrales épaisses. Autres références sur la Figure 3*

with the criteria of differential adult size between sexual dimorphs. Relative morphology and costulation change strongly throughout post-embryonic development in both [M] and [m] (Figs. 3-5,6), excepting H_1/D, which remains almost constant throughout, such as in most eurycephalitines. At ED_1 both dimorphs are statistically identical in growth rates, relative morphology and costulation. At ED_2, from 18mm in diameter, appear some divergences between [M] and [m] in costulation and coiling but their whorl sections remain identical at comparable diameters. Comparisons between MS and MC by means of the confidence-intervals of 95% of the former show they share the same subadult and adult morphogenetic patterns and growth rates, e.i., variation between samples may be attributed to intraspecific variability.

Heterochronic developmental patterns between sexual dimorphs are known in living eulimid gastropods (Mc Namara 1993), cephalopods such as *Argonauta* showing an extreme sexual dimorphism (Wells & Wells 1977: 293), and they have been invoked to explain size and morphological relationships between dimorphs in some lower Jurassic ammonites (Guex 1981). The well established sexual dimorphism in some otoitid species such as *Emileia (E.) multiformis* (GOTTSCHE), *E. (Chondromileia) giebeli* (GOTTSCHE) and *Pseudotoites singularis* (GOTTSCHE) including macro- and microconchs (Westermann & Riccardi 1979) resembles that of the Eurycephalitinae in almost all details. For these cases, and the homologous ones, we should speak of heterochronic sexual dimorphism with complex mature progenetic microconchs which are never duplicate forms of the juvenile macroconch.

According to the above discussion and the results of the precedent study, we conclude the following: 1) our MS, from a single faunal horizon, represents a single dimorphic biospecies (sensu Callomon et al. 1992); 2) the morpho-species *E. vergarensis* (BURCKHARDT) [M] and *X. gottschei* (TORNQUIST) [m] share the same morpho-ornamental patterns and relationships -dimorphic ontogeny- with the [M] and the [m], respectively, of the

TABLE 3 - Statistical measurements for all the studied specimens of *Eurycephalites gottschei* [M&m] throughout the ontogeny. Whorl number (NV) extrapolated for >21mm.
*Paramètres statistiques de la totalité des spécimens d'*Eurycephalites gottschei *[M&m]. NV extrapolée pour D>21 mm.*

Dimorph	Dimnetes(NV)	Character	n	x+k0.95	CV(%)	RO
[M&m]	0.8< D 2mm	U/D	2	0.26	3.8	25-0.27
	(1<NV<2)	W/D	3	0.78	12.3	0.68-0.91
		H_1/D	2	0.46	8.7	0.42-0.50
		H_2/D	2	0.37	18.9	0.30-0.44
		W/H_1	2	1.65	9.1	1.50-1.80
	2<D<4mm	U/D	3	0.23	7.1	0.21-0.25
	(2<NV<3)	W/D	8	0.71±0.06	9.9	0.59-0.82
		H_1/D	9	0.45±0.05	13.3	38-0.53
		H_2/D	7	0.31±0.05	17.4	0.25-039
		W/H_1	8	1.53±0.14	10.6	1.34-1.80
	4<D<8mm	U/D	7	0.17±0.01	7.7	0.14-0.19
	(3<NV<4)	W/D	13	0.55±0.03	8.4	0.48-0.62
		H_1/D	12	0.48±0.05	14.2	0.36-0.59
		H_2/D	6	0.31±0.06	17.5	0.23-038
		W/H_1	11	1.14±0.10	12.9	0.92-1.60
		P	3	11	46.4	6-18
		V	2	33	9.1	30-36
	8<D18mm	U/D	18	0.14±0.01	15.1	0.11-0.18
	(4<NV<5)	W/D	28	0.58±0.02	9.7	0.48-0.71
		H_1/D	26	0.49±0.01	6.7	0.43-0.55
		H_2/D	13	0.30±0.02	12.1	0.22-0.35
		W/H_1	23	1.20±0.05	9.6	1.04-1.47
		P	8	10±2	20.0	7-13
		V	7	37±4	11.4	32-46
[M]	18m<60	U/D	21	0.13±0.01	14.9	0.10-0.16
	(5<NV<6.5)	W/D	32	0.66±0.03	10.9	0.49-0.82
		H_1/D	31	0.49±0.01	6.3	0.44-0.57
		H_2/D	19	0.26±0.02	17.6	0.19-0.36
		W/H_1	29	1.36±0.07	12.4	1.00-1.76
		P	22	11±1	14.8	8-14
		V	23	34±3	19.1	25-51
	D>60mm	U/D	19	0.09±0.01	23.4	0.03-0.12
	(NV>6.5)	W/D	19	0.64±0.03	9.8	0.54-0.77
		H_1/D	19	0.52±0.02	6.8	0.46-0.62
		H_2/D	6	0.23±0.02	6.9	0.21-0.26
		W/H_1	19	1.25±0.06	10.5	1.05-1.53
		P	12	4±3	93.0	0-9
		V	19	26±1	9.1	21-29
[m]	D>18mm	U/D	25	0.15±0.01	14.0	0.10-0.20
	(NV>5)	W/D	26	0.60±0.02	8.4	0.55-0.78
		H_1/D	25	0.46±0.01	6.5	0.40-0.54
		H_2/D	17	0.27±0.01	7.5	0.24-0.31
		W/H_1	25	1.32±0.05	9.0	1.09-1.64
		P	25	9±1	17.0	7-13
		V	25	26±2	22.5	13-38

MS; 3) these two morpho-species therefore constitute a sexual dimorphic pair, and they must be given the same, single specific name. This dimorphism pointed out for adult size, coiling and ornamentation, arises from the progenetic microconch (truncated in somatic development), modified terminally for the dimorphic characters by mature changes in coiling and, a combination of epigenetic outgrowths with acceleration in costulation, all with respect to the macroconch.

The heterochronic relationships between the dimorphs (sexes) of a single species are comparable to those which occur between ancestor and heterochronic descendant species in phylogenetical processes. In both cases the processes are genetically determined; hormonally controlled in the former and hormonally "induced" in the latter. In the case of dimorphism, sexual or not, the heterochronic pattern is one of horizontal, intraspecific variation, but in that of phylogenetical scale it represents vertical, evolutionary change.

TAXONOMY OF THE DIMORPHIC SPECIES

Eurycephalites vergarensis (BURCKHARDT) has a vertical range confined to the Vergarensis Zone where it is the only recorded species of the genus (Riccardi & Westermann 1991; Riccardi et al. 1989; Parent in prep.). The vertical range of *Xenocephalites gottschei* (Tornquist) seems to be some broader than that of the [M], its base at the top of the Steinmanni Zone (Upper Bathonian) and its top at the base of the Bodenbenderi Zone (Lower Callovian).

Once demonstrated the dimorphic correspondence between the two nominal morpho-species they may be united under a single, common specific name although the two respective types come from somewhat distant localities and there is no guarantee that they are of the same age, thus they could not therefore formally be coupled as lectotype/allotype. But after much analysis it was taken the decision to unite them taking in account that all the known material of the two morpho-species was studied, and consequently, that the statistical inferences here obtained are meaningful.

The most simple and conservative alternative is to designate the pair as *E. vergarensis* (Burckhardt, 1903) [M&m], including *X. gottschei* as a synonym; nevertheless it is not suitable since *Macrocephalites gottschei* Tornquist, 1898 has publication priority over *Macrocephalites vergarensis* Burckhardt, 1903. Moreover the genus *Xenocephalites* Spath, 1928 includes the microconchs of several macroconch nominal genera (*Eurycephalites, Lilloettia, Stehnocephalites, Iniskinites*), as was suggested by Riccardi & Westermann (1991: 72; see Parent & Argüello in prep.), and could be expected to be gradually "emptied" with the advance of the knowledge, to be supressed once dimorphic correspondences between its nominal species and the corresponding macroconchs are fully established. Conversely the genus *Eurycephalites* Spath, 1928 comprises well defined macroconch species which biostratigraphic and geographic ranges are clearly delimitated, and their phyletic relationships have been worked out with close certainty. Thus the most appropiate name is:

Eurycephalites gottschei (Tornquist, 1898) [M&m]
Macroconch: "*Eurycephalites vergarensis*" (Burckhardt, 1903)
Microconch: "*Xenocephalites gottschei*" (Tornquist, 1898)

SYSTEMATIC DESCRIPTION

Superfamily STEPHANOCERATACEAE Neumayr, 1875
Family SPHAEROCERATIDAE Buckman, 1920
Subfamily EURYCEPHALITINAE Thierry, 1978 (1976)
(inc. Paracephalitinae Tintant & Mouterde, 1981)

Genus *Eurycephalites* Spath, 1928

Type species.- *Macrocephalites gottschei* (Tornquist, 1898). Spath (1928) originally designated *"Macrocephalites vergarensis"* Burckhardt, 1903 but this is a junior synonym of *"M. gottschei"* Tornquist.

Diagnosis - Dimorphic. Shell globose, slightly compressed to depressed with subquadrate to ovate whorl section; involute to occluded umbilicus with rounded slope and shoulder. Slightly flexuous projected primaries dividing on flanks into 2 or 3 secondaries which cross the venter without interruptions. In the macroconchs ribbing fadding away progressively from the inner flanks to venter on body chamber; in the microconchs becoming sparse and prominent.

Remarks - Almost all the microconchs are retained pro temp. in the genus *Xenocephalites* Spath, 1928. These two genera were founded at the same time, so if they are to be united, the choice of senior synonym is arbitrary. The macroconch is preferable because it is richer in characters hence more precisely interpretable chronologically (Callomon, pers. com.), an operational concept.

Eurycephalites gottschei (Tornquist, 1898) [M&m]

Figs. 2,6; Tables 1-3

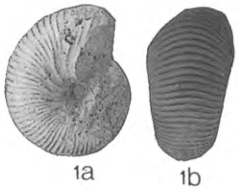
Synonymy - See Riccardi & Westermann (1991: 36, 76).

Lectotype - Tornquist's (1898: pl. 8, fig. 4) original microconch, designated as the lectotype of *"X. gottschei"* by Riccardi et al. (1989: 567).

Allotype - The macroconch figured by Burckhardt (1903: pl. 2, figs. 18-20, pl. 3, fig. 4) designated as lectotype of *"E. vergarensis"* by Riccardi et al. (1989: 565).

Material - The standard sample: 5 adults [M] (LPB 026-028, 030, 031) and 35 juveniles and subadults [M] (LPB 029/1-4, 111, 113-115/1-3, 117, 118, 121-123, 126-133, 137, 142, 147-150, 155, 157, 158), 19 subadults and adults [m] (LPB 112, 124, 125, 135, 139, 141, 143-146, 151-154, 156, 159, 160, 161, 400). The complementary material (complete information in Riccardi & Westermann 1991): 14 subadults and adults [M]

FIGURE 6 - **1-11.** *Eurycephalites gottschei* (Tornquist, 1898) [M&m]. **1a,b:** Complete juvenile [M], compressed variant (LPB 029/4); the ventral view showing the arched ventral ribs. **2-4:** Complete juveniles [M] (LPB 029/1, 128, 127). **5a,c:** Complete juvenile [M] (LPB 154). **6a,b:** Complete subadult [M] (LPB 122). **7a,b:** Complete subadult [M] (LPB 150). **8a,b:** Incomplete adult [M] (LPB 028). **9a,b:** Incomplete adult [m] (LPB 112). **10a, b:** Complete adult [m] (LPB 144). **11a,b:** Complete adult [m] (LPB 151). All figures natural size. The points indicate the end of the phragmacone. All specimens come from the same single faunal horizon in the Vergarensis Zone (Lower Callovian) at Chacay Melehué, Argentina. ***1a,b:*** *juvénile complet [M] (LPB 029/4), variant comprimé* ***2-4:*** *juvéniles complets [M] (LPB 029/1, 128, 127).* ***5a,c:*** *juvénile complet.* ***6a,b:*** *[M] subadulte complet.* ***7a,b:*** *[M] subadulte complet.* ***8a,b:*** *[M] adulte incomplet.* ***9a,b:*** *[m] adulte incomplet.* ***10a,b:*** *[m] adulte complet.* ***11a,b:*** *[m] adulte complet. Toutes les figures x 1. Les points indiquent la fin du phragmacône. Tous les spécimens proviennent d'un même horizon faunique, Zone à Vergarensis (Callovien inférieur), Chacay Melehué, Argentine.*

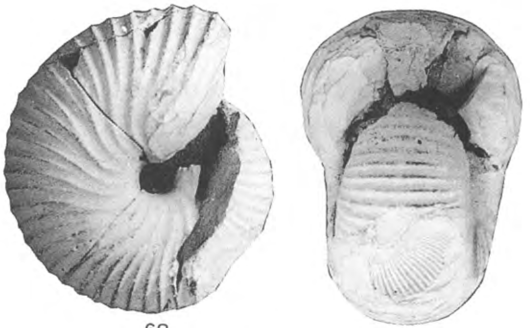

1a 1b

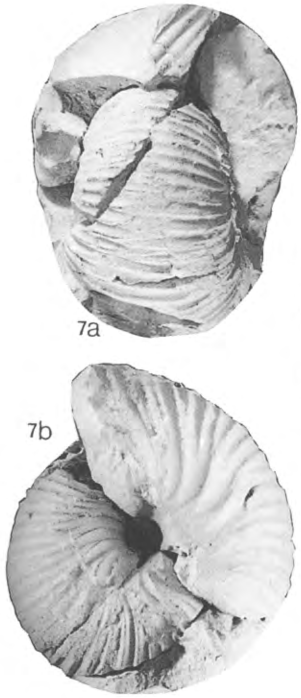

2


3


4


5a 5b 5c


6a 6b


7a
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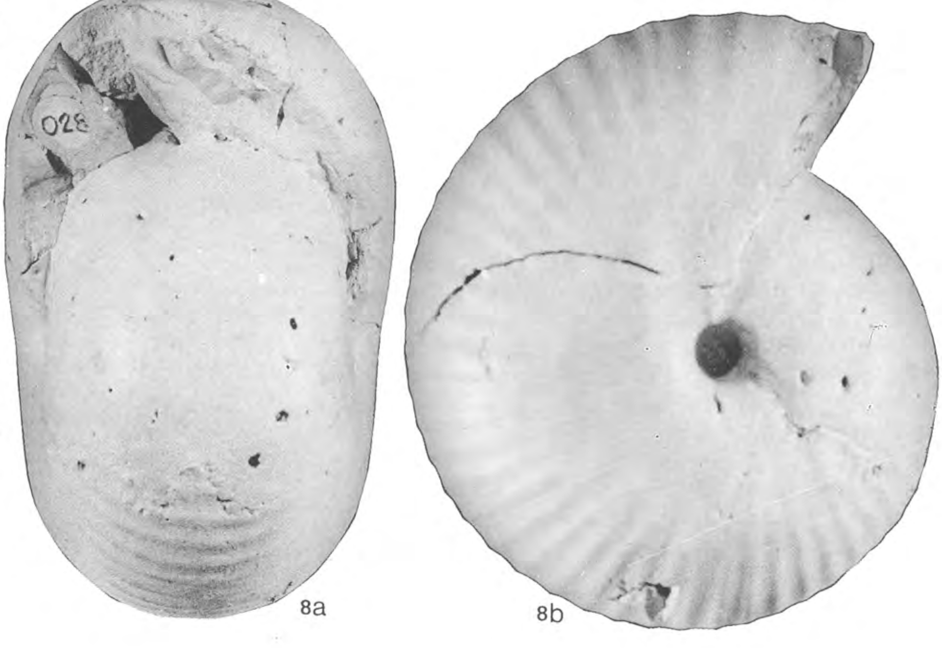
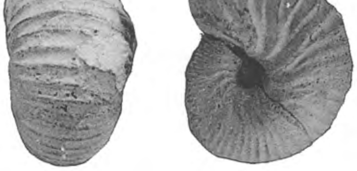


8a 8b


9a 9b


10a 10b


11

(FCENBA 7395: ALLOTYPE, TUB 671207/1 [2 specimens], MLP 12650-53, 12655, 12657, 12658, 12664-66, 23481), and 7 subadults and adults [m] (GAUG 496/448: LECTOTYPE, MLP 12767, 12769-73).

Biometry (Tab. 1-3) - All measurements at $D<18$mm come from the standard sample; mean values for $D<4$mm may be somewhat biased due to small sample size.

Description - Macroconch: The protoconch is smooth fusiform, transversely elongated to the direction of coiling, 0.55mm in width and 0.34mm in diameter. The siphuncle, central throughout the first whorl, migrates to the ventral region at the beginning of the second one. Through the two first whorls ($0.80<D<4$mm) the shell is smooth, globose and very evolute with a subcircular whorl section and a wide umbilicus with a very low slope. At 3-4mm in diameter stout, blunt, fairly prorsiradiate primary ribs appear from the inner third of the flank and cross the broadly curved venter radially. On the third whorl ($4<D<8$mm) the conch is much more compressed ($W/D=0.55$) and involute ($U/D=0.17$), the whorl section high with flanks converging to the narrow rounded venter. Umbilical slope is subvertical with a broadly rounded shoulder. Relative whorl height remains almost constant throughout development (H_1/D: 0.46->0.52). On the fourth whorl ($8<D<18$mm) the shell becomes more inflated ($W/D=0.58$), depressed and involute ($U/D=0.14$); the section becomes subcircular with broadly rounded venter and convex flanks which pass over a rounded shoulder to an almost vertical slope. Costulation reaches the highest density ($P=7$-13, $V=32$-50) at about 16-20mm in diameter. Fine primaries, originating at the umbilical wall, are bent backward and project onto the inner-middle third of the flank where they bifurcate, and, with 1-2 intercalatories, cross the venter more or less radially. Ventral ribs are never interrupted nor fade, and in the most compressed specimens describe a low adapical arch (Fig. 6.1b). In the fifth whorl ($18<D<40$mm) the shell remains globose and becomes increasingly involute and depressed. Whorl section at this size is subrectangular to rounded with flat to fairly convex flanks and the venter is broadly rounded. From $D>18$-20mm the costulation becomes gradually coarser and lower in ventral density (V = 25-35 at $D=40$mm).

The adult body chamber begins at $D=50$-60mm in almost all specimens, being 0.70-0.75 whorls long. The whorl section is subrectangular, wider than high (W/H_1= 1.05-1.53), with subparallel flanks which converge on the rounded, almost flat venter. Relative umbilical width varies from 0.03 to 0.12, umbilical slope is almost vertical and shoulder rounded. From $D=40$-50mm the body chamber is perumbilically smooth, and the costulation remains confined to the ventral region with 20-30 stout ventral ribs along the last half of the whorl. Aperture is simple with a lateral, shallow constriction which never reaches the venter.

Microconch: The phragmacone is identical to that of the macroconch up to the beginning of the fifth whorl, about 18-20mm in diameter, where the adult body chamber begins. Distinctive morphology is only developed on the adult body chamber, which is about 0.75-0.80 whorls long and egressive (U/D= 0.14-0.20). The whorl section is rounded to subrectangular ($W/H_1=1.09$-1.64), with a broad rounded to flat venter, fairly convex flanks, and a rounded umbilical shoulder which tends to disappear in the most evolute and large individuals. The fine and dense costulation at the beginning of the body chamber, becomes very much coarser on the last half of the whorl. 7-13 primaries, originate rectiradiately at the umbilical shoulder rise on the inner half of the flank where they bifurcate. The secondaries and some intercalatories ($V=13$-30) project and cross the venter subradially.

Remarks - The macroconch of *Eurycephalites rotundus* (TORNQUIST) may be distinguished from that of *Eurycephalites gottschei* (TORNQUIST) from $D=10$-15mm by the more compressed whorl section with smooth flanks; the microconchs by the bigger final adult size and coarser ribbing on the body chamber of that of *E. gottschei*. *Stehnocephalites gerthi* (SPATH) [M] differs from the macroconch of *E. gottschei* from $D=15$-25mm in diameter by the wider umbilicus and more depressed, stout whorl section. *Lilloettia steinmanni* (SPATH) [M] may be distinguished onwards from its inner whorls too, by its more closed umbilicus and the more compressed whorl section with flanks converging into a narrow and somewhat acute venter.

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REFERENCES

ALBERCH P., GOULD S.J., OSTER G.F. & WAKE D. 1979 - Size and shape in ontogeny and phylogeny. *Paleobiology* 5, (3): 296-317.

BURCKHARDT C. 1903 - Beitrage zur Kenntis der Jura- und Kreideformation der Cordillere. *Palaeontographica,* Abt. A, 50: 1-144.

CALLOMON J.H. 1981 - Dimorphism in Ammonoids. *In* M.R. HOUSE & J. R. SENIOR (eds.), *The Ammonoidea.* Systematic Association Special Volume 18: 257-273, Academic Press, London.

CALLOMON J.H., DIETL G. & NIEDERHÖFER H.-J. 1992 - On the true stratigraphic position of *Macrocephalites macrocephalus* (SCHLOTHEIM, 1813) and the nomenclature of the standard Middle Jurassic "Macrocephalus Zone". *Stuttgarter Beiträge zur Naturkunde,* B185, 65 p.

DOMMERGUES J.-L. 1986 - Translation des trajectories ontogénétiques et résultats hétérochroniques; un modèle. *Comptes Rendus de l'Académie des Sciences de Paris,* 302, II, 19: 1211-1213.

DOMMERGUES J.-L. 1987 - L'evolution chez les Ammonitina du Lias Moyen (Carixien, Domérien Basal) en Europe. *Documents du Laboratoire de Géologie de. Lyon,* 98, 297 p.

DOMMERGUES J.-L., DAVID B. & MARCHAND D. 1986 - Les relations ontogenèse-phylogenèse: applications paléontologiques. *Geobios,* 19, (3): 335-356.

DOMMERGUES J.-L. & MEISTER C. 1986 - Trajectoires ontogénétiques et hétérochronies complexes chez les ammonites (Harpoceratinae) du Jurassique inférieur (Domérien). *Geobios,* Mem. Sp. 12: 207-219.

GUEX J. 1970 - Sur le sexe des ammonites. *Bulletin des Laboratoires de Géologie, Minéralogie, Géophysique et du Musée géologique de l'Université de Lausanne,* 178, 6 p.

GUEX J. 1981 - Quelques cas de dimorphisme chez les ammonoides du Lias Inferieur. *Bulletin des Laboratoires de Géologie, Minéralogie, Géophysique et du Musée géologique de l'Université de Lausanne,* 258: 239-248.

GOULD S.J. 1977 - *Ontogeny and phylogeny.* Harvard University Press edit., Cambridge (Mass.), 501 p.

HALD A. 1952 - *Statistical theory with engineering applications.* John Wiley & Sons Inc., 783 p.

LANDMAN N.H., DOMMERGUES J.-L. & MARCHAND D. 1991 - The complex nature of progenetic species - Examples from Mesozoic ammonites. *Lethaia,* 24, (4): 409-421.

MC NAMARA K.J. 1981 - Paedomorphosis in Middle Cambrian xystridurinae trilobites from northern Australia. *Alcheringia,* 5: 209-224.

MC NAMARA K.J. 1986 - A guide to the nomenclature of heterochrony. *Journal of Paleontology,* 60, (1): 4-13.

MC NAMARA K.J. 1993 - Inside evolution: 1992 Presidential Adress. *Journal of the Royal Society of Western Australia,* 76: 3-12.

PARENT H. & ARGÜELLO F.A. (In preparation): Upper Bathonian and Lower Callovian ammonites from Chacay Melehué (Cephalopoda, Middle Jurassic, Argentina).

RAFF R.A. & KAUFMAN 1991 - *Embryos, Genes and Evolution.* MacMillan Publisher Company edit., 395 p.

REYMENT R.A. & SANDBERG P. 1963 - Biometric study of *Barremites subdifficilis* (KARAKASCH). *Palaeontology,* 6(4): 727-730.

RICCARDI A.C. & WESTERMANN G.E.G. 1991 - Middle Jurassic Ammonoid fauna and Biochronology of the Argentine-Chilean Andes. Part III: Bajocian-Callovian Eurycephalitinae, Stephanocerataceae. *Palaeontographica,* Abt. A 216, (1-3), 110 p.

RICCARDI A.C., WESTERMANN G.E.G. & ELMI S. 1988 - The Bathonian-Callovian ammonite Zones of the Argentine-Chilean Andes. *2nd International of Symposium on Jurassic Stratigraphy*: 347-358.

RICCARDI A.C., WESTERMANN G.E.G. & ELMI S. 1989 - The Middle Jurassic Bathonian-Callovian Ammonite Zones of the Argentine-Chilean Andes. *Geobios,* 22, (5): 553-597.

SNEDECOR G.W. & COCHRAN W.G. 1967 - *Statistical Methods.* 6th edition, Ames. Iowa State University Press, 593 p.

SPATH L.F. 1927-1933 - Revision of the Jurassic cephalopod fauna of Kachh (Cutch). *Palaeontographica Indica,* (N.S. 9) 2: 1-945.

THIERRY J. 1976 - Dimorphisme et polymorphisme chez *Pachyceras* BAYLE (Ammonitina, Stephanocerataceae) du Callovien supérieur (Jurassique moyen). *Haliotis,* 6: 185-218.

THIERRY J. 1978 - Le genre *Macrocephalites* au Callovien Inferieur (Ammonites, Jurassique Moyen). *Mémoires Géologiques Université de Dijon,* 4, 491 p.

TORNQUIST A. 1898 - Der Dogger am Espinazito Pass. *Palaeontological Abhadlungen,* N.F. 3, (2): 3, (135)-69, (210).

WELLS M.J. & WELLS J. 1977 - Cephalopoda: Octopoda. *In* GIESE A.C. & PEARSE J.S. (eds), *Reproduction of marine invertebrates*, 6: 291-336.

WESTERMANN G.E.G. & RICCARDI A.C. 1979 - Middle Jurassic ammonoid fauna and biochronology of the Argentine-Chilean Andes, II. Bajocian Stephanocerataceae. *Palaeontographica,* Abt. A 164: 85-188.

WRAY G.A. & RAFF R.A. 1990 - Pattern and process heterochronies in the early development of sea urchins. *Developmental Biology,* 1: 245-251.

H. PARENT
Instituto de Fisiografía y Geología
Universidad Nacional de Rosario
Pellegrini 250
2000 Rosario, Argentina