N. Jb. Geol. Paläont. Abh. 301/1 (2021), 85–107
Stuttgart, July 2021

Article

The evolution and variation of the Jurassic ammonoid *Stehnocephalites gerthi* (Spath)

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With 14 figures

Abstract: A new bed-by-bed collection of samples of *Stehnocephalites gerthi* (Spath) throughout its stratigraphic range has been studied in order to characterize the variation and phyletic evolution of this Jurassic ammonoid. The study was conducted adopting a partition of the morphologic variation within a species as transients for the phyletic changes in the lineage, and as morphs for the individual variation within the transients. The results of the study show that the phyletic evolution of the species can be described as three transients, which include wide variations in adult size, shell shape and ornamentation. This variation could be studied in detail from the transient III. The variation is very wide and can be described by means of four morphs. These morphs are interpreted as the result of the operation of different developmental heterochronic processes over different sets of charaters in different individuals. It is possible that the conspicuous morphology and ornamentation of the transient II, which correlates with lithogical changes, have originated in environmental changes.

Key words: Eurycephalitinae, Upper Bathonian, evolutionary lineage, ontogeny, intraspecific variation, transients, morphs, developmental heterochronies, Neuquén Basin, Argentina.

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1. Introduction

The rich ammonite fauna of the Upper Bathonian shales of the Los Molles Formation at Chacay Melehué, Argentina in the Neuquén Basin (Fig. 1; see Westermann 1992) is characterized by the occurrence of species of the Eurycephalitinae (Riccardi et al. 1989; Riccardi & Westermann 1991; Parent 1998; Parent et al. 2020). The genus *Stehnocephalites* Riccardi, Westermann & Elmi, 1989, stands out among other representatives of this subfamily due to its abundance. These ammonoids belong to a relatively short-lived lineage, which has been recorded mainly in the Upper Bathonian deposits through the western Neuquén Basin (Fig. 1B). Formerly, this genus seemed to be confined to the depocentre of Chacay Melehué, but it has been much more widely recorded in recent years, from the area of Chacay Melehué towards the northern San Juan Province.

The genus *Stehnocephalites* as well as its type species *Stehnocephalites gerthi* (Spath, 1928) have been described in detail in several papers (Stehn 1923; Riccardi et al. 1989; Riccardi & Westermann 1991; Parent 1998). These are sphaeroconic to subsphaeroconic ammonites when adults, with more or less strong primary ribs, the secondaries and intercalatories crossing the wide venter with even spacing. Two species have been included: *S. gerthi* (Gerthi Subzone, Steinmanni Zone) and *Stehnocephalites crassicostatus* Riccardi & Westermann, 1991 (lower Gottschei Zone). This latter is poorly known; only its holotype was collected in situ; specimens described in Parent (1998) are here reconsidered (discussion below) as merely morphotypes of *S. gerthi*.

S. gerthi was eudemic (sensu Callomon 1985) in the central Neuquén Basin, the breeding area where the phyletic lineage evolved (Riccardi & Westermann 1991; Parent 1998). *S. gerthi* has appeared as

DOI: 10.1127/njgpa/2021/1001
www.schweizerbart.de
0077-7749/2021/1001 $ 5.75

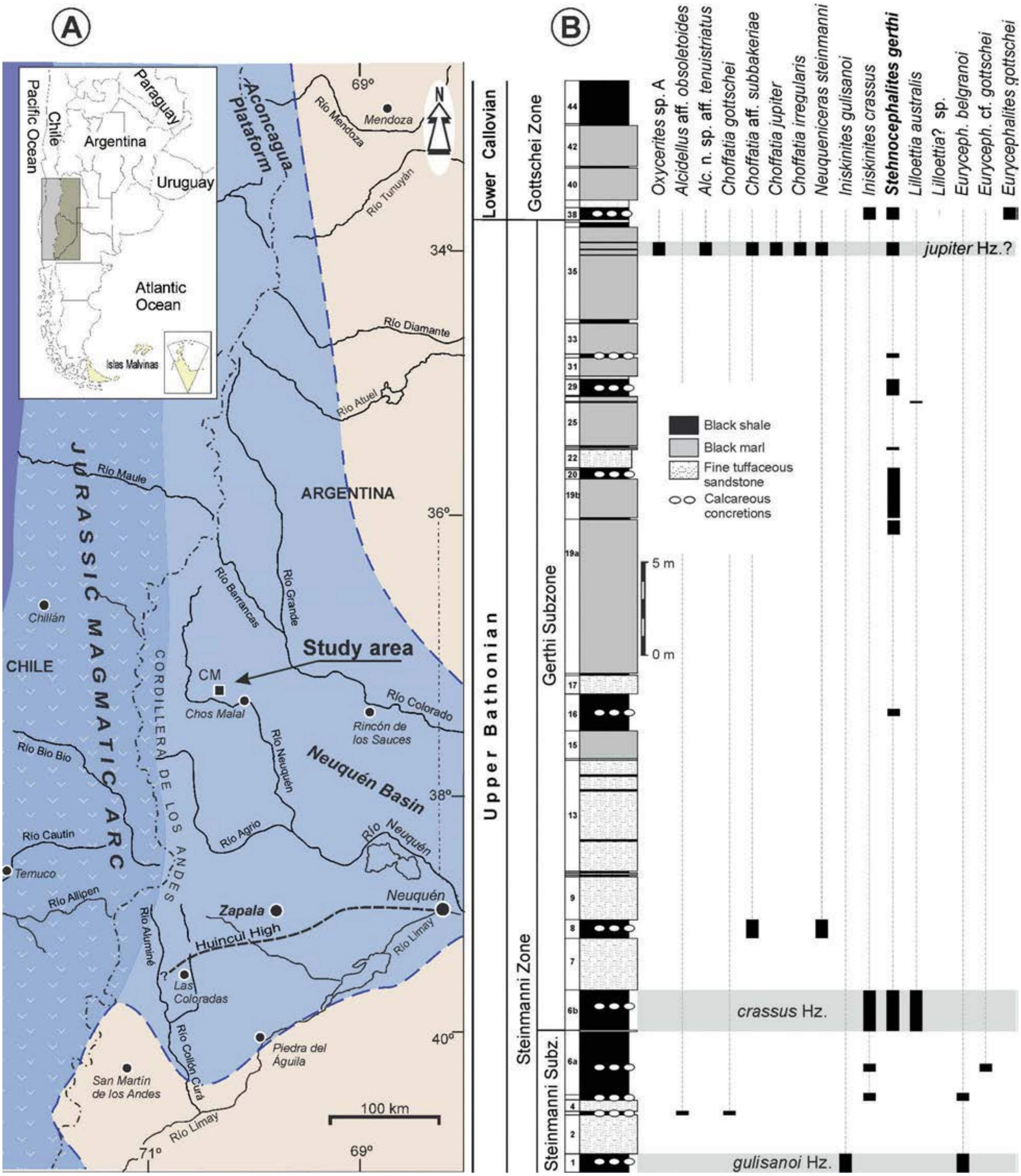

Fig. 1. **A** – The study area in the Neuquén Basin. **B** – Log of the studied section in Chacay Melehué, the ammonite succession, and the chronostratigraphic classification; all simplified from Parent et al. (2020). Locality: Chacay Melehué (CM).

a highly variable species since the description of the collection of Keidel (1910), including the type specimens, by Stehn (1923) as *Macrocephalites diadematus* Waagen, 1875. The remarkably high variability was confirmed by modern collecting, in such a way that the mode of variation was described as a mosaic of morphotypes (Parent 1998) from widely variable adult size, shell-shape and ornamentation combining in different ways (Riccardi & Westermann 1991). However, the variation of the species according to the stratigraphic position of successive samples, showing its phyletic evolution, could not be considered in those papers.

With the objective of studying the patterns of variation and evolution of *S. gerthi* at the finest level of stratigraphic resolution possible, a new collection of the Upper Bathonian (Gerthi Subzone, Steinmanni Zone) ammonite fauna was gathered from a new section (Fig. 1B). This section, the ammonite fauna and the chronostratigraphic classification have been described in a previous paper (Parent et al. 2020). It consists of a succession of black shales and marls with abundant calcareous concretions belonging to the Los Molles Formation (Fig. 1B). Many discontinuity surfaces occur throughout, indicating non-sequences. These erosive discontinuities produce inconspicuous discordances indicating gaps in the record, generated by episodes of very low depositional-rate, probably without any deposition.

From this collection, it was found that the stratigraphic range of *S. gerthi* is longer than previously assumed, ranging downwards at least up to the *crassus* Hz., the base of the Gerthi standard Subzone (Fig. 1B). The material studied by Riccardi & Westermann (1991) and Parent (1998), mostly from the *jupiter* Hz., corresponds to a late segment of the lineage. The specimens collected below the *jupiter* Hz. (part of the new material) show significant differences.

In the present paper, we present the results of the study of the patterns of variation and phyletic evolution of *S. gerthi* based on material collected bed-by-bed from the Upper Bathonian Gerthi Subzone of Chacay Melehué.

After explanation of the concepts of species, variation, and nomenclature adopted here, the ontogeny of the species is described in detail, then the individual and evolutionary variation is discussed. The studied material allows the distinction of segments of the lineage as three transients by means of the shiftings in the range of variation. The latest of these transients shows wide morpho-sculptural variation which is classified as four morphs. These morphs may appear as entangled in a mosaic with complex patterns of variation which are analized here.

2. Species, variation and nomenclature

The wide variability of most ammonoid species (see De Baets et al. 2015 for a review) makes useful and replicable descriptions and characterizations a rather delicate task. Currently there is poor consensus among the authors about interpretation and nomenclature of the observed variability. According to this, I will explain the concepts and nomenclature adopted here for the description of *S. gerthi*, and the interpretation of its variations. The concepts and nomenclature are represented in Fig. 2, showing a theoretical phyletic lineage (Fig. 2A) and its hypothetical fossil record which would be available for sampling (Fig. 2B).

Species as evolving lineages – transients and variants. Here, we consider species as “groups of individuals with comparable ontogeny ranging through a continuous spectrum of variation, often wide and sexually dimorphic, through a more or less long stratigraphic range”. This formulation emphasizes the importance of the ontogeny and sexual dimorphism in ammonite taxonomy and systematics, as well as allowing to consider the species as an evolving lineage. The evolutionary steps of a lineage, the transients, could be considered the closest to the biological species concept (Mayr 2004) as pointed out by Dietze et al. (2005). However, many generations of interbreeding individuals are expected to be preserved mixed in any bed of rock.

The variation, which show the individuals attributed to a single species, may be considered as having two components: (1) the variation observed among the (coeval) individuals (within transients; examples with ammonites of the same size and developmental stage in Sturani 1971, Howarth 1973, Callomon 1985, Weitschat 2008), and (2) that observed through the phyletic evolution of the species (between transients). The two components can be distinguished only from collections of many specimens sampled bed-by-bed through some stratigraphic range. The distinction between these two components may be only operational at some point, for the evolutionary change begins as intraspecific variation (Arthur 2002).

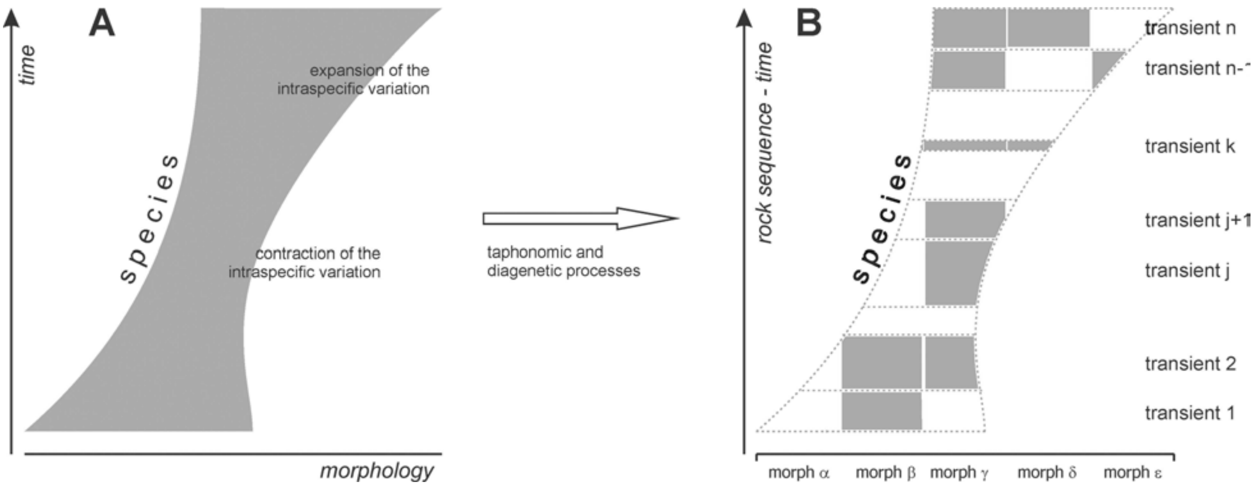

Fig. 2. Segment of phyletic lineage of a theoretical evolving species (**A**) which, after a given taphonomic-diagenetic history, is only patchy preserved (gray trapezoids) in the fossil record by part of its intraspecific variation (morphs) of some steps (transients) of its evolution (**B**). The shape of the representation of the lineage is configured by shifts in the morphologic range of variation through time. In practice, the configuration of the lineage (A) must be inferred from the interpretation of its fossil record (B) according to morphology and stratigraphic succession. The morphologic range appears as discretely composed by different morphotypes of each transient, so that some morphs that persist in the lineage may be wrongly interpreted as different parallel species. The transients are gradually identified according to the advance of knowledge from collections under fine stratigraphic control, and each of them will represent different (typically short) time intervals. The nomenclature of morphs and transients is discussed in the text.

It is widely accepted that through phyletic evolution species shift their ranges of variation through time (Fig. 2A). This is usually recorded in fossil sequences by shiftings in the frequency distribution of intergrading morphotypes (Fig. 2B). However, as the fossil record is essentially incomplete due to taphonomic and diagenetic processes, just patchy portions of the lineages are recorded. This record is in the form of groups of specimens showing different ranges of morphological variation through successive stratigraphic levels (gray trapezoids in Fig. 2B). According to the accumulation of material after more collection, these groups may be gradually conneced by intermediate forms. Some examples in ammonites are shown in Kennedy & Cobban (1976), Callomon (1985), Parent (2001), Parent & Garrido (2020), Scherzinger et al. (2015, 2018), Wierzbowski et al. (2018), and Dietze et al. (2021), among others.

Interfecundity, the key of the biological definition of species (Mayr 2004), is commonly assumed by morphologic resemblance between individuals, even in Zoology – extant and extinct molluscan species are based on morphology, mainly of the shell. Tintant (1952) rightly pointed out that in Palaeozoology the criterium of interfecundity can be assumed from its main consequence: continuous morphologic variation (typically with gaussian or at least bell-shaped distribution). In this sense, it is interesting to note that interfecundity can be tested in living animals for only a limited number of generations, but can not be known if long distant generations are reproductively isolated from older ones at some point of their phyletic evolution. Of course, this uncertainty cannot be solved from the fossil record either. Thus, the problem in Palaeontology is the same that in Biology: the partition of a phyletic lineage as different species is purely contingent and arbitrary – although still useful.

Nomenclature of the intraspecific variants. The nomenclature for the classification of the vertical (stratigraphic) and horizontal (individual) variants (gray trapezoids in Fig. 2B) within a species must allow to denote these variations under Linnean nomenclature and according to the ICZN. Dietze et al. (2005) have pointed out that Waagen (1869) proposed a nomenclatural way to describe the evolutionary steps of a lineage ("Mutation") and the morphological character of an individual or variant ("Varietät"). Choffat (1893: 61–62) discussed the meaning and nomenclature of morphological and temporal variants in ammonites based on the resolutions for zoological nomenclature from the Second International Geological Congress (Bologne, 1881; see Anonymous 1882). These recommendations differ nomenclaturally in some point from the system of Waagen (1869), since the term "mutation" was similarly recommended for the chronological succession of variants, and "varieté" for the geographic variants. This latter is similar but not equivalent to the "varietat" in which the geographic factor is not forced. Choffat (1893) applied the system of "mutation" and "varieté"; a clear example is his description of *Perisphinctes* [*Mirosphinctes*] *bukowskii* Choffat, 1893 from different localities and stratigraphic positions. In this sense, Dietze et al. (2005) discussed and updated the terminology, adopting the use of the terms "transient" (Bather 1927; Callomon 1985) for the former "Mutation", and "variant" ("Varietät" or "varieté"). The category subspecies, which many authors use for the geographic and/or temporal variants supposed in phyletic connection, is here rejected for palaeontological descriptions for the inconsistency of its definition.

The nomenclatural system adopted here follows essentially that of Waagen (1969) and Choffat (1893) in the form discussed in Parent (1998; cf. Dietze et al. 2005) and represented in Fig. 2B: (1) the intraspecific morphologic variants or morphotypes, resulting from the partition of the range of variation, are denoted as "morphs" (this latter must not be in italics), and (2) the intraspecific temporal variants, resulting from the segmentation of a lineage, are denoted as "transients" (steps of the lineage). The fossil record of a lineage composed by successive transients and morphs is represented in Fig. 2B – note that only some morphs of some transients are preserved. This representation shows some persistent morphotypes through time, which under a morphotypic vertical classification would be considered as different species by some. It is clear that these transients will typically include several successive generations mixed. In the ideal situation, the range of variation in each transient should be described, but this requieres large numbers of specimens, mostly well preserved adults, from several stratigraphical levels.

3. Systematic palaeontology

Conventions and remarks: The new material described is housed at the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala (MOZ-PI). Body chamber is abbreviated with Bc and phragmocone with Ph; macroconch (female shell): [M], microconch (male shell): [m]. Measurements: diameter (D), diameter at the last adult septum (D_{ls}) and diameter at adult peristome (D_p), umbilical width (U), whorl width (W), whorl height (H_1), and whorl ventral (or apertural) height (H_2); all given in millimeters [mm]; length of body chamber (L_{BC}) in degrees [°]. Number of primary (P) and ventral (V) ribs per half whorl. These per-half-whorl measurements are more sensitive to the ontogenetic changes than per-whorl, and are less exigent with quality of material. The biometric features of shell-shape are given in the form of dimensionless numbers or "indexes", mainly relative to the corresponding value of D, allowing plain comparisons in a range of size.

The maturity of the specimens is assessed by uncoiling of the body chamber, no matter if septal suture lines are visible and/or preserved or not. Uncoiling refers to a more or less abrupt change in the curvature ratio of the umbilical seam; an irreversible process which if produced in any pre-adult stage would make an anormally coiled ammonite, and is not known in Jurassic planispirally coiled ammonites.

Levels of occurrence of the specimens denoted by the level number in Fig. 1B and the prefix CM (Chacay Melehué).

Order Ammonitida Fischer, 1882
Suborder Ammonitina Fischer, 1882
Superfamily Stephanoceratoidea Neumayr, 1875
Family Sphaeroceratidae Buckman, 1920
Subfamily Eurycephalitinae Thierry, 1978

Genus *Stehnocephalites*
Riccardi, Westermann & Elmi, 1990

Type species: *Indocephalites gerthi* Spath, 1928; by original designation.

Remarks: Within the genus, two nominal species have been described: *Stehnocephalites gerthi* and *Stehnocephalites crassicostatus* Riccardi & Westermann, 1991. This latter is poorly known and its holotype is here considered as a late morphotype of *S. gerthi*.

The type locality of the type species is Chacay Melehué, Neuquén, Argentina (Spath 1928). The geographic distribution of the genus corresponds to the broad area where *S. gerthi* has been recorded, covering most of the Neuquén Basin, from Lonquimay in the southermost end up to the San Juan Province in the northern end. The localites where the record is better known are in northern Neuquén Province, i.e. Rahuecó, C. Melehué, Vega de la Veranada (see Stehn

1923; Stipanicic 1965; Westermann 1967; Riccardi et al. 1989; Riccardi & Westermann 1991; Parent 1998; Parent et al. 2020). Out of its eudemic centre, around the depocentre of the Neuquén Basin in Chacay Melehué-Rahuecó (Fig. 1B) where the species has its highest abundance and covers its full stratigraphic range, it occurs as isolated records in scattered localities. In the southern Mendoza Province, it occurs in Sierra de Reyes (Riccardi & Westermann 1991; Spalletti et al. 2012). Legarreta et al. (1993) cited the occurrence of *S. gerthi* in the Gottschei Zone of Malargüe (southern Mendoza Province) and Barrancas (northernmost Neuquén Province). Ramos et al. (2010: pl. 1, figs. F, G) have recorded the species in the top of the Nieves Negras Formation at Las Minas, Mendoza Province. This ammonite comes from a level of 6 m of concretional shales/mudstones, including some forms of *Choffatia* figured as "*Choffatia andina*?", *Choffatia jupiter* (Steinmann, 1881), and *Neuqueniceras steinmanni* (Stehn, 1923) which likely belong to the upper part of the Steinmanni Zone (discussion in Parent et al. 2020). Álvarez (1997: pl. 11, fig. f) figured an adult macroconch of *S. gerthi* and cited the occurrence of the species in the Los Patillos Formation at Arroyo Las Garzas, Arroyo de las Vegas, and Paso del Espinacito in the San Juan Province.

Sexual dimorphism has remained elusive or hard to determine. In almost all cephalopods, and so in most ammonoids, the males are progenetic with usual modifications and/or outgrowths at the adult stage (Landman et al. 1991; Parent 1997; Klug et al. 2015). It has usually been assumed that *Stehnocephalites* could have *Xenocephalites*-like microconchs, e.g. the specimens figured by Parent (1998: figs. 23F–H and 32A–D). An indisputable microconch, not assignable to the morphogenus *Xenocephalites* Spath, 1928, is described below.

Stehnocephalites gerthi (Spath, 1928)

Figs. 3–13

1923 *Macrocephalites diadematus* Waagen. – Stehn, p. 80, pl. 2, figs. 1–3, pl. 7, fig. 3, pl. 8, fig. 4 (holotype).
*1928 *Macrocephalites gerthi* nom. nov. (*recte* n. sp.). – Spath, p. 175.
1931 *Macrocephalites diadematus* Waagen. – Windhausen: pl. 27, p. 2 (holotype?).
1967 *Macrocephalites* (*Indocephalites*) *gerthi* Spath. – Westermann, p. 72.
1989 *Stehnocephalites gerthi* n. gen. – Riccardi et al., p. 567, pl. 6, figs. 1, 2.
1991 *Stehnocephalites gerthi* (Spath). – Riccardi & Westermann, p. 83, pls. 20–25.
1991 *Stehnocephalites crassicostatus* n. sp. – Riccardi & Westermann, p. 88, pl. 26, figs. 1, 2.
1991 *Stehnocephalites* sp. A. – Riccardi & Westermann, p. 89, pl. 26, figs. 3–5.
1992 *Stehnocephalites gerthi* (Spath). – Westermann, pl. 60, fig. 5.
1997 *Stehnocephalites gerthi* Riccardi & Westermann. – Álvarez, pl. 11, fig. f.
1998 *Stehnocephalites gerthi* (Spath). – Parent, p. 95, figs. 19–23.
1998 *Stehnocephalites crassicostatus* Riccardi & Westermann. – Parent, p. 108, figs. 25, 26.
2010 *Stehnocephalites gerthi* Riccardi & Westermann. – Ramos et al., pl. 1, figs. F, G.
2012 *Stehnocephalites gerthi* Riccardi & Westermann. – Spalletti et al., p. 473, fig. 6D–E.
2020 *Stehnocephalites gerthi* (Spath). – Parent et al., p. 26, fig. 21.

Material: This study is based on the new material, consisting of 40 adult macroconchs, and one microconch; all from levels CM-6b to CM-35 of the section in Fig. 1B. Of these, only sixteen macroconchs were considered in the biometric analysis as they provide the full set of measurements per-individual. More than 300 additional specimens were observed in the field but not collected. The remaining material considered for comparison is that studied in Parent (1998) which included the material of Riccardi & Westermann (1991), all from Chacay Melehué and almost exclusively from levels equivalent to CM-25 to CM-35 of the present section.

Description: The biometric features of the new material are summarized in Fig. 12; for the remaining material see Parent (1998) and Riccardi & Westermann (1991).

Microconch (Fig. 9D): One small adult specimen (c. D = 23 mm), incipiently uncoiled, is considered male because of the variocostation in the body chamber at small size ($P = 8$, $V = 30$).

Macroconch: The early ontogeny, up to about D = 30–35 mm, remains invariable among the individuals, even from the earliest representatives of the species. The ontogeny can be described as four developmental stages (ED) of morphology and ornamentation (based on Parent 1998):

ED$_1$ (Fig. 11E): innermost whorls ($D < 8$ mm). Globose, widely umbilicated (U/D = 0.23–0.30), whorl section suboval depressed (W/H_1 = 1.20–1.60). Feeble primary ribs appear from $D = 4$ mm; at the end of the stage they are P = 10–12.

ED$_2$ (Figs. 7C and 11D, E): juvenile phragmocone ($8 < D < 20$ mm). Inflate platycone, the whorls become compressed (W/H_1 = 0.80–1.00) with flat flanks; narrowly umbilicated (U/D = 0.10–0.15). The whorl section is subrectangular-suboval by reduction of the relative whorl width whereas the relative whorl height remains unchanged. Ribbing fine and dense; primaries more or less flexuous, bi- or trifurcating from the lower half of the flanks, then crossing the venter evenly spaced and unchanged.

ED$_3$ (see Parent 1998: figs. 16, 17, 19D–E): pre-adult and adult phragmocone ($20 < D < D_{ls}$ = 40–100 mm). Sphaeroconic, the whorls revert to a suboval depressed, wider than high, retaining the relative whorl heigth unchanged. Moderately involute (U/D = 0.13–0.25), but variable; the umbilical wall is steep and high, passing through a rounded shoulder to the inflated flanks then to a wide rounded venter. Primary ribs more or less flexuous, sharp, bi- or more rarely trifurcating around the middle of the flank into indistinct secondaries; intercalatory ribs occur irregularly; ventral ribbing unchanged and evenly spaced. This morpho-ornamental stage ends at about the last septum, at variable diameter because of the wide variation of the adult size in the macroconchs.

The individual morpho-sculptural variation becomes higher from about 30–40 mm in diameter, especially in the last half whorl of the adult phragmocone.

ED$_4$ (Figs. 3, 4, 5B, C, 6–8, 9A–C, 10, 11): adult body chamber. Widely variable in morphology and ornamentation. Adult size D_p = 55–150 mm; moderately involute. Whorl section suboval wider than high to subrectangular (W/H_1 = 1.00–1.80). Primary ribs prosocline, curved forward, strong or fine; secondary ribs finer than primaries crossing the venter evenly spaced. In some specimens the bodychamber is smooth. Peristome plain, in some specimens slightly sigmoidal.

Variation: The new material (Fig. 3–11) shows that under fine stratigraphic control, the wide intraspecific variation of the adult macroconchs of *S. gerthi* (Figs. 12, 13) can be decomposed in two components (Fig. 2): (1) that produced by shiftings in the modal morphology and sculpture through the successive populations, here described as three transients, and (2) the variation among the specimens within each transient, here described for transient III (only) as four morphs.

- transient I (Fig. 3; levels CM-6b-16): the earliest representatives known of the species; large adult size, stout, moderately evolute with strong ribbing, the primaries stronger than secondaries and presence of intercalatories. Mean body chamber length 270°. Four specimens.
- transient II (Figs. 4–6; levels CM-19a-19b): Adult size medium to large; subrectangular in whorl section with flattened venter; strong and sharp, sparse rectiradiate primary ribs. Short body chamber, L_{BC} = 180–200°. Eight specimens.
- transient III (Figs. 7–12; levels CM-20-38): very variable adult size, depressed to compressed, subelliptical to subrectangular whorl section, moderately involute to involute. Body chamber length 210-300°. Twenty eight specimens.

The specimens from level CM-20 although incomplete document the morpho-ornamental transition from transient II to transient III: specimens with strong and sharp primaries with a rounded-subrectangular whorl section (Fig. 7A), and others more densely and finely ribbed with wide depressed suboval whorl section (Fig. 7B).

The new specimens of this transient fit the partition of the variation as four morphs (α, β, γ, and δ, defined formerly in Parent 1998). This classification is obtained by leaving the adult size and involution varying within the morphs, whereas the whorl section, density and strength of primary ribbing are considered for the differentiation (Fig. 14). However, the mosaic structure of the variability blur the boundaries in many cases. As noted above the inner whorls, the juvenile stages of the ontogeny (ED$_1$–ED$_2$), are very constant throughout the species.

- morph α: globose, with depressed, wider than high, subelliptical whorl section. Primary ribs rather fine and dense. The holotype belongs to this morph.
- morph β: globose, with depressed, wider than high, subelliptical whorl section. Primary ribs strong and sharp, rather sparse.
- morph γ: more or less compressed, with subcircular, slightly wider than high, whorl section. Primary ribs strong and sparse.
- morph δ: more or less compressed, with subrectangular to subcircular, slightly wider than high, whorl section. Primary ribs fine and dense.

Distribution and age: The geographic distribution of the species is summarized above. The stratigraphic range of *S. gerthi* was formerly established by Riccardi & Westermann (1991) and recently extended downwards by Parent et al. (2020) from the new material (transients I and II). It ranges from the *crassus* Hz., base of the Gerthi Subzone, upper Steinmanni Zone of the Upper Bathonian up to the lower Gottschei Zone of the Lower Callovian (Fig. 1B).

4. Discussion

Facing the high degree of variation between the transients and among their adult macroconchs (Figs. 12, 13), especially in the transient III (Figs. 13, 14), of what is here considered a single species, one could ask where the limits of phenotypic variation within a single ammonite species must be established – or if we are mixing more than one species, or even genera. However, all the specimens show the age, diagnostic morphology, and ornamentation of the genus *Stehnocephalites*, which allow clear separation from the other co-occurring eurycephalitines. On the other hand, all the specimens show (as far as preserved) identical juvenile morpho-sculptural ontogeny with only minor variations of the relative whorl width. Thus, under the adopted framework of classification we have a single species as subject, whose macroconchs are highly variable in adult size, shell shape and ornamentation, but demonstrate a rather invariant juvenile ontogeny.

The holotype of *S. gerthi* is virtually identical in size, shell-shape and ornamentation to the present specimen in Fig. 11A from level CM-35. This morphotype (morph α) is typical of the transient III, which thus would be the type-transient of the species.

The medium-sized adults of the transient II (Fig. 5B, C) are almost indistinguishable from the holotype of *S. crassicostatus* (see Riccardi & Westermann 1991: pl. 26, fig. 1) collected from the Gottschei Zone (formerly Vergarensis Zone; see Parent 1998 and Garrido & Parent 2013). This matching strongly suggests that *S. crassicostatus* is merely a persistent morphotype in the lineage, thus a junior synonym of *S. gerthi*.

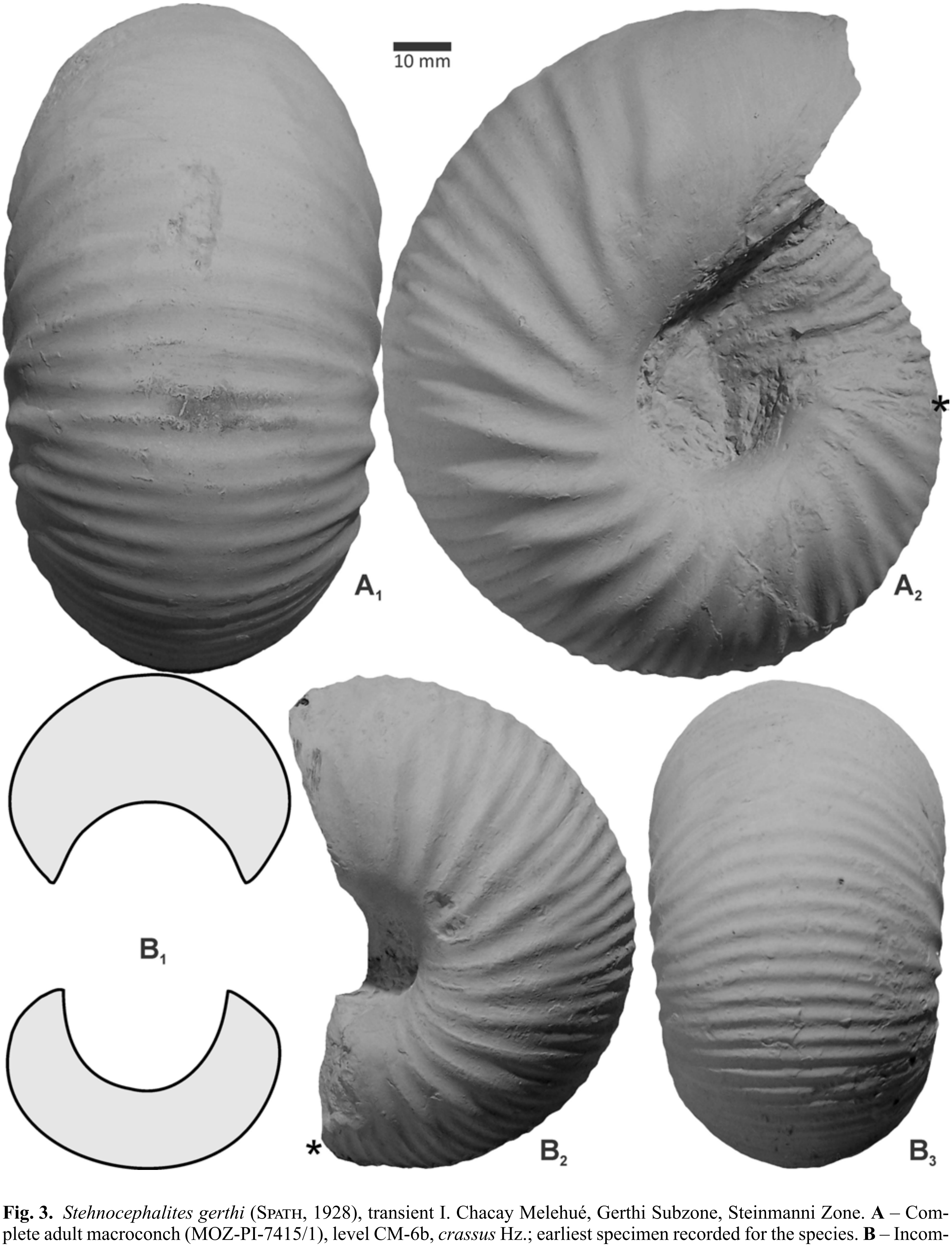

Fig. 3. *Stehnocephalites gerthi* (Spath, 1928), transient I. Chacay Melehué, Gerthi Subzone, Steinmanni Zone. **A** – Complete adult macroconch (MOZ-PI-7415/1), level CM-6b, *crassus* Hz.; earliest specimen recorded for the species. **B** – Incomplete adult macroconch (MOZ-PI-7418), level CM-16; B_1: whorl section, gray shaded body chamber. All natural size (x1). Asterisk at last septum.

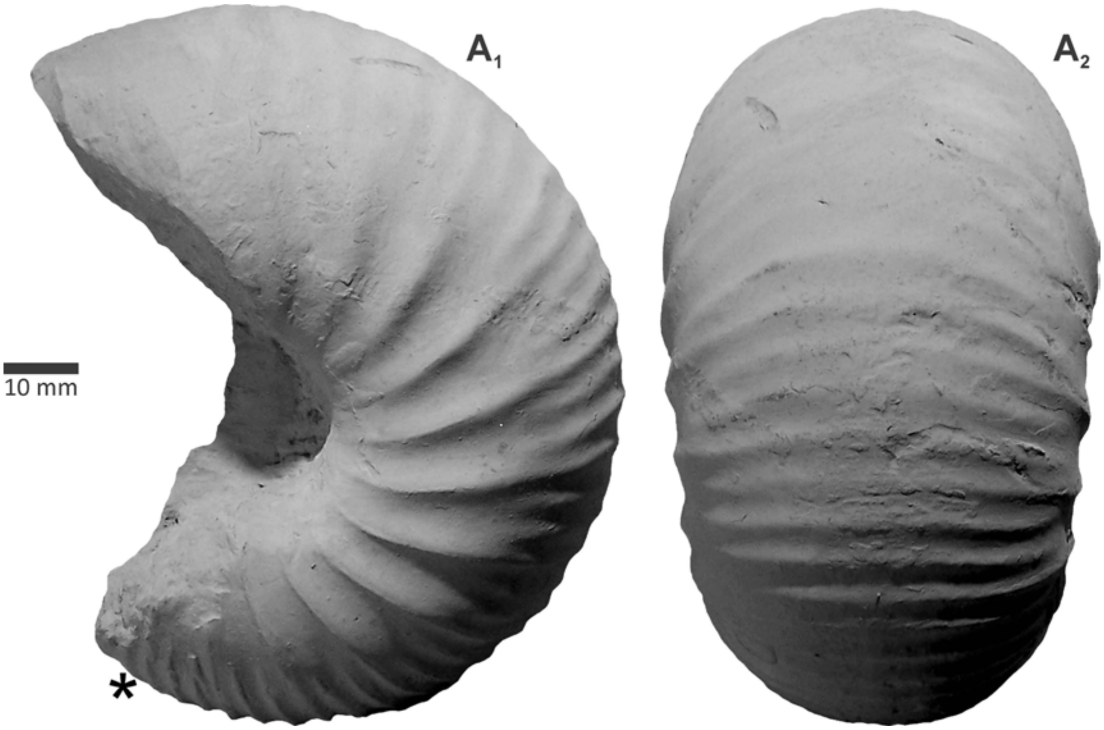

Fig. 4. *Stehnocephalites gerthi* (Spath, 1928), transient II. Chacay Melehué, level CM-19a, Gerthi Subzone, Steinmanni Zone. Adult macroconch with remains of the phragmocone (MOZ-PI-7419/1). – Natural size (x1). Asterisk at last septum.

Fragmentary specimens from level CM-38, where the holotype of *S. crassicostatus* seems to come from, belong to the transient III of *S. gerthi*.

Intraspecific variation: The variation in adult size, shell-shape, body chamber length, and ornamentation of the new material is summarized in Fig. 12, considering the three transients separately; this figure also includes a comparison with the maximum ranges of these characters in the remaining known material (Riccardi & Westermann 1991; Parent 1998) which mostly belongs to the transient III. The Fig. 13 is a summary of the succession of morphotypes of the species, level by level, based on the new material shown in Figs. 3–11. Fig. 14 shows some examples of morphs of the transient III.

Riccardi & Westermann (1991: 83) indicated that they studied limited material consisting of adult macroconch body chambers without phragmocones. This material was mainly collected from a relatively short interval (about 10 m) in the upper part or the Steinmanni Zone at Chacay Melehué, equivalent to the interval of levels CM-25-35 of the present section (Fig. 1B). Thus, their material belongs to the transient III. Indeed, each one of the specimens they figured can be matched with one of those of the transient III described above, or some morphotypes with those in Parent (1998). Riccardi & Westermann (1991) noted that the umbilical diameter, whorl section and ribbing vary in such a way that almost each specimen is unique in some features. However, this complex pattern of variation of the macroconchs can be classified in four morphs as described above.

However, the ontogeny remained undescribed until Parent (1998) studied better preserved and more abundant material from the same stratigraphic interval. From this material, the ontogeny was described for first time, and a detailed statistical description of adult size, shell-shape, sculpture and length of the body chamber of the species was elaborated. This statistical framework, based on the whole material known at that time (including that of Riccardi & Westermann 1991), provides the actual maximum ranges and estimation of the theoretical ranges corresponding to the transient III of the species. Some extreme morphotypes of this transient, extremely inflated or finely ribbed which

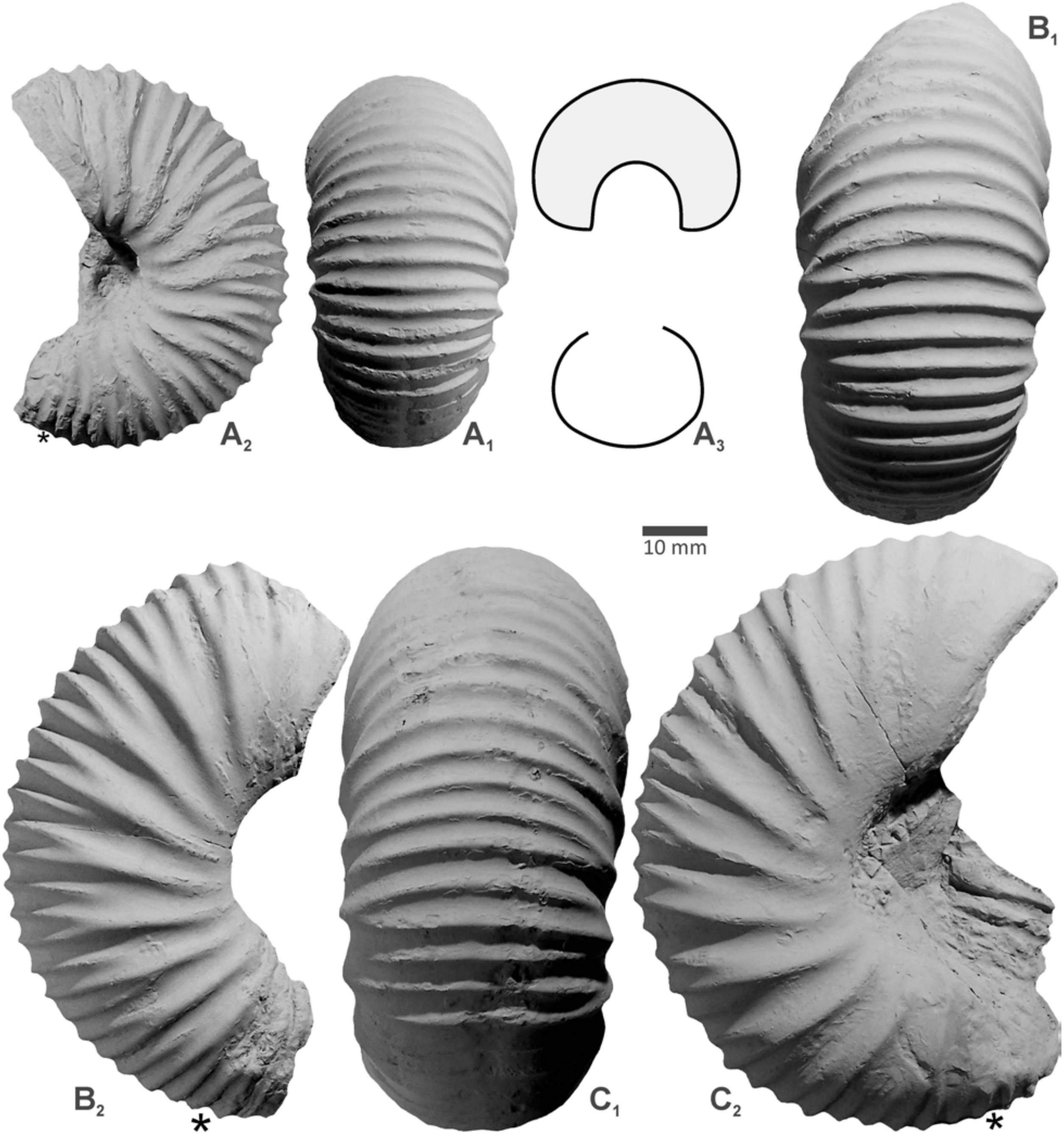

Fig. 5. *Stehnocephalites gerthi* (Spath, 1928), transient II. Chacay Melehué, level CM-19b, Gerthi Subzone, Steinmanni Zone. **A** – Juvenile macroconch with incomplete phragmocone (MOZ-PI-7420/2); A_3: whorl section, body chamber gray shaded. **B** – Adult macroconch body chamber (MOZ-PI-7420/3). **C** – Adult macroconch body chamber with incomplete phragmocone (MOZ-PI-7420/1). – All natural size (x1). Asterisk at the last septum.

are not represented in the new material, were figured in Parent (1998: figs. 20, 21A, B, 23C–E; see also Fig. 14). These extreme morphotypes are very scarce and thus under-represented in the new collection, but the totality of the new specimens of transient III fall well within the ranges of the former study.

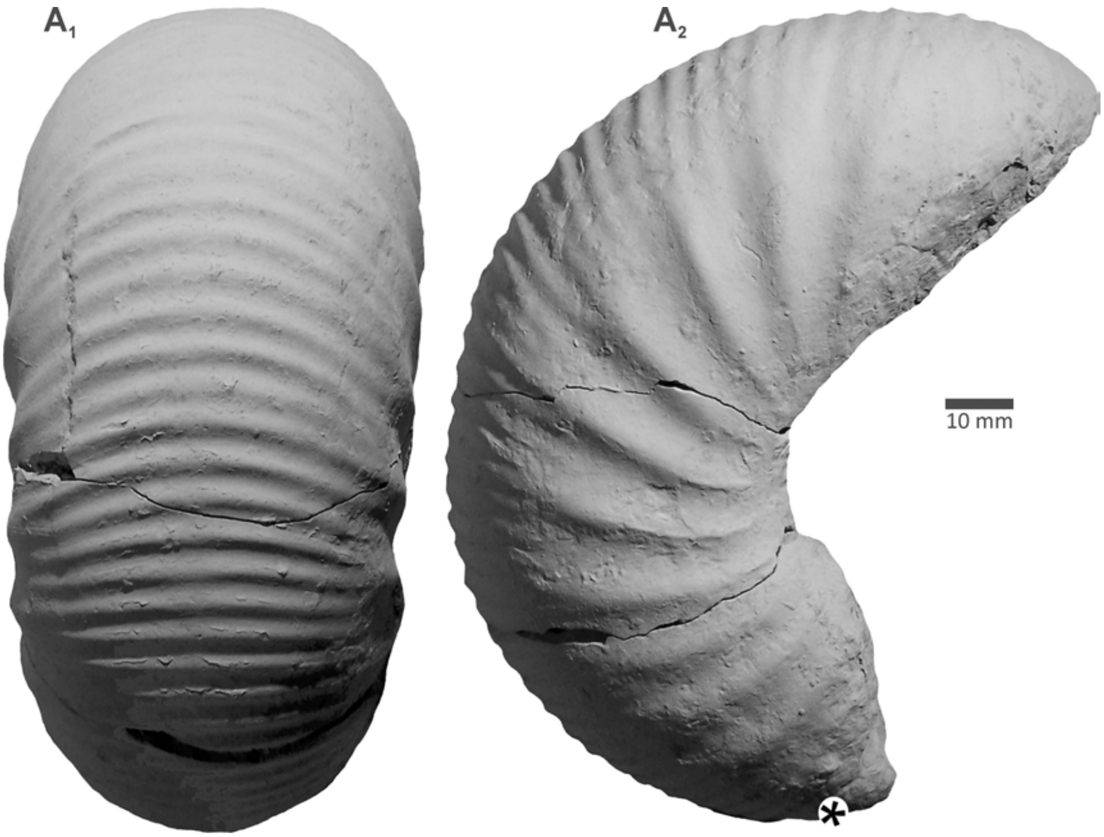

Fig. 6. *Stehnocephalites gerthi* (Spath, 1928), transient II. Chacay Melehué, level CM-19b, Gerthi Subzone, Steinmanni Zone. Adult macroconch body chamber (MOZ-PI-7420/5). – Natural size (x1). Asterisk at the last septum.

The macroconchs of the earliest representatives known of the species, the transient I, are scarce and their total range of variation is poorly understood. The few specimens available do not show substantial levels of variation, which may be a result of low sample size within transient I.

The macroconchs of the conspicuous transient II show a distinct but narrow range of morpho-sculptural and body chamber length variation, although with wide ranges in adult size.

According to the material known of the species, the only transient with enough material available for detailed studying of the intra-transient variation is the transient III.

Developmental processes and the individual variation in the transient III: Concerning the processes that produce the wide intraspecific variation in the transient III, the author had concluded (Parent 1998) that the mosaic of morphotypes is produced by (1) developmental heterochronies operating from the pre-adult stage, and (2) a low degree of covariation among characters from the pre-adult stage (Fig. 12G, H). However, the present study shows that this interpretation should be reformulated, in the sense that the low levels of covariation are a product of the combination of different heterochronic processes operating over different sets of characters.

According to McNamara (1986), the heterochronic processes by which the ontogeny can be modified are six, producing peramorphic (acceleration, hypermorphosis, and pre-displacement) or paedomorphic (neoteny, progenesis, and post-displacement) patterns of variation. The heterochronic changes may affect the whole organism, but more often different organs or growth fields can undergo heterochronies (or remain unaffected) independent of what is going on elsewhere (McKinney & McNamara 1991: 14). This interpretation is herein applied to the ammonite shell, as composed of different morphogenetic or growth fields cor-

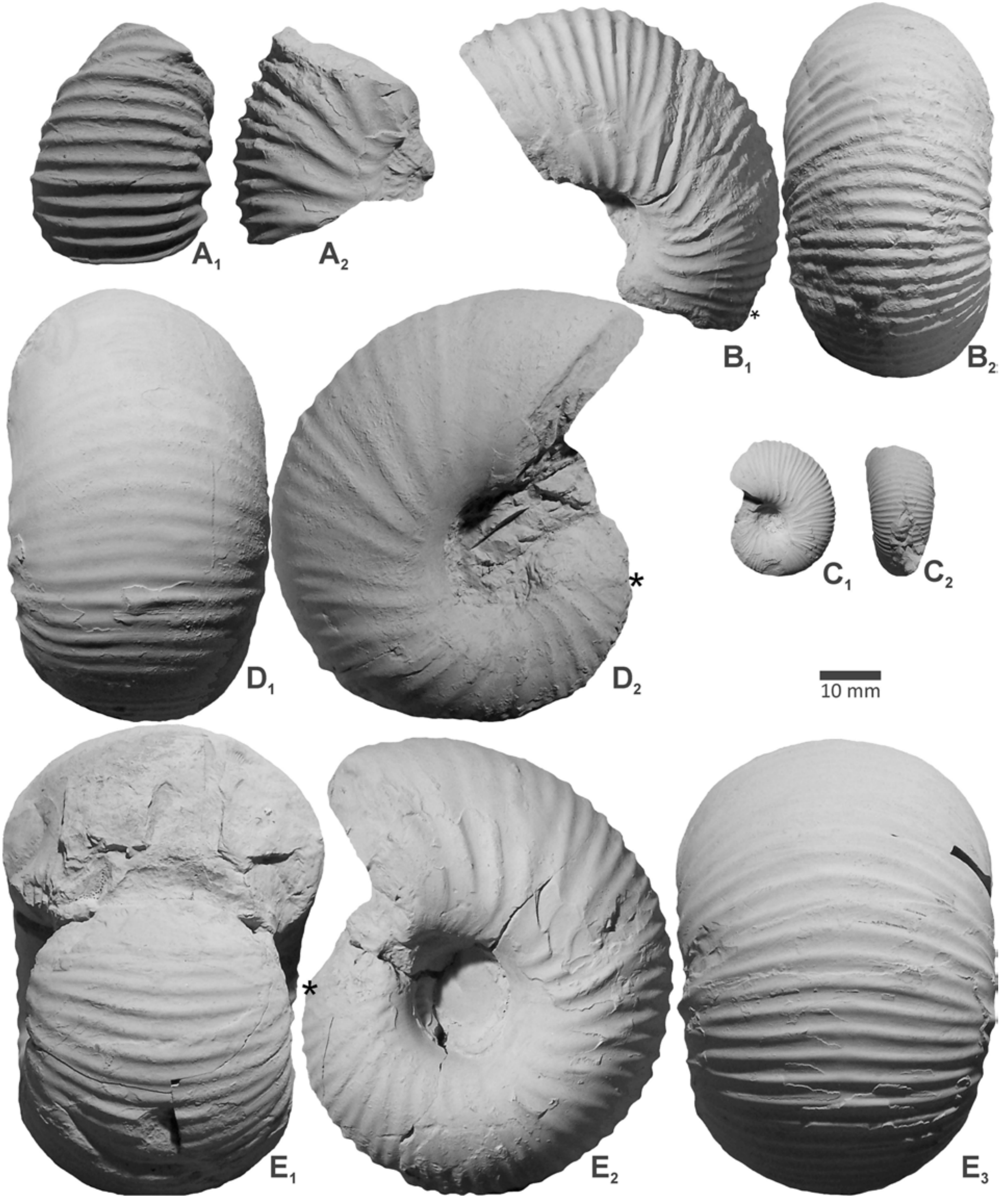

Fig. 7. *Stehnocephalites gerthi* (Spath, 1928) transient III, Chacay Melehué, levels CM-20 and CM-23, Gerthi Subzone, Steinmanni Zone. **A** – Fragmentary macroconch body chamber (MOZ-PI-7421/1), level CM-20; this specimen is an intermediate form between transients II and III. **B** – Incomplete adult? macroconch body chamber (MOZ-PI-7421/2), level CM-20. **C** – Inner whorls of a macroconch (MOZ-PI-7422/1), level CM-23. **D** – Complete adult macroconch (MOZ-PI-7422/2), level CM-23; coarsely ribbed morphotype. **E** – Complete adult macroconch (MOZ-PI-7422/3), level CM-23; inflated and densely ribbed morphotype – All natural size (x1). Asterisk at the last septum.

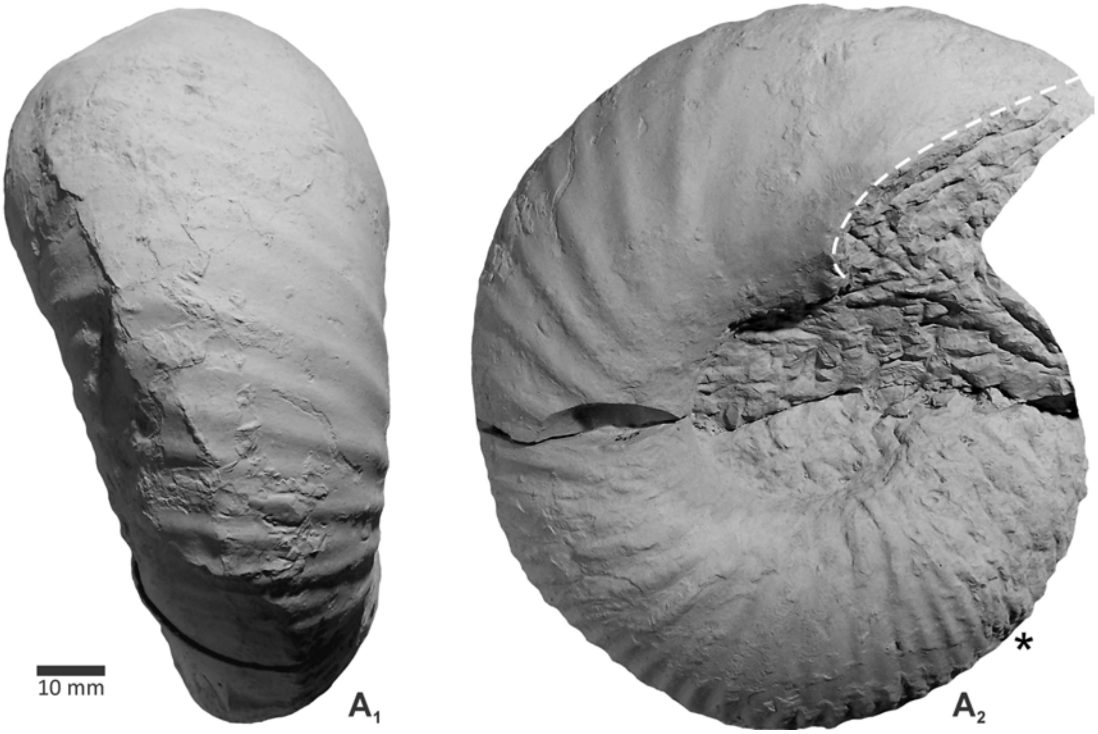

Fig. 8. *Stehnocephalites gerthi* (Spath, 1928), transient III. Chacay Melehué, level CM-30, Gerthi Subzone, Steinmanni Zone. Complete adult macroconch (MOZ-PI-7424/1); large-sized and coarsely ribbed morphotype. – Natural size (x1). Asterisk at the last septum.

responding to ornamental structures and dimensional sets of characters. These, considered in dimensionless mode, are: involution (U/D-H_2/D) and whorl section (W/D-H_1/D); additionally adult size at peristome (D_p), body chamber length (L_{BC}), and number and strength of primary ribbing.

In *S. gerthi* there is a concurrence of paedo- and peramorphic processes producing variants or morphotypes in which different characters or sets of characters are affected. The interpretation of heterochronies consists of comparing a given ontogeny against one taken as standard of reference; here we choose the holotype (Riccardi et al. 1989: pl. 6, figs. 1, 2) represented by the practically identical specimen in Fig. 11A. We present here some examples of heterochronic interpretation of the variations in *S. gerthi*.

The sample of umbilical trajectories of the transient III studied by Parent (1998) can be interpreted as a spectrum of paedo- and peramorphic variants. This is an example of the populational behaviour of a single character, but the individuals undergo other different heterochronies concurrently, producing the variation in mosaic. This mosaic is produced by the combination of different heterochronic processes operating in each individual. The wide intraspecific variation of transient III (Figs. 13, 14) is such that if not for the vast number of specimens known of the species, forming a continuum of morphologic intergradation, and the knowledge of the invariant ontogeny, it would be laudable to suspect the presence of several species.

The levels of covariation between dimensional characters are measured by the correlation between shell dimensions and the diameter D as indicator of size. The correlation coefficient, $r = \mathrm{cov}(x, y)/(\mathrm{SxS}_y)$ (see Cramer 1947: 264–265), is a dimensionless measurement of the covariation between dimensions, thus allowing direct comparison unaffected by size. The early juvenile ontogeny, ED_2 (D = 8–20 mm), shows high covariation between all characters with the size (D), slightly decreasing through ED_3 (D = 20–65 mm), but remaining high. These developmental stages are the juvenile part of the shell which, as described above, is almost invariable in all the well-preserved, known specimens. In the adult stage ED_4 the covariation H_1-D

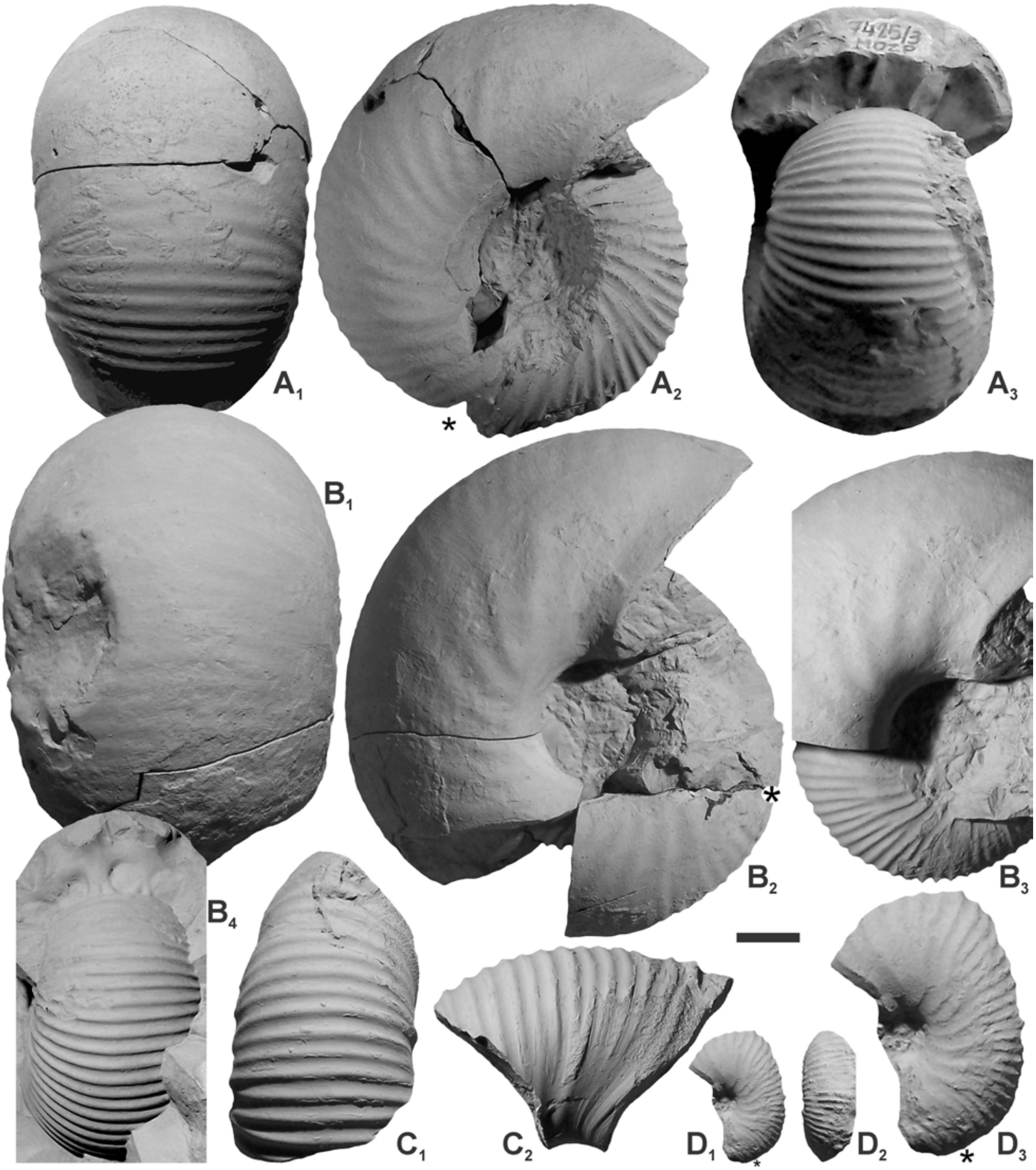

Fig. 9. *Stehnocephalites gerthi* (Spath, 1928), transient III. Chacay Melehué, level CM-32, Gerthi Subzone, Steinmanni Zone. **A** – Complete adult macroconch (MOZ-PI-7425/3). **B** – Complete adult macroconch (MOZ-PI-7425/5). **C** – Fragment of body chamber (MOZ-PI-7425/2); compressed variant with sharp ribbing recalling transient II. **D** – Complete? adult microconch (MOZ-PI-7425/1); D_3: lateral view x2. – All natural size (x1) except D_3 (x2). Asterisk at the last septum.

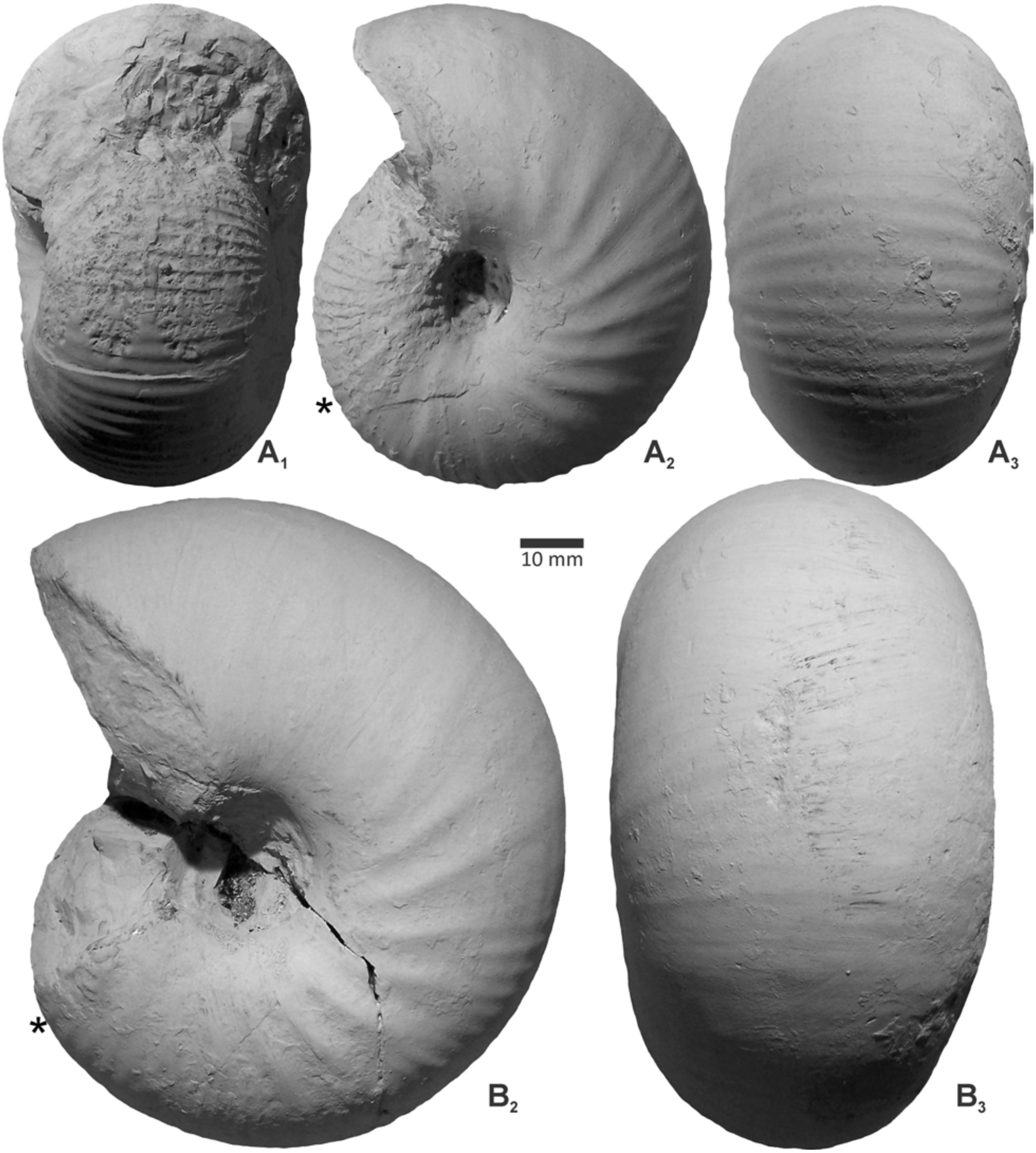

Fig. 10. *Stehnocephalites gerthi* (Spath, 1928), transient III. Chacay Melehué, level CM-32, Gerthi Subzone, Steinmanni Zone. **A** – Complete adult macroconch (MOZ-PI-7425/6). **B** – Complete adult macroconch (MOZ-PI-7425/8). – Natural size (x1). Asterisk at the last septum.

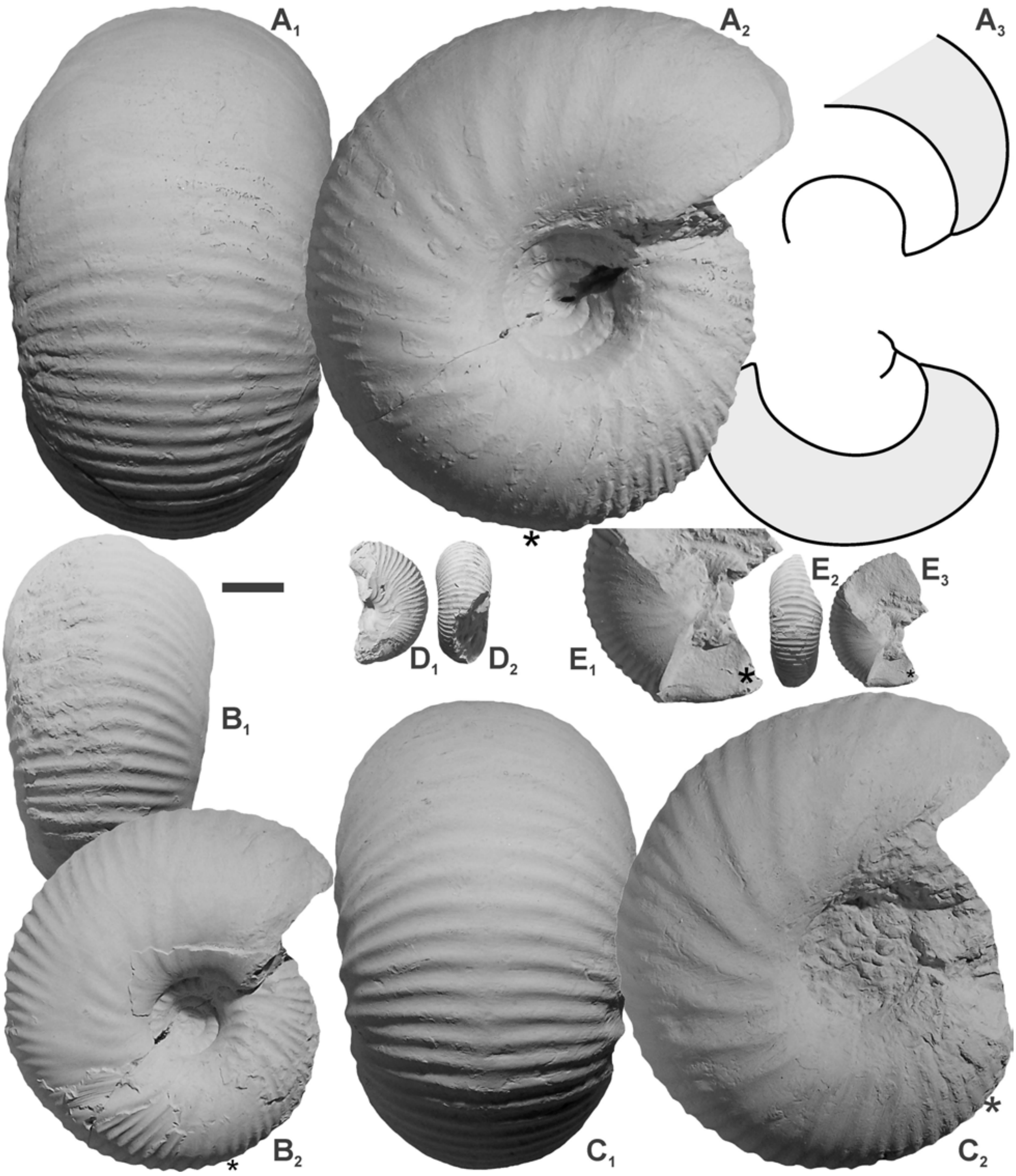

Fig. 11. *Stehnocephalites gerthi* (Spath, 1928), transient III. Chacay Melehué, level CM-35, Gerthi Subzone, Steinmanni Zone. **A** – Complete adult macroconch (MOZ-PI-7430/17), large, stout, and evolute morphotype, almost identical to the holotype; A_3: whorl section through the peristome (body chamber shaded). **B** – Complete adult macroconch (MOZ-PI-7430/18), small, densely ribbed morphotype. **C** – Complete adult macroconch (MOZ-PI-7430/19), medium-sized, coarsely ribbed morphotype. A–C refigured from Parent et al. (2020: fig. 21). **D** – Inner whorls of a large macroconch (MOZ-PI-7430/25), densely ribbed subplatyconic (stage ED_2) at about D = 20 mm. **E** – Juvenile macroconch (MOZ-PI-7430/23) showing the innermost whorls smooth at D = 3.2 mm, densely ribbed at D = 6.2 mm, and the outer whorl (D = 19.9 mm) platyconic and densely ribbed. – All natural size (x1). Asterisk at last septum.

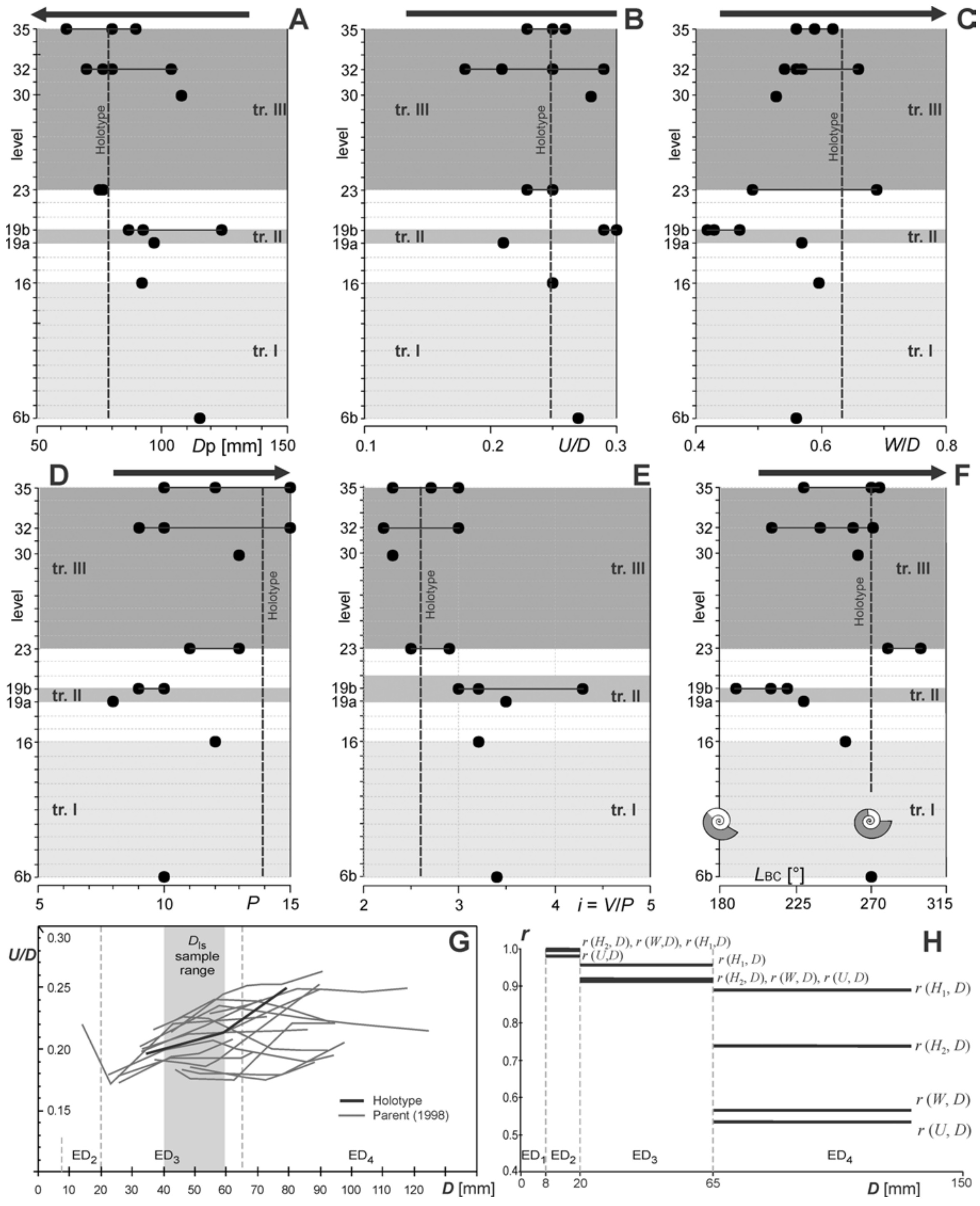

Fig. 12. *Stehnocephalites gerthi*. **A**–**F** – Biometry of adult macroconchs of transients I–III of the new material. The maximum ranges corresponding to material of transient III in Parent (1998) are indicated above each graph by bold bars, with arrowhead if exceed the range of the present graphs. Sample sizes of the new material considered: *n*(tr. III) = 10, *n*(tr. II) = 4, *n*(tr. I) = 2. A: Adult diameter at peristome; B: relative umbilical diameter; C: relative whorl width; D: number of primary ribs; E: ratio of ventral to primary ribs; F: length of body chamber (life position according to Westermann 1996). **G** – Trajectories of relative umbilical diameter of selected specimens. **H** – Ontogeny of the relative covariation (measured by *r*) between shell dimensions and size in transient III. G, H: Only data from Parent (1998); measurements for ED_1 insufficient for analysis.

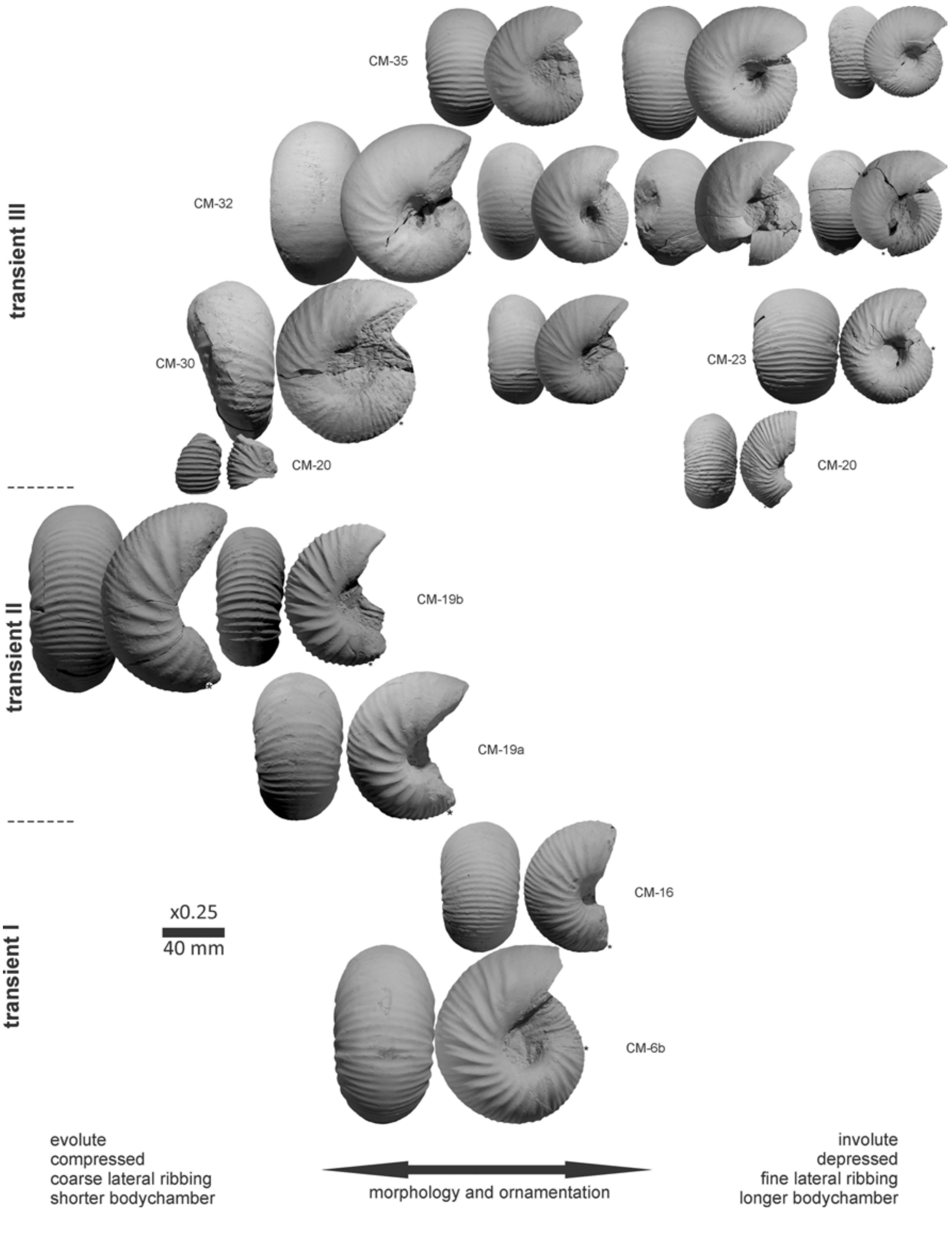

Fig. 13. *Stehnocephalites gerthi* (Spath, 1928). Succession of adult macroconchs (reproduced at one quarter size from previous figurations) representing the morpho-ornamental evolution of the phyletic lineage. The specimens at each level are approximately arranged according to the morphology and ornamentation which characterize the morphs α, β, γ, and δ. The picture obtained has the structure of the model in Fig. 2B which allows to visualize the shifts of the intraspecific variation of the succeeding transients and their internal variation. Since the four morphotypes cannot be arranged along a single line intergrading completely, some specimens are not very exactly placed in the general framework. Some specimens are flipped for ease interpretation. – All x0.25.

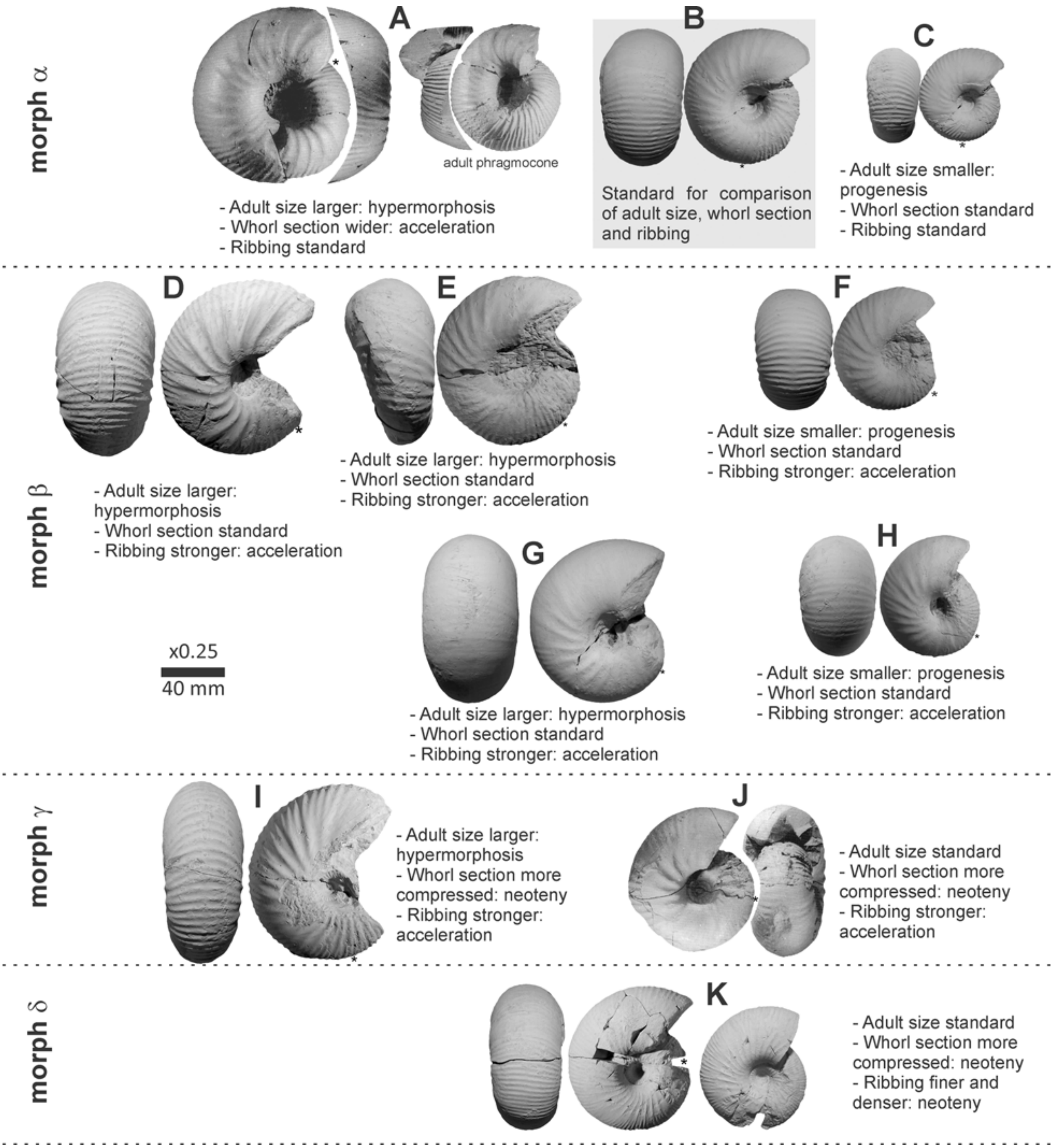

Fig. 14. **A–H** – *Stehnocephalites gerthi* (Spath, 1928) [M], transient III, complete adult macroconchs of the four morphs (α, β, γ, and δ). These variants cover most of the known variation in the species. The shell shape and size are interpreted as modulated by heterochronic processes as indicated for each specimen. The specimen B (morph α, indistinguishable from the holotype, is chosen as the standard for comparison. Vertical alignment nearly according to adult size. A, D, I–K reduced and refigured from Parent (1998) after additional preparation. B, C, E–H reduced and reproduced from Figs. 8, 10, 11. – All x0.25. Asterisks at last septum.

remains high, but becomes lower for H_2-D, and very low for W-D and, especially, for U-D. The lowering covariation is produced according to the different sizes (D) at which the rates of growth of the dimensions U, W, H_1, and H_2 shift, that is their heterochronic development (e.g., Fig. 12H). The association of low covariation for U and W and high for H_1 and H_2 points to the rule of covariation (Westermann 1996; Hammer & Bucher 2005; De Baets et al. 2015; Monnet et al. 2015), but in the form discussed in Parent et al. (2010), where the whorl overlaping (H_2/H_1) is the primary factor controlling the whole shell-shape.

Similar cases of intraspecific variation based or modulated by developmental heterochronies have been described for ammonites of different ages (e.g., Meister 1988; Meister 1989; Hantzpergue 1989: 80; Hammer & Bucher 2006; Parent et al. 2011: 69; Frau et al. 2016: fig. 5).

Intraspecific variation between transients – phyletic evolution: Parent (1998) founded a correlation between morphology and lithofacies in the form that the more depressed and inflated specimens predominate in shaly beds, whereas more compressed specimens are found in marly beds. This pattern is confirmed and refined from the present sampling under higher stratigraphic resolution. The occurrence of *S. gerthi* through its stratigraphic range is mainly in the thin levels of shales. In the thick bank of marls (CM-19a-b) the species shows a shift in morphology and ornamentation into the transient II (Figs. 1B, 13).

The marly bank CM-19 could have been formed by synsedimentary accumulation of carbonates from the depositional environment, or by early and/or late diagenetic processes involving carbonate migration (C. Garrido, pers. comm. 13/02/2021). If the calcareous contents would be synsedimentary, thus reflecting the environmental conditions at the time of deposition, then this bank must represent a period of greater productivity and thus the presence of a richer micro- and invertebrate macrofauna than in shale-producing environments. However, these conditions must be considered with caution because the fossils in the bank CM-19 are scarce, other than ammonites.

The patterns of intraspecific variation according to facies are well documented, although the causes are diversely discussed (e.g., Marchand 1984; Jacobs et al. 1994; Westermann 1996; Weitschat 2008; Wilmsen & Mosavinia 2011; Lukeneder 2015; Lehmann et al. 2016; Klein & Landman 2019; Monnet et al. 2015). If one accepts a defensive function of ribbing and ornamentation in general, it could be that the stronger ribbing from juvenile whorls in transient II, was an adaptation for better resistance to predation by animals attracted by this supposedly more favorable environment. Alternatively, they may have had some hydrodynamic benefit, improving certain life habits in these different environmental conditions (D.J. Peterman, pers. comm. 05/04/2021). From the work of Ward (1981) it seems reasonable to assume that fine ornamentation would have had benefitial effects on the hydrodynamics (see Chamberlain & Westermann 1976), whereas the strong ornament would not, but in fact being effective as a defense to predation and impact. Furthermore, the short bodychamber of the individuals of transient II (Fig. 12F) would confer higher stability to the animal (Westermann 1996; Naglik et al. 2015), an additional advantage for escaping from predators, and for catching prey.

5. Conclusions

The genus *Stehnocephalites* ranges, at least, the whole Gerthi Subzone of the Steinmanni Zone (Upper Bathonian) and the lower Gottschei Zone (Lower Callovian; Fig. 1B). It seems to include the single species *S. gerthi*, while *S. crassicostatus* is considered a synonym. *S. gerthi* evolved from *Iniskinites crassus* Riccardi & Westermann, 1991 in the upper Steinmanni Zone (Riccardi & Westermann 1991; Parent 1998; Parent et al. 2020). The geographic distribution of *S. gerthi* includes much of the western Neuquén Basin, from northern Neuquén Province up to southern San Juan Province. The best record is known in the study area, Chacay Melehué.

The whole known fossil record of *S. gerthi* allows the reconstruction of the lineage from its origin up to its apparent extinction in the lower Gottshei Zone. According to the morpho-ornamental changes of the macroconchs through the stratigraphic range of the species, three transients have been distinguished. The variation observed within transients can be classified as four morphs, although well characterized only in the latest one for the time being.

The intraspecific variation of the females of the species is very wide through its phyletic evolution. However, there is a trend of reduction of adult size at peristome correlated with an increase in density of the primary ribbing. The relative umbilical and whorl width, and the body chamber length do not show significant trends, other than the shorter body chamber in transient II. However, there is a clear trend of reduction of the index *V/P* which is produced by the increase in the number of primary ribs while the density of the ventral ribbing is mantained almost unchanged through the lineage. The transient II shows some excursions from these trends since the specimens are the most compressed in whorl section with lower number of primaries and shorter body chambers.

In the latest transient (and most likely in the others) the variation is produced by the concurrence of different paedo- and peramorphic heterochronies operating over different sets of characters in different individuals, producing a mosaic of morphotypes.

It seems possible that the conspicuous morphology and ornamentation excursion of the transient II is an adaptation for defense from preying as suggested by interpretation of the lithology.

The intraspecific variation is mainly produced by heterochronic development of sets of characters in combination with variable sizes and ages of maturation, while the sequence of ornamental stages and the juvenile ontogeny remain rather invariable.

This latter conclusion seem applicable to most, if not all, ammonoids.

However, for the understanding of the typically wide variation and evolution of ammonites and for classification, one must insist in the crucial importance of considering the type of material compared. It is essential to make distinction between adult or juvenile, and between complete, incomplete or phragmocone and/or body chamber. For this, the only definite criterium of maturity is the uncoiling of the bodychamber which, in different degrees, is developed in the Ammonitina.

Acknowledgements

Sergio Cocca (Zapala) and Oscar D. Capello (Rosario) gave expert assistance during field-work. Alberto C. Garrido (Zapala) and Luciano Brambilla (Rosario) have given important discussion on some aspects of the present study. D.J. Petermann (Utah), as referee of the journal, gave a valuable review for improving the manuscript.

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Manuscript received: April 25th, 2021.
Revised version accepted by the Stuttgart editor: June 16th, 2021.

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