Heterotopy and heterochrony in the palaeotaxodont bivalve *Natasia boliviensis* (Babin and Branisa) from the Early Ordovician of northwestern Argentina

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Cabezal: Heterototopía en tironucúlidos del Ordovícico argentino.

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Abstract . In the last few years several contributions concerning heterochronic processes have been produced, but only few papers dealing on heterotopy have been published. Material of *Natasia boliviensis* (Babin and Branisa, 1987) from the Early Ordovician of northwestern Argentina includes specimens at different growth stages, from smaller, juvenile individuals with taxodont dentition, to larger adult shells displaying actinodont dentition. Ontogenetic development of dentition is tentatively interpreted as resulting from heterotopic changes from an unknown praenuculid ancestor, whereas changes in shell outline could be explained by mean of heterochrony.

Resumen. En los últimos años se publicaron numerosas contribuciones sobre procesos heterocrónicos pero son escasos los análisis de los cambios en la forma (espaciales) o heterotópicos. La especie *Natasia boliviensis* (Babin y Branisa, 1987), del Ordovícico Temprano del Noroeste argentino, está representada por abundantes ejemplares en distintas etapas de desarrollo que incluyen individuos juveniles con dentición de tipo taxodonte hasta individuos adultos con dentición actinodonte. El desarrollo ontogenético de la dentición en esta especie se interpreta tentativamente como un caso de heterotopía a partir de un antecesor praenuculido desconocido. Los cambios producidos en el contorno de las valvas, en cambio, pueden ser atribuidos a un proceso heterocrónico.

Key words. Heterotopy. Tironuculids. Early Ordovician.

Palabras clave. Heterotopía. Tironuculidos. Ordovícico Temprano.

Introduction

In the recent decades the evolutionary trends involving developmental changes have focused mostly on heterochrony, that involves changes over time in the rate and timing of development (Gould, 1977; McNamara, 1990, 2001). On the other hand, there are only a few examples of morphological change by heterotopy, which implies evolutionary changes in spatial patterning of development (Zelditch and Fink, 1996). As long as heterochrony is characterized by a parallelism between ontogeny and phylogeny, a novelty resembling a different developmental stage of an ancestral form, heterotopy results in changes in the form respect to the ancestral morphology. As Zelditch and Fink (1996) suggested, a pure heterochrony or a pure heterotopy are very rare, and probably most developmental changes involve both temporal and spatial changes in a variable degree.

As Arthur (2000) stated, developmental reprogramming is an essential aspect in the evolutionary theory. In this frame, it is important to explore the ontogenetic patterns in the fossil record. The aim of the present work is to analyze the developmental pattern of *Natasia boliviensis* (Babin and Branisa. 1987) on the basis of a series of differently sized specimens collected from the upper Floian (*O. evae*-*O. intermedius* biozones) Acoite Formation. Studied material comes from the western slope of the Cordillera Oriental, south of the Los Colorados village, northwestern Argentina. This study discuss the hypothesis that the hinge pattern of the genus *Natasia* Sánchez (1995) evolved from a *Praenucula*-like palaeotaxodont by a heterotopy, and its shell outline resulted from a peramorphic heterochronic modification. Although there are no records of its probable ancestor, the earliest ontogenetic stages of the *Natasia* dental pattern strongly suggest a *Praenucula*-like ancestor.

Tironuculid genera

Tironuculids are included in the Subclass Palaeotaxodonta. Morris and Fortey (1976) placed them in the Family Praenuculidae, and subsequently Babin (1982) erected the Family Tironuculidae Babin (1982), which is morphologically close to the praenuculids, and both families were included in the Superorder Nuculiformii Gray by Carter *et al*. (2000). The tironuculids are characterized by dental changes throughout growth, from a taxodont-like to an actinodont-like pattern, and include the genera *Tironucula* Morris and Fortey (1976), from the Darriwilian of Spitsbergen, *Ekaterodonta* Babin (1982), from Floian beds of the Montagne Noire, and *Natasia* Sánchez (1995), from the Floian of Central Andean Basin (southern Bolivia-northern Argentina). Placement of tironuculids into Nuculiformii is supported by the juvenile stages of *Natasia* and the possible juvenile specimens of *Ekaterodonta*, but equivalent ontogenetic stages in *Tironucula* have not been reported.

Morris and Fortey (1976) erected the genus *Tironucula* on specimens displaying a combination of actinodont and taxodont teeth. Larger specimens (adults) of *Tironucula jugata* Morris and Fortey (1976) show taxodont, chevron-like anterior teeth. The left valve displays a single posterior tooth with the upper arm of the chevron posteriorly deflected extending along the hinge plate to form a posterior actinodont-like tooth. The right valve possesses two posterior actinodont-like teeth. Three ontogenetic stages can be recognized trough growth: (1) small (about 0.1 mm) edentulous specimens, (2) shells bearing a single ovoid anterior tooth, and (3) shells with two ovoid anterior teeth. No posterior teeth developed at these stages (Morris and Fortey, 1976, p. 702, plate 1, figs. 2-4), the taxodont pattern being attained in the adult. Morris and Fortey (1976) did not mention specimens of intermediate (0.9 to 4.5 mm wide) size, so it is possible that teeth became taxodont during this not recorded stages.

Ekaterodonta courtessolei Babin, (Babin, 1982) shows three to four elongated anterior teeth, and a posterior series of 10 to 15 taxodont-like teeth from which the upper arm of the first chevroned tooth elongated and runs parallel to the dorsal margin forming a lamellar element. The series of chevroned teeth are joined to the lamellar dorsal tooth. The complete ontogenetic series in *E. courtessolei* remains unknown, but it striking that the specimens are associated to small, taxodont-hinged specimens resembling *Praeleda* Pfab or some related taxa (Babin, 1982, p. 39).

The species *Ekaterodonta boliviensis* Babin and Branisa was erected on specimens from Floian beds of the Sella Formation (southern Bolivia) (Babin and Branisa, 1987). Subsequent collections of this species from the coeval Acoite Formation (northwestern Argentina) allowed to erect the genus *Natasia* Sánchez (1995). Argentine material of *Natasia boliviensis* (Babin and Branisa) includes specimens ranging from 1mm to 10 mm in length showing a complete transition from taxodont-like to actinodont-like dentition.

Ontogeny of *Natasia boliviensis*

In a previous contribution, numerous specimens collected from a single stratigraphic level were analyzed leading to define four growing stages (Sánchez, 1995). However, it is important to note that these stages were recognized only in order to simplify the description because there are no interruptions in the growth series. The first step corresponds to smallest specimens (1 to 2 mm length) having a well-developed taxodont hinge, including a complete series of anterior and posterior chevroned teeth. Because there are not specimens smaller than 1 mm, the existence of a single-tooth stage like in *Tironucula* cannot be demonstrated. Departing from this ‘taxodont-like’ stage, a series of transformations in the anterior and posterior dental series occur, but changes in each series are different. As result, the largest specimens display a peculiar dentition formed by a posterior series of actinodont-like teeth, and an anomalous anterior series of not chevroned nor actinodont teeth.

Changes during growth in *Natasia boliviensis*

Transformations in the anterior, subumbonal, and posterior dental series are different throughout growth, and consequently they are discussed separately. In the posterior series (figure 1.1) development begins in the most distal tooth with the reabsorption of the chevron angle that produces a separation of the arms (figure 1.2). At this stage, both the dorsal and ventral arms underwent a constriction that fragment the original branches in two segments from the dorsal arm and two from the ventral one which form two parallel series (figure 1.3). The modified arms of this tooth merged to the first formed elements beginning the formation of two actinodont-like teeth. Successive similar changes from the distal to the proximal teeth continues until the complete formation of two actinodont-like teeth, parallel to the dorsal margin (figure 1.4-6).

There are not enough specimens having well-preserved anterior dental series to know all the developmental stages. Available specimens belonging to an intermediate ontogenetic stage display anterior teeth showing a series of right not-chevroned elements (figures 2.6, 10), but unfortunately previous stages filling the gap between this stage and the juvenile chevron teeth are lacking. In the adult hinge, some elements merged to form an irregular pattern of V-shaped to Y-shaped teeth. Even though no intermediate stages are preserved, it seems likely that the growth pattern strongly differs from that of the posterior dental series. The subumbonal series does not show changes through growth.

The above description suggests a dissociate genetic control of the three dental series. Such a dissociation has been a norm in all the palaeotaxodont bivalves, although the degree of its incidence could have been different. In genera having a simple dental pattern, like *Suria* Sánchez (1997), there are only small differences between the anterior and posterior series, concerning to the direction of the chevron angles and the size of anterior and posterior teeth, which seems to be correlated to the hinge size. In this and other similar cases, a high degree of genetic association can be deduced. A similar low degree of dissociation could be present in *Concavodonta* Babin and Melou (1972), in which the chevrons of both dental series display an opposite direction. Since modifications during growth resulted in very different anterior and posterior dental patterns, the genetic dissociation in tironuculids seems to have been higher than in the above mentioned palaeotaxodonts. Thus, it is possible that dental series in palaeotaxodonts were controlled by variable degrees of genetic association, from a strong association, with a few differences in orientation and size of dental elements, to a strong dissociation, resulting in very different patterns of growth.

N. boliviensis also underwent through growth notable changes in the shell outline. Smaller (juvenile?) specimens have a more or less triangular shell outline (figures 2.1, 2), which changes to subquadrate in large (older?) individuals (figure 2.6). Changes from a triangular to a subquadrate shell outline could be explained by a different growing rate, with a rapid development of the posterior half of the shell with regard to the anterior half, that is, these allometric changes have followed a peramorphic heterochronic pattern.

On the contrary, dental transformations as described above could not be explained by allometry. Reabsorption and displacement of parts of the original chevrons are modifications in space, not allometric changes, and consequently, these changes only could be explained by heterotopy.

Comparative analyses among tironuculids

Dental patterns in adult stages of the three tironuculid genera look different. Adults of *Tironucula* maintain a taxodont style in the anterior dental series, and the actinodont-like pattern developed only in the posterior hinge. *Ekaterodonta* displays a reverse pattern: the anterior series is formed by actinodont-like teeth, and the posterior one by taxodont-like elements joined to the dorsal arm of the first chevroned tooth. Adult specimens of *Natasia* show well-defined actinodont-like teeth in the posterior hinge, and taxodont-like, non chevroned elements, in the anterior and subumbonal areas. Although dental transformations in *Natasia* are greater than those observed in *Tironucula*, both genera share a similar pattern in the adult, with actinodont teeth in the posterior series and taxodont teeth in the anterior hinge, a different condition than that seen in *Ekaterodonta*.

According to the above described features of anterior and posterior dental series, adults of *Natasia* show closer similarities with actinodont-hinged bivalves than both, *Tironucula* and *Ekaterodonta*. In the teeth number and continuous series of teeth, the adult specimens of *Natasia* resemble the Family Cycloconchidae Ulrich. However, this similarity does not imply a phylogenetic relationship between tironuculids and cycloconchids, as mentioned below.

Discussion and conclusions

Juvenile specimens of *N. boliviensis* are closely related to *Praenucula expansa* Pfab 1934, described and figured by McAlester (1968) in both dentition and shell outline (compare figures 2.1, 2 and 2.4). However, as Jaecks and Carlson (2001) stated, phylogeny is one of the most important components to define heterochrony (and also heterotopy), and we do not know the phylogenetic relationships between tironuculids and praenuculids. Depending on these relationships dental changes in *Natasia* could represent an heterotopic process starting from a *Praenucula*-like ancestor, or a paedomorphic heterochronic process leading from *Natasia* to the praenuculids. Due to the presence of a taxodont dentition in the early growth stages, tironuculids have been included into the palaeotaxodonts, but there are not clear evidence as to whether tironuculids or praenuculids were the ancestors. Indirect evidence would suggest that praenuculids are the ancestors of tironuculids: 1, The palaeotaxodont record possibly predates that of tironuculids. *Afghanodesma* Termier and Termier is from strata dated as Early Ordovician (Tremadocian) of Afghanistan by Desparmet *et al*. (1971), although this age has been questioned by Babin and Hammann (2001) because it is not supported by paleontological evidence; 2, the geographic expansion of praenuculids, that predates that of tironuculids; and 3, the greater diversification of praenuculids with regard to that of tironuculids. Because there are not evidence enough to support the origin of tironuculids from praenuculids, this possibility is only tentatively accepted until ontogenetic stages of some praenuculid species are known.

On the basis of dental morphology of *Tironucula*, Morris and Fortey (1976) suggested that nuculoid hinge derived from a more primitive actinodont dentition. However, growth changes in *Ekaterodonta* and *Natasia* suggest an opposed option: lamellar teeth arose from enlargement of the arms of chevroned teeth (Babin, 1982). The origin of both, actinodont and nuculoid dental types was carefully analyzed by Sánchez and Babin (1998), which concluded that there is not a direct relationship between these dentitions, but both developed independently in different bivalve clades. In agreement with this conclusion, Babin and Hammann (2001) proposed an hypothetic “Cambrian proterodont” type from which both dentitions originated.

The recently erected Family Intihuarellidae, from the Early Ordovician of the Cordillera Oriental (northwestern Argentina), suggests that intihuarellids could have been the probable ancestors of cycloconchids (Sánchez and Vaccari, 2003). Consequently, the heterochronic process verified in *Natasia boliviensis* -and partially in the other tironuculids- can be viewed as an isolated event without descendents. Besides, the lamellar teeth of tironuculids are homoplasious of the true actinodont teeth of cycloconchids and related groups.

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FIGURE CAPTIONS

Figure 1. Schematic drawing of ontogenetic stages in *Natasia boliviensis* (Babin and Branisa) / *Dibujo esquemático de los estadíos ontogenéticos en* Natasia boliviensis *(Babin y Branisa)*. Left: original scheme from Sánchez, 1997; right, detail of the successive changes in the posterior hinge / *A la izquierda: esquema tomado de Sánchez, 1997; a la derecha, detalle de los cambios sucesivos en la charnela posterior*. 1, taxodont, chevroned teeth (from the specimen figured in figure 2.1) / *dientes taxodontes en chevron (a partir del ejemplar figurado en la figura 2.1)* ; 2, transformation of the distal (V) tooth / *transformación del diente distal (V)*; 3, transformation of following (IV) tooth begins (see figure 2.3) / *comienza la transformación del diente siguiente (IV) (ver figura 2.3)*; 4,

transformation of the following (III) begins, the distal part shows two small actinodont-like teeth (from specimens figured in figures 2.5 and 2.9) / *comienza la transformación del diente III, la parte distal muestra dos pequeños dientes de tipo actinodonte (a partir de los ejemplares figurados en las figuras 2.5 y 2.9)*; 5, advanced stage (from the specimen figured in figure 2.7) / *estadío avanzado (a partir del ejemplar figurado en la figura 2.7)*; posterior actinodont-like teeth completed (from specimens figured in figure 2.6 and 2.10) / *dientes posteriores de tipo actinodonte completados (a partir de los ejemplares figurados en las figuras 21.6 y 2.10).* a, anterior adductor muscle / *músculo aductor anterior*; lig, ligament / *ligamento*.

Figure 2. Ontogenetic stages of *Natasia boliviensis* (Babin and Branisa) / Estadíos ontogenéticos en *N. boliviensis* (Babin y Branisa). 1, 2, first stage / *primer estadío*. 1, left valve with anterior and posterior taxodont, chevroned teeth / *valva izquierda con dientes anteriores y posteriores taxodontes, en chevron*, CEGH-UNC 13613 (x 10); 2, two young specimens showing shell outline and adductor anterior muscle scar / *dos ejemplares juveniles mostrando el contorno de la valva y el músculo aductor anterior*, CEGH-UNC 13615a (x 6,5); 3, second stage / *segundo estadío*. Right valve, note broken posterior chevrons / *Valva derecha, nótense los dientes posteriores en chevron rotos,* CEGH-UNC 13609 (x 10); 5, 7, 9, third stage / *tercer estadío*. 5, right valve / *valva derecha*, CEGH-UNC 13615b (x 11). 7, an advanced form of the third stage / *una forma avanzada del tercer estadío*, CEGH-UNC 7023 (x 9), 9, right valve, note two short actinodont teeth in the posterior extremity of hinge / *valva derecha, nótense los dos cortos dientes actinodontes en la extremidad posterior de la charnela*, CEGH-UNC 13612 (x 7); 8, enlarged view of hinge of specimen from figure 5 / *vista ampliada de la charnela del ejemplar de la figura 5*, (x 17); 6, 10, fourth stage/*cuarto estadío*. 6, right valve/*valva*

derecha, CEGH-UNC 13606 (x 8,5); 10, right valve / *valva derecha*, CEGH-UNC 13607 (x 6). Note the actinodont teeth in the posterior hinge, and the anterior Y-shape teeth in both specimens / *nótense los dientes actinodontes en la charnela posterior y los dientes en forma de Y en la anterior en ambos ejemplares*. 4. *Praenucula* sp. Left valve, Don Braulio Formation, Sandbian, Precordillera / *valva izquierda, Formación Don Braulio, Sandbiano, Precordillera*. CEGH-UNC 16170b (x 3). All specimens preserved as internal molds / *Todos los ejemplares preservados como moldes internos.*