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Ontogenetic variation of statolith shape in the short-finned squid *Illex coindetii* (Mollusca, Cephalopoda)

Variacion ontogénica del estatolito de la pota *Illex coindetii* (Mollusca, Cephalopoda)

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ABSTRACT

Changes in statolith morphology of *Illex coindetii* are described from specimens ranging from 42 to 379 mm mantle length obtained during trawling activities in the North-eastern Atlantic. The growth of the statolith was differentiated in five developmental stages. It has been observed that the wing of the statolith has two different growth patterns, from the ventral zone to the dorsal one and viceversa. The rostral angle of the statolith varied during its ontogenetic growth from an obtuse angle to a 90° angle. The dorsal zone of the statolith is here named as dorsal dome, and the lateral and ventral zone the lateral dome.

RESUMEN

En este trabajo se describen los cambios en la morfología del estatolito de *Illex coindetii*. El estudio se llevo a cabo mediante el análisis de 341 ejemplares con longitudes del manto comprendidas entre 42 y 379 mm. Estos animales se capturaron en la pesquería de arrastre desarrollada en el Atlántico noreste. El crecimiento del estatolito fue diferenciado en cinco estadíos de desarrollo. Se observaron dos patrones diferentes de crecimiento del ala del estatolito, desde la parte ventral a la dorsal y viceversa. El angulo rostral varía en el crecimiento ontogénico del animal, desde un ángulo marcadamente obtuso a un ángulo recto. El crecimiento en longitud máxima y en anchura del estatolito se enlentece al llegar a la maduración de los animales. Se propone una variación en la nomenclatura del estatolito de esta especie.

KEY WORDS: *Illex coindetii*, statolith, morphology, North-eastern Atlantic.
PALABRAS CLAVE: *Illex coindetii*, estatolito, morfología, Atlántico noreste.

INTRODUCTION

Cephalopods play an important role in the trophic web of marine ecosystems as both predators and prey of many marine species (AMARATUNGA, 1983). These marine molluscs have been cited as components of the diet of such top predators as marine mammals (XAMPENY AND FILELLA, 1976; CLARKE, 1980, 1986; CLARKE, MARTINS AND PRINCE, 1993; GONZÁLEZ, LÓPEZ, GUERRA AND BA-

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RREIRO, 1994), large teleosteans (BOUXIN AND LEGENDRE, 1936; BELLO, 1991; GUERRA, SIMÓN AND GONZÁLEZ, 1993; CLARKE, CLARKE, MARTINS AND SILVA, 1995), sea-birds (RODHOUSE, CLARKE AND MURRAY 1987; CLARKE, CROAXALL AND PRINCE, 1991; FURNESS, 1994; CROAXALL AND PRINCE, 1996) and cephalopods (RASERO, GONZÁLEZ, CASTRO AND GUERRA, 1996, RODHOUSE AND NIGMATULLIN, 1996). Beaks, statoliths, chitinous sucker rings and, to a lesser extent, gladius, were the main structures which allowed a positive identification to the taxonomic level of species in studies about trophic relationships between cephalopods and other marine animals. These hard structures remain unaltered in the stomach contents of their predators and represent an important source of information on the trophic relationships where these animals are involved.

Statoliths of cephalopods are small hard paired structures composed by calcium carbonate in the form of aragonite. They are situated in fluid-filled cavities termed statocysts inside the cartilaginous skulls of the cephalopods belonging to the subclass Coleoidea (CLARKE AND MADDOCK, 1988a). The statolith and the macula (statoconia system) constitute the receptor organ for detection of gravity. This is one of the functions of the statocysts, in which the level of sophistication is equivalent to the vertebrate vestibular system (YOUNG, 1960, 1989; STEPHEN AND YOUNG, 1982; BUDELMANN, 1978, 1988, 1990).

Statoliths are also the structures most frequently used for studies on age and growth. The statoliths of many cephalopod species show growth increments, which have been shown to have a daily periodicity of deposition in several species (see JACKSON, 1994).

Since teuthoid statoliths are apparently species-characteristic and have a greater likelihood of fossilisation than other cephalopod structures, they have become very important for identification of fossil species (CLARKE AND FITCH, 1975, 1979). The applications of image analysis which have been used in the morphological study of the statoliths, both recent and fossil, have shed light on certain phylogenetic relationships among cephalopods (CLARKE AND MADDOCK, 1988a; 1988b). As was done with shape analysis of fish otoliths (CAMPANA AND CASSELMAN, 1993), the statolith morphology of cephalopods has been used also for stock discrimination (BORGES, 1995).

As ontogenetic changes do exist in the statolith (MORRIS AND ALDRICH, 1984; GUERRA AND SÁNCHEZ, 1985; CLARKE AND MADDOCK, 1988b; BRUNETTI AND IVANOVIC, 1991), some remains on the reliability of this approach about this subject. From descriptions based solely on one statolith from one specimen, the result of the analysis of shape can be altered (LOMBARTE, SÁNCHEZ AND MORALES-NÍN, 1995) and a correct prey identification could also be uncertain.

The aim of this study was to determine the changes in the statolith shape for the ommastrephid squid *Illex coindetii* (Vérany, 1839) during its ontogenetic growth.

MATERIALS AND METHODS

341 specimens of *Illex coindetii* were collected in the North-eastern Atlantic (Fig. 1) from November 1991 to October 1992. Fishing was carried out at depths ranging from 100 and 350 m over the Galician continental shelf. The animals were sexed, measured to the nearest mm mantle length (ML), weighed (to 0.1 g) and assigned a maturity stage according to LIPINSKI (1979). The squid ranged from 48 to 379 mm ML. The statoliths were removed from the head and preserved in 96% ethanol. Statolith major axis and maximum width were recorded. Then, the statoliths were measured using an eyepiece graticule. Terms used in descriptions were assigned following the nomenclature established by CLARKE (1978).

Measurements were made using an image analysis system (IAS); the equipment used is reviewed by MACY (1995). The description of the each develop-

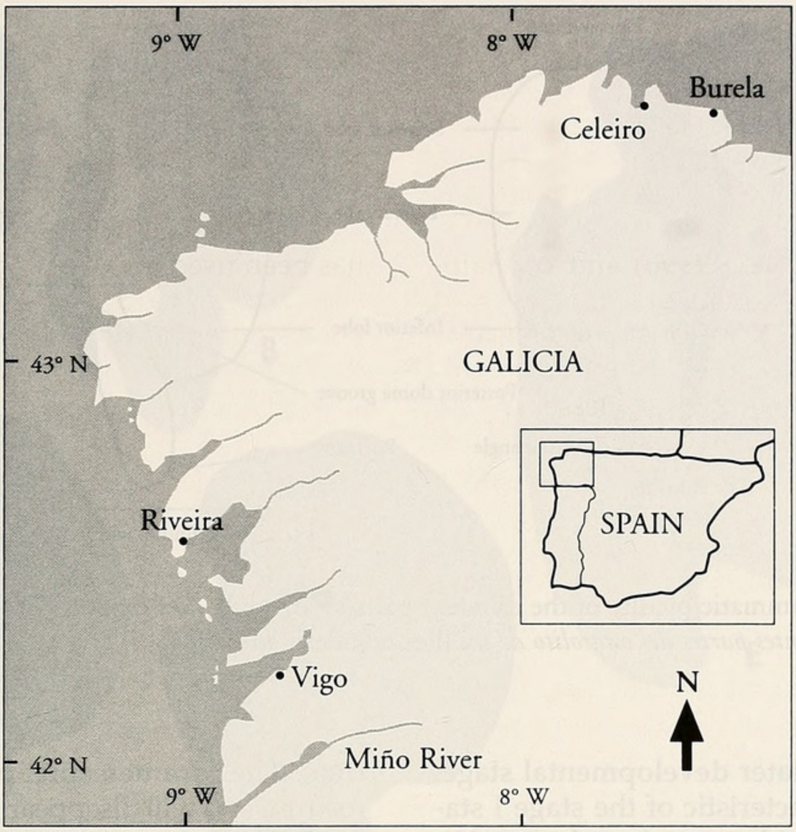

Figure 1. *Illex coindetii.* Fishing area where the samples were obtained.
Figura 1. Illex coindetii. Area de pesca donde se obtuvieron las muestras.

mental stage of the statolith was made based on microphotographs.

RESULTS

Statolith morphology: Statolith maximum length ranged from 0.47 (female of 48 mm ML) to 1.66 mm (female of 360 mm ML). No significant differences ($p<0.05$) between maximum length and maximum width of male and female statoliths of equivalent ML were found at any stage of development. Therefore, sex does not affect the growth of the statolith in *Illex coindetii*.

Figure 2 shows a diagrammatic picture of the different parts of an adult *Illex coindetii* statolith in posterior and anterior view. Terms used in descriptions and the measurements made are also shown. Some characteristic features were observed in these statoliths: a) there is continuity between the dorsal dome and the lateral dome. This feature can be observed between the superior and inferior lobes of the lateral dome as well; b) the posterior dome groove is very patent; c) the rostrum is short and an anterior rostral lobe does not exist; d) the wing is very broad; e) the medial fissure is well developed and also has a small posterior indentation; f) the dorsal spur is very clear.

Statolith development: Although the above description refers to a late developmental stage of the statolith in an adult animal, the way to reach this definitive stage is quite complex. Thus, the statolith has become increasingly complex and passed through different stages which implies growth in different planes. These stages can be described as follows (Fig. 3):

Stage I: Statoliths of immature animals ranging from 50 to 80 mm ML. The medial fissure is not yet visible but will be situated under the dorsal dome. This area will be the surface where the wing will connect with the body of the

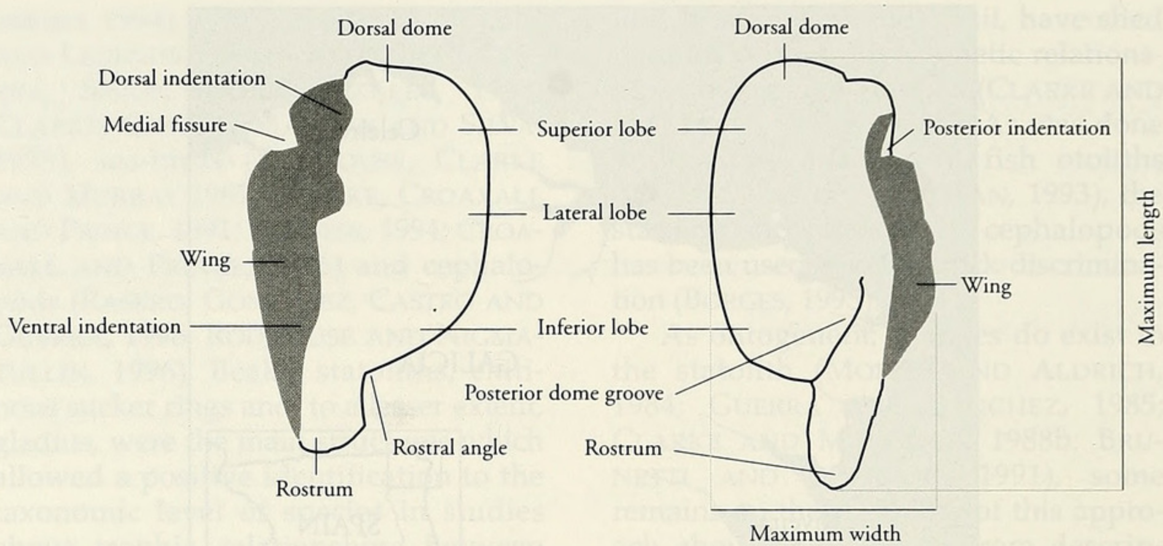

Figure 2. Diagrammatic picture of the different parts of an adult *Illex coindetii* statolith.
Figura 2. Diferentes partes del estatolito de un Illex coindetii *adulto.*

statolith in a later developmental stage. Another characteristic of the stage I statolith is the wide rostral angle (>140°). The primordium of the rostrum is also visible in the ventral zone of the statolith. It is virtually impossible to differentiate the dorsal dome, the superior and inferior lobes of the lateral dome, being round the general shape.

Stage II: This developmental stage includes the statoliths of animals with ML between 90 and 130 mm. The main characteristic of this stage is the growth of the rostrum, and the change in shape of the statolith, which is enlarging the ventral direction. Small dark zones in the ventral zone can be distinguished. This crystallisation will form the wing of the statolith. The wing formation is observed in two directions, from the rostrum to the dorsal plane of the statolith and from the dorsal dome to the ventral plane. There is a slight differentiation between superior and medium lateral dome.

Stage III: This stage is remarkably different from the preceding one. It appears in submature and mature squid ranging from 130 to 200 mm ML. The enlargement of the rostrum continues and the formation of the wing spans from the ventral to the dorsal zone. The medial fissure is small. A zone devoid of crystallisation called the foramen appears for the first time. The foramen runs parallel to the rostrum and will disappear gradually. The rostral angle is getting narrow and at this stage it forms almost a 90° angle.

Stage IV: Mature animals between 200 and 250 mm ML. The developmental stage is close to definitive conditions. The foramen is partially or totally occluded and the wing is formed along the entire statolith. As the statolith grows, the lobes become more distinct. Practically, the rostral angle is 90°.

Stage V: This stage describes the statoliths of mature specimens bigger than 250 mm ML. There are only minor changes in morphology from stage IV. Crystallisation in the wing is stronger and the foramen is totally occluded. The formation of the wing emphasises the medial fissure.

Figure 4 illustrates the relationship between the mantle length and the maximum length and width of the *Illex coindetii* statolith.

DISCUSSION

This paper gives a description of different developmental stages of *Illex coindetii* statoliths, based on observations of the statolith growth. There are important changes in shape of the statolith

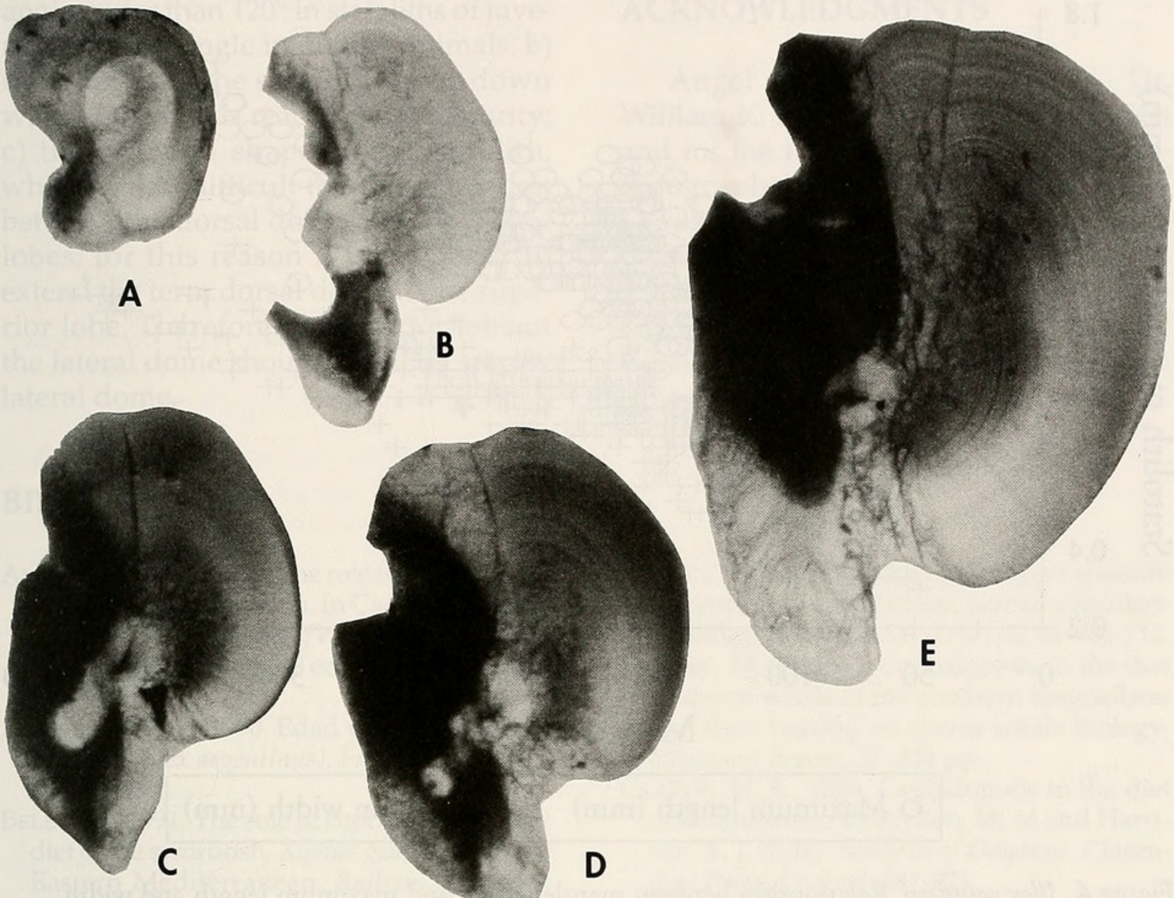

Figure 3. Stages of development for the statolith of *Illex coindetii.* A: Stage I, maximum statolith length (MSL)= 0.67 mm and maximum statolith width (MSW)= 0.40 mm; B: Stage II, MSL =0.90 mm and MSW= 0.63 mm; C: Stage III, MSL= 1.13 mm and MSW= 0.80 mm; D: Stage IV, MSL= 1.20 mm and MSW= 0.80 mm; E: Stage V, MSL= 1.53 mm and MSW= 1.03 mm.

Figura 3. Estadíos de desarrollo del estatolito de Illex coindetii. *A: Estadío I, longitud máxima del estatolito (LME)= 0,67 mm y anchura máxima del estatolito (AME)= 0,40 mm; B: Estadío II, LME= 0,90 mm y AME= 0,63 mm; C: Estadío III, LME 1,13 mm y AME= 0,80 mm; D: Estadío IV, LME= 1,20 mm y AME= 0,80 mm; E: Estadío V, LME= 1,53 mm y AME= 1,03 mm.*

through the life cycle of *Illex coindetii*. Considering the statolith of ommastrephids, it is important to note the difficulty in differentiating between the dorsal dome and the superior and inferior lobes described by CLARKE (1978) for teuthoids. This observation agrees with SÁNCHEZ (1981) for *Illex coindetii* specimens from Mediterranean waters and ARKHIPKIN (1990) and BRUNETTI AND IVANOVIC (1991) for *Illex argentinus.* It was also observed that the rostral angle for statoliths of *Illex coindetii* juveniles is clearly higher than 140° and progressively it is getting narrower until it reaches 90° in mature animals.

Stages I and II correspond to specimens ranging from three to five months of age. The description coincides with stages I and II defined for *Illex argentinus* (BRUNETTI AND IVANOVIC, 1991) and the "definitive stage" noted by MORRIS and ALDRICH (1984). The shape of the statolith is enlarged to the ventral side and it grows in the ventral zone. The formation of the wing converges from two different directions, from the dorsal zone to the ventral one and vice-versa.

Stage III of the statolith of *Illex coindetii* corresponds to submature and mature animals between five and eight months of age ranging from 130 to 200

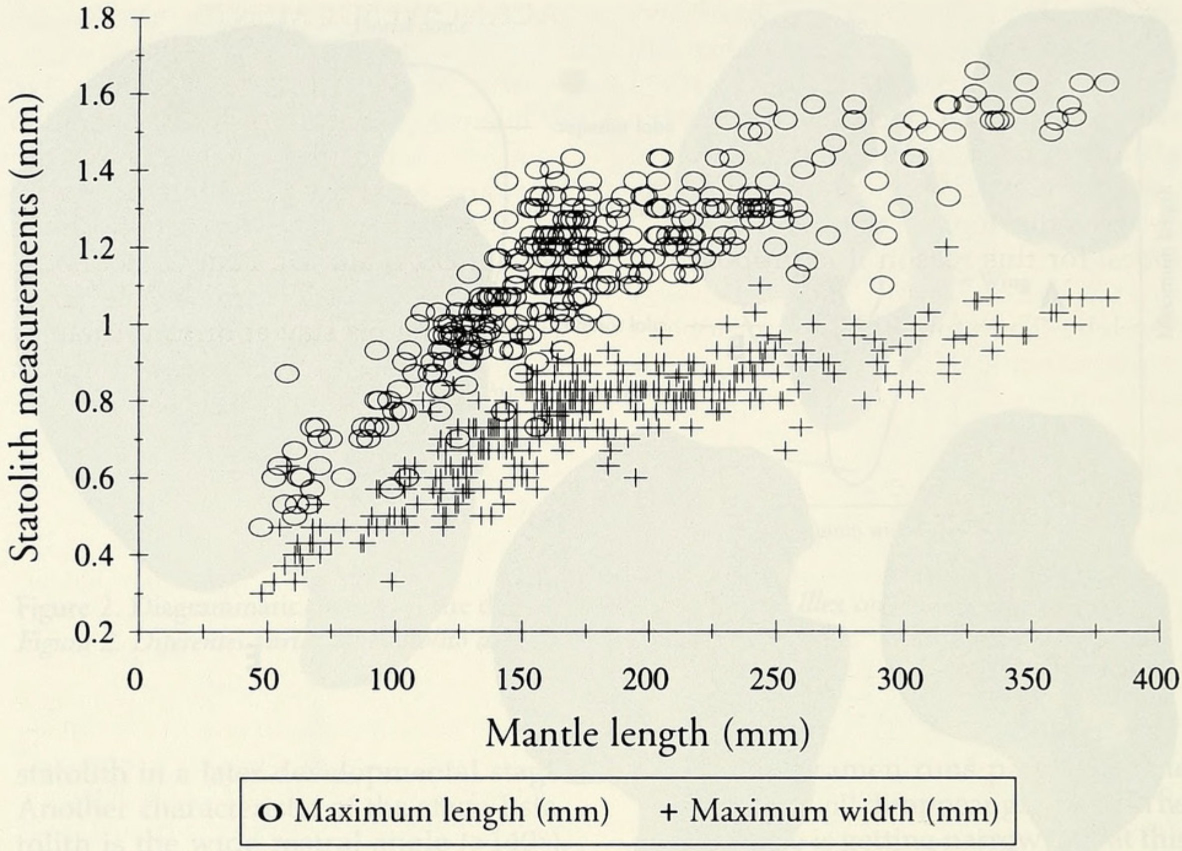

Figure 4. *Illex coindetii.* Relationship between mantle length and maximum length and width .
Figura 4. Illex coindetii. *Relación entre la longitud del manto y la anchura y longitud máximas.*

mm ML. The union of the wing with the dorsal dome of the statolith was observed in this stage, which agrees with the observations of MORRIS AND ALDRICH (1984) for the "juvenile stage" of *Illex illecebrosus* and stage III of ARKHIPKIN (1990) and BRUNETTI AND IVANOVIC (1991) for *Illex argentinus*. From this stage onwards, the growth of the statolith slows down; this could be related with the process of maturation of the animals as showed in the Figure 4. In stage III appears for the first time the foramen, which was noted as a characteristic feature of ommastrephids. This is a lack of crystallisation that runs parallel to the rostrum. It is formed when both planes of the wing grow, connecting over the medial part of the statolith, leaving one distinct zone between this point and the body of the statolith.

Stages IV and V are very similar in shape. However, a main difference can be found when the foramen disappears completely in stage V. Stage IV of *Illex coindetii* corresponded to animals of between 200 and 250 mm ML and ages ranging from eight to ten months. Finally, the statoliths of animals bigger than 250 mm ML and older than ten months are included in the stage V. These statoliths are similar to those described by MORRIS AND ALDRICH (1984) for the "advanced stage" in statoliths of *Illex illecebrosus*, to the stage VI observed by BRUNETTI AND IVANOVIC (1991) for *Illex argentinus* and the statolith described by SÁNCHEZ (1981) for an adult *Illex coindetii* specimen from the Mediterranean Sea.

On the whole, it can be concluded that the shape of the statolith changes gradually from the juvenile stage until it reaches a definitive stage of development. There are three features to be noticed during the growth of the *Illex coindetii* statolith: a) the variation of the rostral angle, getting narrow progressively, from an angle wider than 120° in statoliths of juveniles to a 90° angle in mature animals; b) the growth of the statolith slows down when the animals reach sexual maturity; c) the rounded shape of the statolith, which makes difficult the differentiation between the dorsal dome and the lateral lobes; for this reason it is proposed to extend the term dorsal dome to the superior lobe. Therefore, the inferior lobe of the lateral dome should be called simply lateral dome.

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