The strange apical system of the genus *Pourtalesia* (Holasteroida, Echinoidea)

T. Saucede & B. David
Biogéosciences, Dijon, France

R. Mooi
California Academy of Sciences, San Francisco, California, USA

ABSTRACT : The apical system of the genus *Pourtalesia* displays a plate architecture that falls so far outside that typical of other echinoids that plate homologies remain problematic. Our results, in accordance with the Extraxial-Axial Theory (EAT), show that the typical holasteroid pattern found in the smallest specimens undergoes a series of disturbances that result in a multiple disjunction accompanied by isolation or disappearance of certain genital plates. Therefore, we propose a radically new interpretation of the apical architecture of the genus that agrees with: 1) the Ocular Plate Rule as interpreted through the EAT; 2) patterns observed in the other genera of the family as well as in the sister-group (plexechinids); and 3) the patterns known from Paleocene holasteroids. In the context of the EAT, the genus *Pourtalesia* appears to represent the extreme in a reduction of the extraxial part of the body wall that is a general feature of all the echinoids.

Keywords: Apical system, Pourtalesiidae, Extraxial-Axial Theory.

1 INTRODUCTION

The family Pourtalesiidae consists of seven extant abyssal genera, which are distributed worldwide. The most best known and striking feature of this family is certainly the strange shape characterizing each genus. However, this strange shape is not the only odd thing about these abyssal echinoids. They also display an original plate pattern which drastically departs from the classical pentameral, radiating architecture of most echinoids (see earlier investigations of the oral side in David 1985, David 1987, David 1990). This paper focusses on the plate architecture of the apical system -- an architecture that is so different from that typical of other echinoids that plate homologies remain problematic.

According to Mooi et al. (1994), the body wall of echinoderms is constructed of two major components : axial elements and extraxial elements. Supported by embryology (David & Mooi 1996, David & Mooi 1998), this model, the Extraxial-Axial Theory (EAT), proposes a new system of skeletal homologies among echinoderms.

The EAT suggests that almost all the test of echinoids consists of axial skeleton, the extraxial skeleton being restricted to the scales present on the periproctal membrane, and to the genital plates (Fig. 1). The axial skeleton is organized into five growth zones that follow the Ocular Plate Rule (OPR). According to the OPR, each growth zone is closely associated with an ocular plate and comprises an ambulacrum surrounded by two half-interambulacra, one on each side. New plates in both the ambulacra and interambulacra are formed next to the ocular plate, concomitantly shifting each column adorally.

During the BIOGAS program (1972 — 1981), 69 specimens of *Pourtalesia miranda* Agassiz 1869 were collected in the Southern part of the Bay of Biscay at a depth of 2100 meters. Ranging from 1 to 21 millimeters in length, the specimens in this sample provide an opportunity to describe the ontogeny of the apical system and to explore its plate organization and homologies.

2 THE APICAL SYSTEM OF *POURTALESIA*

Interpreting the plate architecture of the apical side of *Pourtalesia miranda* is not straightforward (Fig. 2a). The first step in interpretation consists of the identification of the five growth zones, and of the five ocular plates heading them. Determination of growth zone boundaries has to agree with the OPR, which implies that an ocular plate is to be found at the adapical extremity of each ambulacrum, and that a given ocular plate cannot be surrounded by more

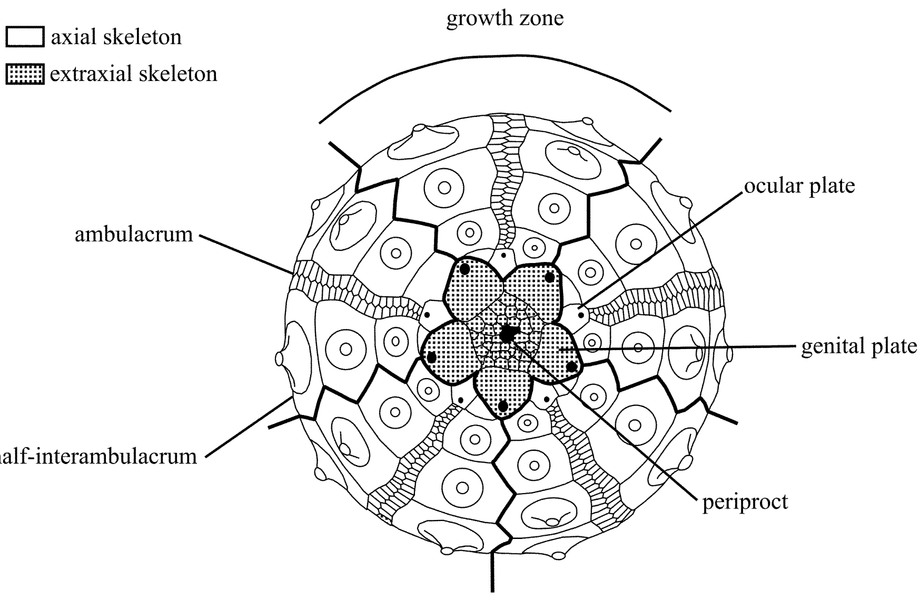

Figure 1. The test of a regular echinoid as interpreted through the EAT. Modified after David & Mooi (1999).

than one row of interambulacral plates in a growth zone. The second step consists of the identification of extraxial elements, and particularly of genital plates. In *P. miranda*, the drawing of growth zone

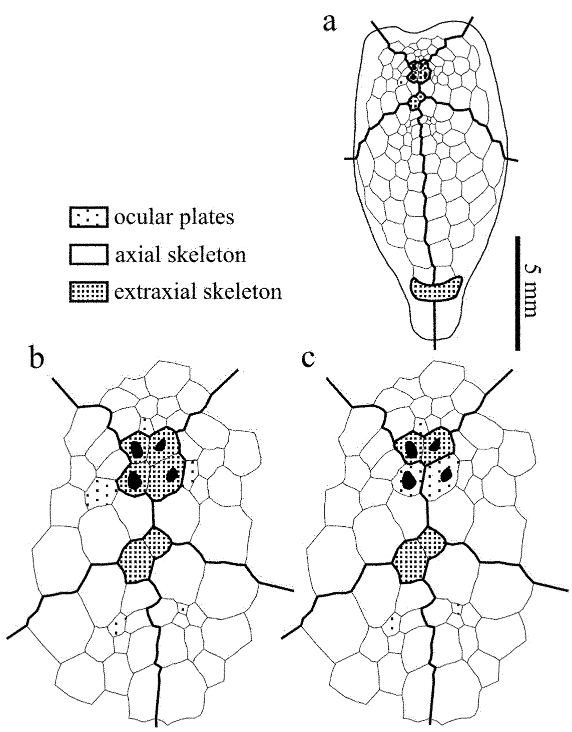

Figure 2. Plate pattern in *Pourtalesia*. a) General architecture of the apical surface. b) Classical interpretation of the architecture of the apical system with the four gonopores opening in four grouped genital plates. c) New proposed interpretation of the apical system with two gonopores opening in ocular plates (see text for explanation). Heavy lines mark the boundaries between the growth zones.

boundaries isolates two plates in the center of the apical system (Fig. 2b). These two plates must be identified as extraxial elements because their independence from any growth zone implies that their growth does not follow the OPR. The four central plates in which gonopores open are likely to be four genital plates. The classical interpretation proposed by Lovén (1883) fits this pattern, except that he regarded the two isolated extraxial plates as supplementary plates from interambulacrum 5.

However, growth zone boundaries can be identified slightly differently (Fig. 2c). According to this second hypothesis, the two isolated extraxial plates are actually genital plates without gonopores, and the two plates bearing the posterior gonopores are ocular plates (i.e. axial skeleton). Although it is quite unusual to have gonopores opening in axial elements, we will explore the possibility that this second interpretation is the correct one. The following arguments in favor of this possibility concern: (1) comparison with other holasteroids; (2) anatomy of the water vascular system; (3) ontogenetic arguments; (4) phylogenetic data; (5) paleontological data.

3 HOLASTEROID PLATE PATTERN

The interpretation we favor makes it easier to compare the apical architecture of *Pourtalesia miranda* and the typical holasteroid apical pattern. The same genital-ocular alternate pattern occurs in *P. miranda* as in a holasteroid such as *Stereopneustes relictus* (Fig. 3). Therefore apical plates of *P. miranda* can be identified on the grounds of

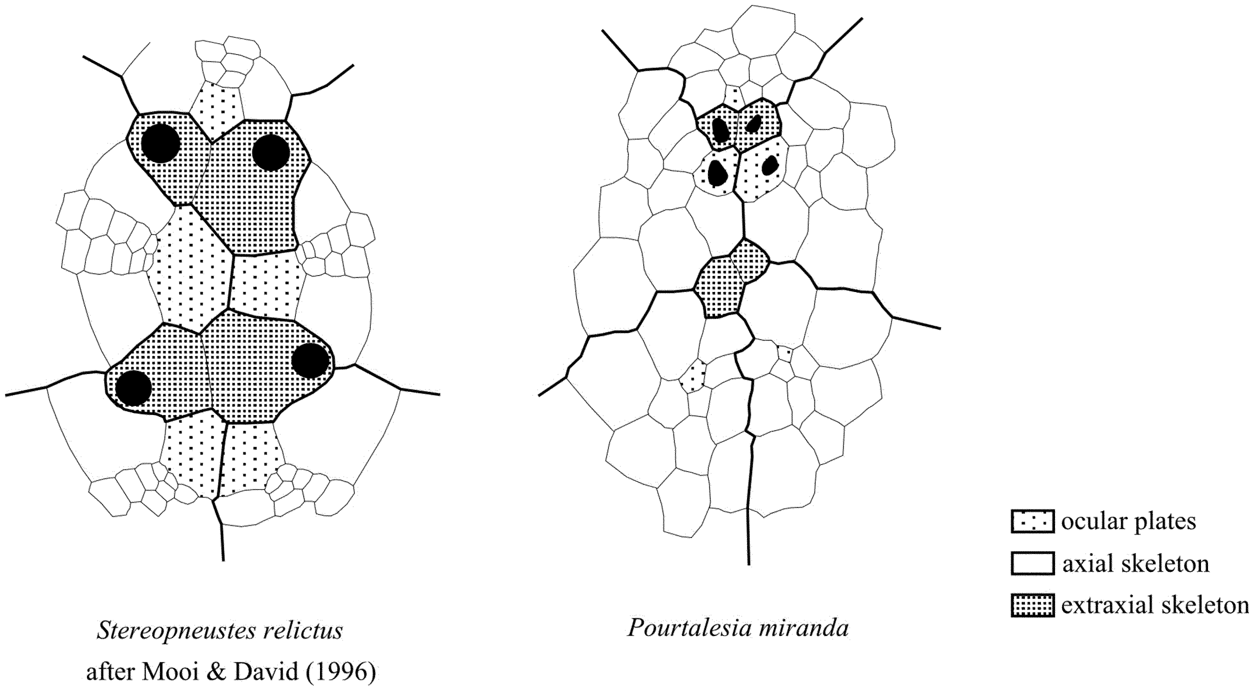

Figure 3. Comparison between the typical holasteroid apical system (here represented by *Stereopneustes relictus*) and the apical system of *Pourtalesia miranda*. Both display an alternating pattern between ocular and genital plates.

the homology between relative plate positions. However, compared with the holasteroid apical pattern, the apical system of *P. miranda* displays several peculiarities. Firstly, as already mentioned, posterior gonopores open in ocular plates rather than in genital plates. Secondly, the apical system appears broken into three units : (1) a trivium formed by the three anterior ocular plates and the two anterior genital plates; (2) two isolated and unperforated extraxial plates that must be homologous to the posterior genital plates of other holasteroids; (3) the two posterior oculars that are additionally separated one from the other.

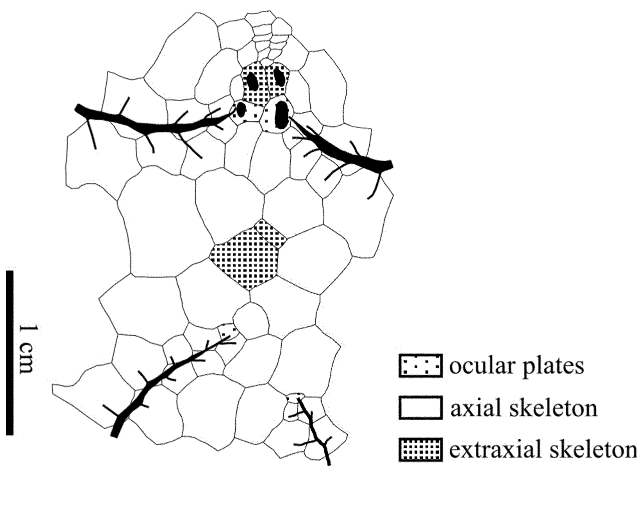

Figure 4. Internal view of a specimen of *Pourtalesia debilis*. Posterior gonopores open in the anterior paired ocular plates.

4 ANATOMICAL DATA

The internal view of a specimen of *P. debilis*, characterized by the same apical architecture as *P. miranda*, allowed us to map the water vascular vessels that run along their respective ambulacra. Their apical extremity ends in a terminal podium that always passes through an ocular plate. In this way, ocular plates can be easily and accurately identified by looking at the apical extremity of the water vessels. It is therefore evident that each of the two plates bearing the posterior gonopores are actually ocular plates (Fig. 4).

5 ONTOGENETIC DATA

Compared with a typical holasteroid apical system, the apical system of *Pourtalesia* is highly transformed by a series of disjunctions between ocular and genital plates. However, in the very first stage of the development, juveniles display a non-disrupted apical architecture, with disruptions appearing as growth proceeds.

At 3.1 mm in length, specimens display a classical holasteroid pattern, except for the absence of one anterior genital plate (Fig. 5a). The madreporic plate can be identified anteriorly by the presence of a single hydropore. Ocular plates can be identified at the apical extremity of their respective ambulacrum. Consequently, the two plates located between the anterior and the posterior ocular plates are the two posterior genital plates.

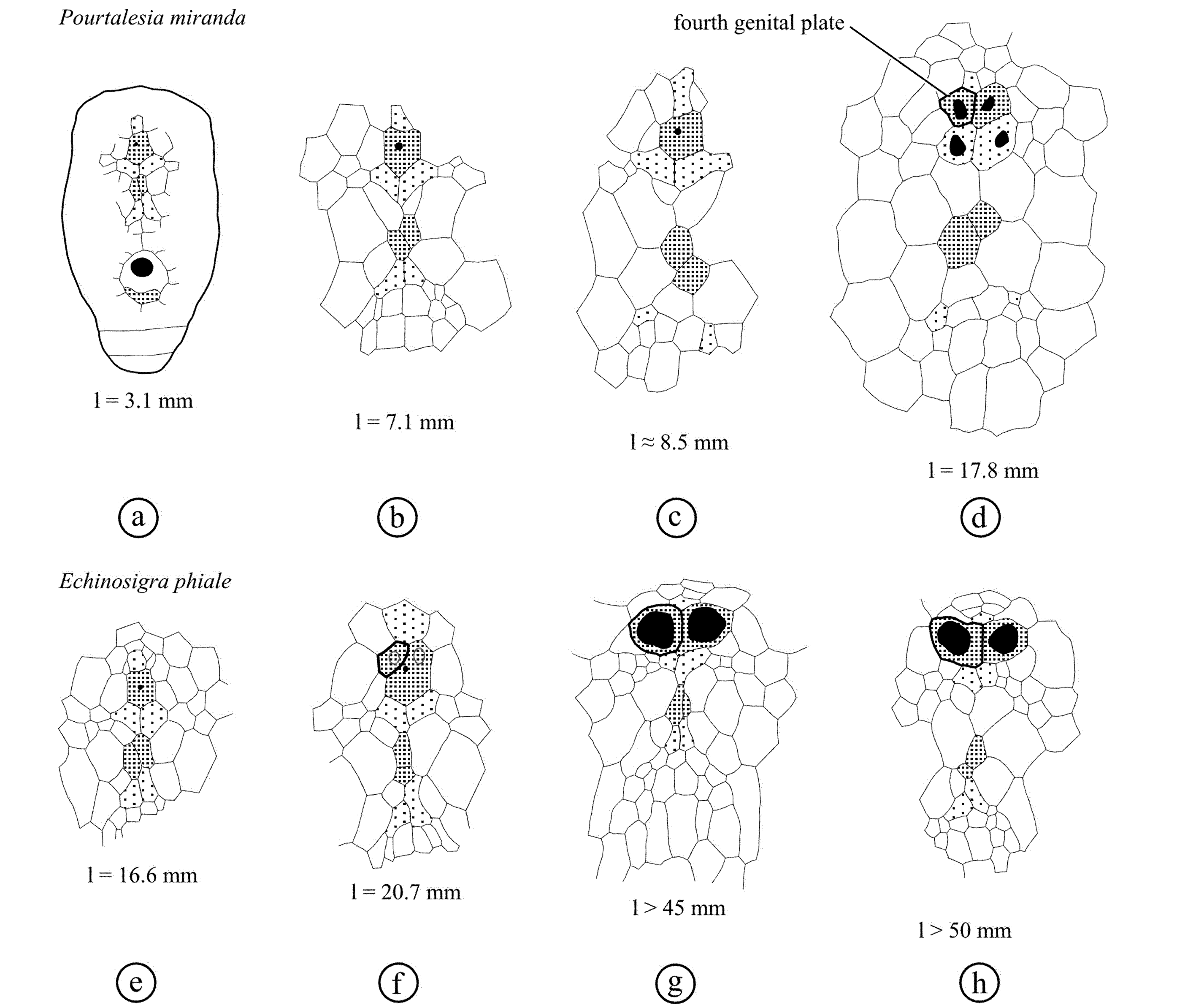

Figure 5. Ontogeny of the apical system in *Pourtalesia miranda* and *Echinosigra phiale*. In both apical systems, a fourth genital plate is formed when gonopores open. The triple disjunction of the apical system can be seen only in *Pourtalesia*.

The first disruption occurs in a specimen 7.1 mm long, and consists of a first disjunction between the anterior paired ocular plates and the two posterior genital plates (Fig. 5b). As a result, the apical system separates into an anterior unit (the trivium) and a posterior one (the bivium) associated with the two posterior genital plates.

At about 8.5 mm long, the apical elongation continues, and the posterior genitals separate from the bivium (Fig. 5c). This leads to the pattern observed in adult specimens. The double disjunction that separates the posterior ocular plates from the posterior genital plates, as well as the posterior oculars from each other, is complete.

Gonopores open at about 18 mm long (Fig. 5d), but the plate pattern observed at 8.5 mm does not undergo any change except for the appearance of a fourth, left anterior genital plate.

Hence the ontogeny of the apical system supports the plate homology established above. The last question remaining to be addressed is the absence in juvenile stages of the left anterior genital plate that appears only later in the ontogeny.

The survey of the 69 specimens of the BIOGAS sample does not provide us with any information that could answer this question. The data come instead from specimens of *Echinosigra phiale* also collected during the BIOGAS program. According to David (1990), the genus *Echinosigra* is the closest relative to *Pourtalesia*. The apical architectures of both are similar but only two gonopores are present in adult *Echinosigra*, ocular plates remaining unperforated. As in *P. miranda*, juveniles possess a single anterior genital plate (the madreporic plate) in which hydropores open, but two anterior genital plates can be seen in the adults.

At 16.6 mm long, the juvenile pattern observed in *Pourtalesia* remains evident (Fig. 5e). A specimen of 20.7 mm in length displays the exact stage at which gonopores open (Fig. 5f). The left gonopore opens in a plate located on the left anterior edge of the madreporic plate. The plate is enclosed by the madreporic plate, the anterior ocular plate, and the third and fourth growth zones, but is not in contact with the close ocular plate situated just posteriorly. However in larger specimens, this "*de novo* genital" enlarges without moving adorally, contacts the ocular plate situated posteriorly, and attains about the same size as the madreporic plate (Fig. 5g).

In accordance with the OPR and the degree of flexibility in the formation of extraxial elements, the "*de novo* genital" could be axial or extraxial. If it is considered axial, it must belong to growth zone III, and to interambulacral column 3.a. This axial interpretation would imply a kind of "locking" of the plate number in that column -- once formed, this plate grows without moving adorally. However, some specimens (Fig 5h) show that a new plate can be added to that half-interambulacrum (3.a) after this "*de novo* genital" has appeared in the series. This new interambulacral plate is positioned normally with respect to the rest of the interambulacrum. It is connected by its whole width to the adjacent adoral interambulacral plate, thus isolating the "*de novo* genital" to exclude it from the axial series. If this plate is considered extraxial, its sudden appearance would not contradict the EAT because extraxial elements can be formed at any time during the growth of echinoids. This is best illustrated by the development of periproctal scales, or by apical pouches in the brooding holasteroids *Antrechinus* (David & Mooi 1990, Mooi & David 1993).

6 PHYLOGENETIC DATA

Similar apical architectures can be seen in other genera of the family as well as in the sister-group, the Plexechinidae (Mooi & David 1996). This supports the interpretation we have given to the apical system of *Pourtalesia*, and shows that it is not an isolated phenomenon.

The pourtalesiid *Cystocrepis* displays the closest architecture to *Pourtalesia* within the family. Both anterior ocular plates are perforated by two gonopores as well, but in contrast to the situation in *Pourtalesia*, the plates are separated from each other.

Similar disjunctions affecting apical systems can also be observed in some plexechinids. This is particularly true for the species *Plexechinus cinctus*, *P. hirsutus* and *P. sulcatus*. However the family presents some peculiar patterns. In *P. sulcatus* the posterior genital plates are isolated from other apical elements as in Pourtalesiidae, but the posterior ocular plates remain connected together. Moreover a supplementary disjunction occurs between the anterior paired ocular plates and the anterior genital plates, although they are always connected in Pourtalesiidae.

7 PALEONTOLOGICAL DATA

The apical disruptions observed in *Pourtalesia* are not restricted to recent holasteroids. The extreme architecture observed in Pourtalesiidae may have its origins in the Paleocene genus *Galeaster*. On the basis of characters other than those of the apical system, this holasteroid is considered by Solovjev (1994) as basal for the family.

In *Galeaster*, the apical system displays some features in common with the recent members of the family: (1) Two gonopores open in the anterior ocular plates; (2) a simple disjunction separates the posterior ocular plates from the posterior genital plates. However, the madreporic plate seems to be the only anterior genital plate in which the anterior gonopores may open. Furthermore, the posterior genital plates are not yet isolated from the anterior part of the apical system.

Disjunctions are not as advanced in *Galeaster* as in *Pourtalesia*, but fossil data suggest that the phenomenon is already present in the earliest members of the family.

8 CONCLUSIONS

Our interpretation of the apical system of *Pourtalesia*, in accordance with the EAT and the growth zones model, sheds light on a very striking apical pattern. It is supported by a variety of evidence, i.e. plate homology with other holasteroids, anatomy of soft tissues, and anatomical, ontogenetic, phylogenetic, and paleontological data concerning plate architecture.

The body wall of echinoderms is composed of extraxial and axial elements. These two skeletal components are present in very different proportions among echinoderms. For example, in the Paleozoic camptostromatoids, the main part of the test is constructed of extraxial skeleton (Mooi & David 1998, David & Mooi 1999). The axial skeleton is represented only by narrow ambulacra. In asteroids the axial skeleton is more developed, but the extraxial part remains well-represented. The most apomorphic expression in the events leading to a reduction of the extraxial part of the skeleton is found in echinoids, in which almost all the test consists of axial skeleton.

In the context of the EAT, the genus *Pourtalesia* appears to represent an even more pronounced extreme in the reduction of the extraxial part of the body wall that is a hallmark of echinoids. First, two gonopores open through axial plates (the ocular plates) instead of through extraxial elements. Unperforated genital plates are not unknown in echinoids, as well illustrated by the genus *Leodia* (Clypeasteroida). However, in *Leodia*, gonopores open between axial plates (interambulacral plates in this case) but not through them, making Pourtalesiidae unique in this respect. The extreme is realized in some specimens of *Pourtalesia,* in which one posterior genital plate seems to be lacking.

It is not surprising that the extreme reduction of the extraxial part of the skeleton be realized in *Pourtalesia*. David (1990) has shown that pourtalesiid diversity is the expression of peramorphic trends. According to Mooi & David (1997) the reduction of the extraxial part of the skeleton in echinoids is also a peramorphic feature. Hence the evolution of the apical system of *Pourtalesia* caps a series of events that characterizes the overall history of the echinoids.

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