

Evolution to the extreme: origins of the highly modified apical system in pourtalesiid echinoids

THOMAS SAUCEDE^{1*}, RICH MOOI² and BRUNO DAVID¹

¹UMR CNRS Biogéosciences, Université de Bourgogne, 6 bd Gabriel, 21000 Dijon, France

²California Academy of Sciences, Golden Gate Park, San Francisco, California, USA

Received October 2002; accepted for publication June 2003

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. A new approach using the Extraxial–Axial Theory (EAT) that develops homologies for the Echinodermata is proposed. The exploration of apical plate patterns throughout ontogenetic sequences shows that the typical holasteroid pattern found in the youngest specimens undergoes a series of disturbances that result in a multiple disjunction accompanied by isolation or disappearance of certain genital plates. We propose a new interpretation of the apical architecture of the genus that agrees with: (1) the plate addition processes as predicted by the EAT; (2) patterns observed in other genera of the Pourtalesiidae as well as in its sister-group (plexechinids); and (3) the patterns known from Palaeocene 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. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 137–155.

ADDITIONAL KEYWORDS: apical system – deep sea – echinoid – Extraxial–Axial Theory – extreme morphology – plate architecture – Pourtalesiidae.

INTRODUCTION

THE EXTRAXIAL–AXIAL THEORY

According to Mooi, David & Marchand (1994), the body wall of echinoderms is constructed of two major components: axial elements and extraxial elements. This model, or EAT (for Extraxial–Axial Theory), describes a system of skeletal homologies among all echinoderms, and is supported by embryology (David & Mooi, 1996, 1998).

Most of the body wall of early Palaeozoic echinoderms is made of extraxial elements, with the axial part of their body wall generally restricted to a few components radiating from the mouth on the oral side of the test. In the context of the EAT, the evolutionary pattern for the phylum as a whole can be viewed as a reduction of the extraxial part of the skeleton, with a compensatory increase in the axial part. This evolutionary pattern reaches its extreme in echinoids,

because almost the entire test of echinoids consists of axial skeleton – the extraxial skeleton is 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 OPR (for Ocular Plate Rule). Following this mechanism, each growth zone is closely associated with an ocular plate and comprises an ambulacrum surrounded by two half-interambulacra, one on each side. New ambulacral and interambulacral plates are formed next to the ocular plate and move downwards to the oral side while they grow and as further plates are added behind.

THE FAMILY POURTALESIIDAE

The family Pourtalesiidae belongs to the order Holasteroidea (Mortensen, 1950), which includes, in part, heart urchins originating in the Early Cretaceous (David, 1988). With a worldwide distribution, the Pourtalesiidae contains seven extant genera, all of which are abyssal as with all other extant holasteroids. Pourtalesiids are bizarre sea

*Corresponding author. E-mail: thomas.saucede@u-bourgogne.fr

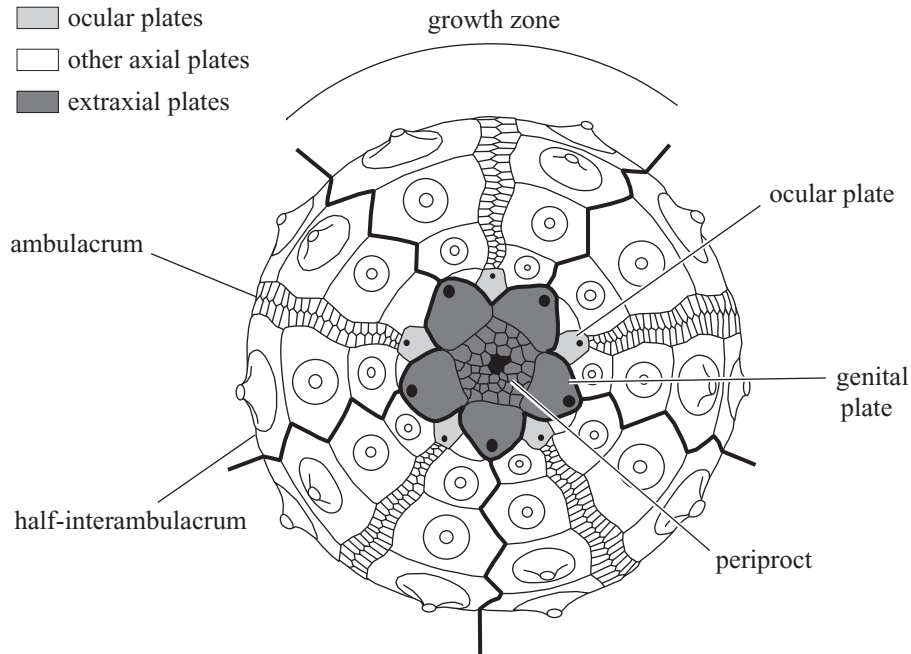


Figure 1. The axial and extraxial parts of a 'regular' echinoid's test. The axial skeleton constitutes almost the entire test and is organized into five growth zones. The extraxial skeleton is restricted to the scales present on the periproctal membrane and to the genital plates.

urchins whose most striking features are the strange shape and architecture displayed by each genus. They are easily distinguished by the general features of their tests, by the architecture of the oral side, and by pedicellariae. Previous work, particularly on oral surface plate patterns (Mironov, 1978; David, 1985, 1987, 1990; Gage, 1987; Mooi & David, 1996), has revealed a unique plate pattern that departs drastically from the classical five-fold radiating architecture of most echinoids (see former investigations of the oral side in David, 1985, 1987, 1990), but little work has focused on the aboral side (Agassiz, 1881, 1904; Lovén, 1883; Saucède *et al.*, 2003).

Recently, Saucède *et al.* (2003) demonstrated the strangeness of pourtalesiid aboral architecture, particularly that of the apical region, and proposed a new interpretation of plate homology in the apical system of the genus *Pourtalesia*. A series of disjunctions separates the apical system into three parts and isolates the posterior genital and ocular plates from the rest of the apical system. More surprisingly, posterior gonopores open in ocular plates (that is in the axial skeleton) rather than in genitals (extraxial skeleton). The identification of such atypical plate patterns invites investigation of the origin of extreme morphologies in pourtalesiids as well as questions concerning the evolution of the clade and its relationships with other holasteroid groups.

ESTABLISHMENT OF POURTALESIID APICAL DISRUPTIONS

We studied a large number of juvenile specimens of *Pourtalesia* and *Echinosigra* obtained by dredging during the INCAL and BIOGAS deep-sea programmes. These samples afforded us an opportunity to explore the ontogeny of the apical system and the establishment of disruptions that take place in the apical systems of pourtalesiids, leading to a better understanding of the adult apical architecture and setting the peculiarities of the apical system of pourtalesiids in the context of apical evolution of extant holasteroids. Interpreting the apical system of pourtalesiids through the EAT, particularly with regard to the expression of the extraxial skeleton, should lead to placement of the pourtalesiids in the overall evolutionary pattern of irregular echinoids, as well as the Echinodermata in general.

MATERIALS

POURTALESIA AND *ECHINOSIGRA*

Pourtalesia and *Echinosigra* are the two best-known genera of the Pourtalesiidae, thanks to material collected over a period of more than a century. Together they constitute the basic material from which plate architectures and homologies were originally determined by us, and from which conclusions were made

and confirmed by study of other members of the family.

The genus *Pourtalesia* is the most diverse, including a dozen species. Specimens of eight of these species (Table 1) were examined in collections at the University of Burgundy (Dijon, France) and the California Academy of Sciences (San Francisco, USA). The most interesting sample consisted of 69 specimens of *Pourtalesia miranda* (Agassiz, 1869) collected during the

BIOGAS programme (1972–1981) in the southern part of the Bay of Biscay (north-east Atlantic) at a depth of 2100 m. Ranging from 1 to 21 mm in length, these specimens provided an opportunity to describe the ontogeny of the apical system and to explore its plate organization and homologies.

About 100 juveniles and adult specimens of *Echinosigra phiale* (Thomson, 1873), plus numerous fragments, collected during the INCAL programme

Table 1. Origin of extant and fossil specimens surveyed in the study

Studied species	Observed specimens	Studied literature
Pourtalesiids		
<i>Pourtalesia miranda</i>	69 juvenile and adult specimens – BIOGAS (Bay of Biscay) and INCAL (Rockall Trough) programmes	Agassiz (1904)
<i>Pourtalesia laguncula</i>	4 juvenile and adult specimens – <i>R/V Albatross</i> (off the coasts of Japan and California)	Lovén (1883)
<i>Pourtalesia aurorae</i>	3 juvenile and adult specimens – ANTARKTIS VII, EPOS 3 cruise (Weddell Sea)	Koehler (1926)
<i>Pourtalesia alcocki</i>	15 adult specimens – EUMELI cruise (East Atlantic)	Koehler (1914)
<i>Pourtalesia wandeli</i>	2 adult specimens – WALDA cruise (Angola Basin)	
<i>Pourtalesia debilis</i>	2 adult specimens – <i>R/V Marion Dufresne</i> MD 03 (South Indian Ocean) and MD 04 (Kerguelen) cruises	Koehler (1926)
<i>Pourtalesia tanneri</i>		Agassiz (1904)
<i>Pourtalesia heptneri</i>		Mironov (1974a)
<i>Pourtalesia jeffreysi</i>	29 adult specimens – NORBI cruise (Norwegian Sea)	Lovén (1883)
<i>Echinosigra phiale</i>	100 juvenile and adult specimens – INCAL and BIOGAS programmes; <i>R/V Challenger</i> cruise (Rockall Trough)	Agassiz (1881)
<i>Helgocystis carinata</i>		
<i>Spatagocystis challengeri</i>		Agassiz (1881); Mironov (1978)
<i>Echinocrepis rostrata</i>		Mironov (1973)
<i>Ceratophysa ceratopyga</i>		Lovén (1883); Mironov (1976)
<i>Cystocrepis setigera</i>	1 adult specimen – collections of the California Academy of Sciences (San Francisco)	Agassiz (1904)
Extant holasteroids		
<i>Plexechinus planus</i>	A dozen adult specimens – ANTARKTIS VII, EPOS 3 programme	Mironov (1978); Mooi & David (1996)
<i>Plexechinus cinctus</i>		Agassiz (1904)
<i>Plexechinus sulcatus</i>		David & Mooi (2000)
<i>Plexechinus hirsutus</i>	1 adult specimen – collections of the California Academy of Sciences San Francisco)	Lovén (1883); Agassiz (1904);
<i>Urechinus naresianus</i>		Mooi & David (1996)
<i>Urechinus antipodeanus</i>		Mooi & David (1996)
<i>Calymne relicta</i>		R. Mooi (pers. comm.)
Fossil holasteroids		
<i>Basseaster rostratus</i>		Solovjev (1994)
<i>Pomaster parvus</i>		Solovjev (1994)
<i>Galeaster sumbaricus</i>		Poslavskaja & Moskvina (1960); Solovjev (1994)
<i>Galeaster minor</i>		Poslavskaja & Moskvina (1960);
		Solovjev (1994)
<i>Galeaster carinatus</i>		Solovjev (1994)
<i>Galeaster dagestanensis</i>		Solovjev (1994)

(Porcupine Seabight, north-east Atlantic), made up another excellent sample by which to study the ontogeny of apical architecture (Table 1).

OTHER POURTALESIIIDS

All the other genera of the family are monospecific (except for the two species attributed to *Echinocrepis*), and are known from very few specimens (see David, 1990, for a review). Fortunately, illustrations and descriptions of the apical system can be found in the literature for each genus (see Table 1). Although the interpretation of apical architecture sometimes relies on only a few drawings, these could be revised and corrected in some cases. For example, apical systems of *Ceratophysa* and *Echinocrepis*, poorly illustrated by Agassiz (1881), were re-examined by Lovén (1883) who produced completely different and far more accurate drawings. However, this is not the case for every species, and for some genera, such as *Helgocystis*, the only available data consist of imprecise descriptions or figures. Another difficulty comes from the small number of individuals available for many species, preventing analysis of intraspecific variation.

The only other direct observations we have been able to make were on a specimen of *Cystocrepis setigera* (Agassiz, 1898) dredged off the coast of Oregon (Table 1). Another specimen of *Cystocrepis* dredged by the *R/V Albatross* was described and figured by Agassiz (1904). *Helgocystis carinata* (Agassiz, 1879) is known from very few specimens, and the only description and drawing of the apical system can be found in Agassiz (1881). A specimen of *Ceratophysa ceratopyga* (Agassiz, 1879) dredged by the *Challenger* was described by Agassiz (1881), but the drawing of the apical system is confusing and different from the revised figure of Lovén (1883), which is of a better quality and is considered herein as correct. Drawings of the apical systems of six other specimens of *Ceratophysa* can be found in Mironov (1973, 1976). *Echinocrepis cuneata* (Agassiz, 1879) was described by Agassiz (1881) but, as for *Ceratophysa*, the drawing of the apical system was greatly improved by Lovén (1883). Mironov (1973, 1976) described and drew the apical systems of two specimens of *Echinocrepis rostrata* (Mironov, 1973). Specimens of *Spatagocystis challengerii* (Agassiz, 1879) were dredged on two occasions a century apart. One of the specimens from the *Challenger* was described by Agassiz (1881), but the drawing of the apical system of another specimen was very different (Agassiz, 1904). The first drawing is barely interpretable. Indeed, Agassiz (1904) recognized that details were not sufficiently brought out in the first illustrations, and Mortensen's (1950) description agrees with the second drawing. For these reasons, the first descriptions will not be considered here.

The apical system of a *Spatagocystis* collected during the 16th cruise of the *R/V Mendeleyev* was described and drawn by Mironov (1978). Finally, Mironov (1996) described the new monotypic genus *Rictocystis*, and illustrated the apical system of *Rictocystis jensenae* (Mironov, 1996). He considers *Rictocystis* as morphologically similar to *Echinosigra* and *Helgocystis*. However, the morphology of these two genera is very different, making this statement difficult to interpret. This means the genus cannot be considered here.

THE SISTER-GROUP

Apical disjunctions are also observed in some plexechinid and urechinid sea urchins. Both families consist of extant abyssal holasteroids that arose at the end of the Cretaceous (David, 1988; Solovjev, 1994) and constitute the sister-group of the Pourtalesiidae–Calymnidae clade (Mooi & David, 1996). Apical disjunctions are well documented in the literature for *Plexechinus cinctus* (Agassiz, 1898), *Plexechinus hirsutus* (Mortensen, 1905), *Plexechinus sulcatus* (David & Mooi, 2000), *Plexechinus planus* (Mironov, 1978), *Urechinus naresianus* (Agassiz, 1879) and *Urechinus antipodeanus* (McKnight, 1974) (Table 1). The species *Calymne relictata* (Thomson, 1877) is the only representative of the Calymnidae (Mortensen, 1907), a family considered to be the closest to the Pourtalesiidae (Mooi & David, 1996; David & Mooi, 2000). Apical disjunctions have been noted in the apical architecture of this species as well (Table 1).

DATA FROM FOSSILS

Except for seven poorly preserved specimens from the Middle Miocene of Japan (Kikuchi & Nikaido, 1985) attributed to *Pourtalesia*, pourtalesiids are unknown in the fossil record. However, it might still be possible to establish approximate times of origin for the peculiarities of pourtalesiid apical systems by determining whether they could already be present in fossil echinoids close to the family.

Palaeontological affinities of the family have been discussed since the time of its discovery. Lovén (1883) emphasized the fact that the apical disjunctions of the Pourtalesiidae were reminiscent of those found in *Collyrites*, particularly because he interpreted isolated posterior genital plates as homologous to the supplementary plates present in disasteroids. Mortensen (1950) also derived the Pourtalesiidae from Disasteridae, via *Cardiolampas*, because of the apical disjunctions and the vertical position of the peristome. Poslavskaya & Solovjev (1964) were the first to show close affinity between Pourtalesiidae and the Late Cretaceous holasteroid *Galeaster*. However, for Mintz (1966), the origin of Pourtalesiidae from *Galeaster* or

any other holasteroid is not easier to support than an origin from the disasteroids. However, this was based on a misunderstanding of apical disjunctions that Mintz considered homologous both in pourtalesiids and in disasteroids. Solovjev (1974, 1994) proposed *Galeaster* as the first pourtalesiid, as well as the genera *Basseaster* (a corystid according to Foster & Philip, 1978) and *Pomaster* as the first urechinid. David (1988) presented a cladistic analysis that supported the Late Cretaceous origin of Pourtalesiidae from a group of holasteroids that includes *Stegaster*, *Galeaster* and *Guettaria*. We follow Solovjev (1974, 1994), and consider the genera *Basseaster*, *Pomaster* and *Galeaster* as plausible stem-groups for Recent holasteroids. Apical systems of species attributed to these three genera were studied from descriptions and drawings found in the literature (Table 1).

RESULTS

PROBLEMATIC PLATE HOMOLOGY IN POURTALESIID APICAL SYSTEMS

Interpreting the plate architecture of the apical region of *Pourtalesia* is not straightforward (Fig. 2A). Mooi & David (1997) showed that the OPR and the growth zone concept could advance understanding of the apical architectures in echinoids. The first step in the interpretation consists of the identification of the axial part of the skeleton, that is to say the five growth zones and the five ocular plates heading them. Determination of growth zone boundaries has to agree with the OPR, which implies that ocular plates are expected at the apical extremity of their respective ambulacrum, and that a given ocular plate cannot be surrounded by more than one row of interambulacral plates in a growth zone. The second step consists of the identification of extraxial elements, particularly genital plates (that is, plates that cannot fit into any growth zone). In spite of this precise methodology, two hypotheses arise to explain the apical architecture of *Pourtalesia*.

In the first hypothesis, the growth zone boundaries isolate two plates in the centre of the apical system (Fig. 2B). These two plates must be identified as extraxial because their independence from any growth zone implies that their placement does not follow the OPR. Finally, the four central plates in which gonopores open are likely to be four genital plates. The classical interpretation proposed by Lovén (1883) and Mortensen (1950) fits this pattern, except that they regarded the two isolated extraxial plates as additional plates detached from interambulacrum 5.

In the second hypothesis, growth zone boundaries are identified slightly differently (Fig. 2C). The same two extraxial plates are excluded from growth zones,

but they are now identified as genital plates without gonopores, and the two plates bearing the posterior gonopores are interpreted as ocular plates (i.e. axial skeleton). Although it is unusual to have gonopores opening in the axial part of the skeleton, we retain this second hypothesis because it is supported by: (1) the anatomical survey of the water vascular system; (2) the comparative study of the apical system of *Pourtalesia* and the conservative apical pattern that characterizes all holasteroids; and (3) the study of the ontogeny of apical systems in *Pourtalesia* and *Echinograna*.

THE WATER VASCULAR SYSTEM

Inside views of specimens of *Pourtalesia alcocki* (Koehler, 1914) and *Pourtalesia debilis* (Koehler, 1926) allowed a survey of the water vascular vessels that run along their respective ambulacra. The axial skeleton, and particularly the ambulacra, are closely associated with the water vascular system (David & Mooi, 1996). Indeed, during growth, tube-feet are budded off from each vessel one by one as ambulacral plates are laid down above and grow around the tube feet (Gordon, 1926a,b). The apical extremity of each water vascular vessel ends with a terminal tentacle (primary podium) that always crosses the associated ocular plate. New axial elements (ambulacral and interambulacral plates) always appear close to the terminal tentacle in such a way that each tentacle + ocular set heads a growth zone (David & Mooi, 1999). In this way, ocular plates can be easily and accurately identified by looking for the apical extremity of the radial vessels. It is clear that, in *Pourtalesia*, vessels of the ambulacra II and IV end on the two plates that also bear the posterior gonopores (Fig. 3). Such anatomical observations strongly support the hypothesis suggesting that posterior gonopores do open in ocular plates II and IV rather than in genitals.

COMPARISON WITH THE CLASSICAL HOLASTEROID PLATE PATTERN

All holasteroids share a common basic apical pattern called an intercalary apical system. In this type of apical system, ocular plates II and IV meet at the mid-line so as to separate anterior and posterior parts of the system (Durham & Wagner, 1966). The interpretation we have favoured makes it easier to compare the apical architecture of *Pourtalesia* and the typical intercalary apical systems of holasteroids such as that in *Stereopneustes relictus* (de Meijere, 1902) (Fig. 4). According to this hypothesis, the antero-posterior distribution of the apical plates of *Pourtalesia* fits the typical holasteroid pattern: ocular plates II and IV do meet at the mid-line, separating anterior genital plates from posterior ones. However, this arrangement is remarkable

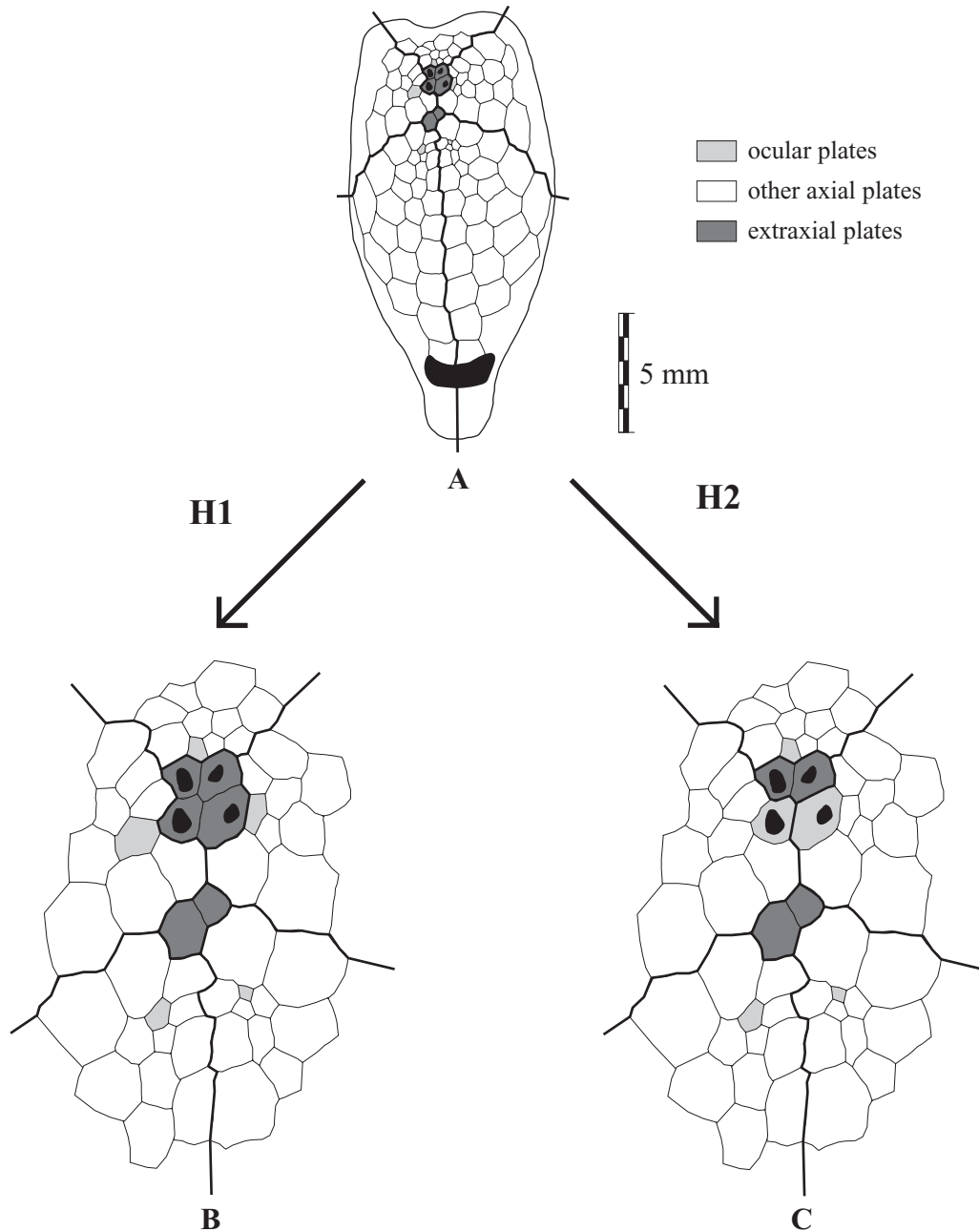


Figure 2. Two hypotheses that can be used to explain the apical architecture of *Pourtalesia*. In the first hypothesis, the four central plates in which gonopores open are interpreted as four genital plates. In the second hypothesis, the two plates bearing the posterior gonopores are identified as ocular plates.

in two aspects. First, as already mentioned, posterior gonopores open in ocular plates and not in genital plates. Second, the apical system appears to be broken into three units: (1) a trivium formed by the three anterior ocular plates (oculars II, III and IV) and the two anterior genital plates (genitals 2 and 3); (2) two isolated and unperforated extraxial plates that are homologous to the posterior genital plates of other

holasteroids (genitals 1 and 4); (3) two posterior oculars (oculars I and V) that are separated from each other.

ONTOGENETIC DATA

Apical disjunctions

Compared with the typical holasteroid apical system, the apical system of an adult *Pourtalesia* is highly

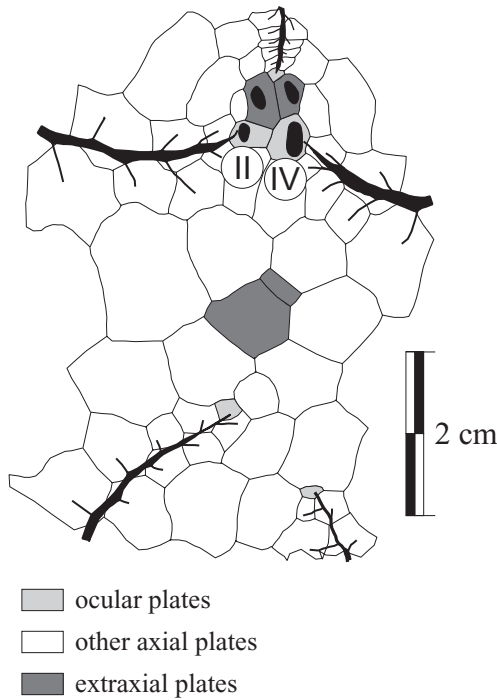


Figure 3. The water vascular system of *Pourtalesia*. Each vessel ends with a terminal tentacle that crosses the associated ocular plate. Vessels of the ambulacra II and IV end on ocular plates II and IV, which also bear the posterior gonopores.

transformed by a series of disjunctions between ocular and genital plates. However, the survey of the BIOGAS sample of *P. miranda* as well as of two young *Pourtalesia laguncula* (Agassiz, 1879) shows that in the very first stages of development, juveniles of *Pourtalesia* display an undisrupted apical architecture, and that disruptions become progressively more marked during growth.

At 3.1 mm long, specimens of *P. miranda* display a typical holasteroid pattern, except for the absence of one anterior genital plate (Fig. 5A). The madreporic plate (i.e. genital 2) can be identified in the anterior part of the apical system by the presence of a single hydropore. An ocular plate can be recognized at the apical extremity of each ambulacrum. It follows that the two plates located between the anterior and the posterior ocular plates are the two posterior genital plates.

Disruption of this pattern was observable in a specimen as small as 7.1 mm long, and consists of a disjunction between the anterior paired ocular plates (II and IV) and the two posterior genital plates (1 and 4) (Fig. 5B). As a result, the apical system separates into an anterior unit (the trivium) and a posterior one (the bivium) that includes the two posterior genital plates.

At about 8.5 mm long, apical extension has continued so that the posterior genitals separate from ocular plates I and V (Fig. 5C). This leads to the pattern observed in adult specimens. Disjunctions that sepa-

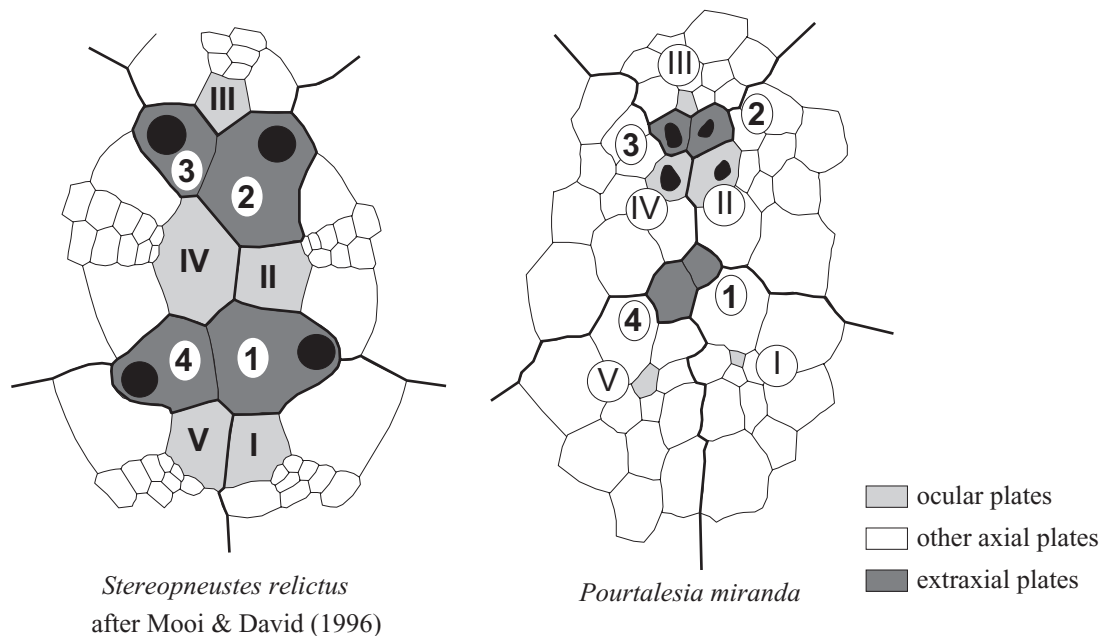


Figure 4. Comparison between the apical architecture of *Pourtalesia* and the plesiomorphic intercalary apical system of *Stereopneustes relictus*. The apical system of *Pourtalesia* appears to be broken into three units.

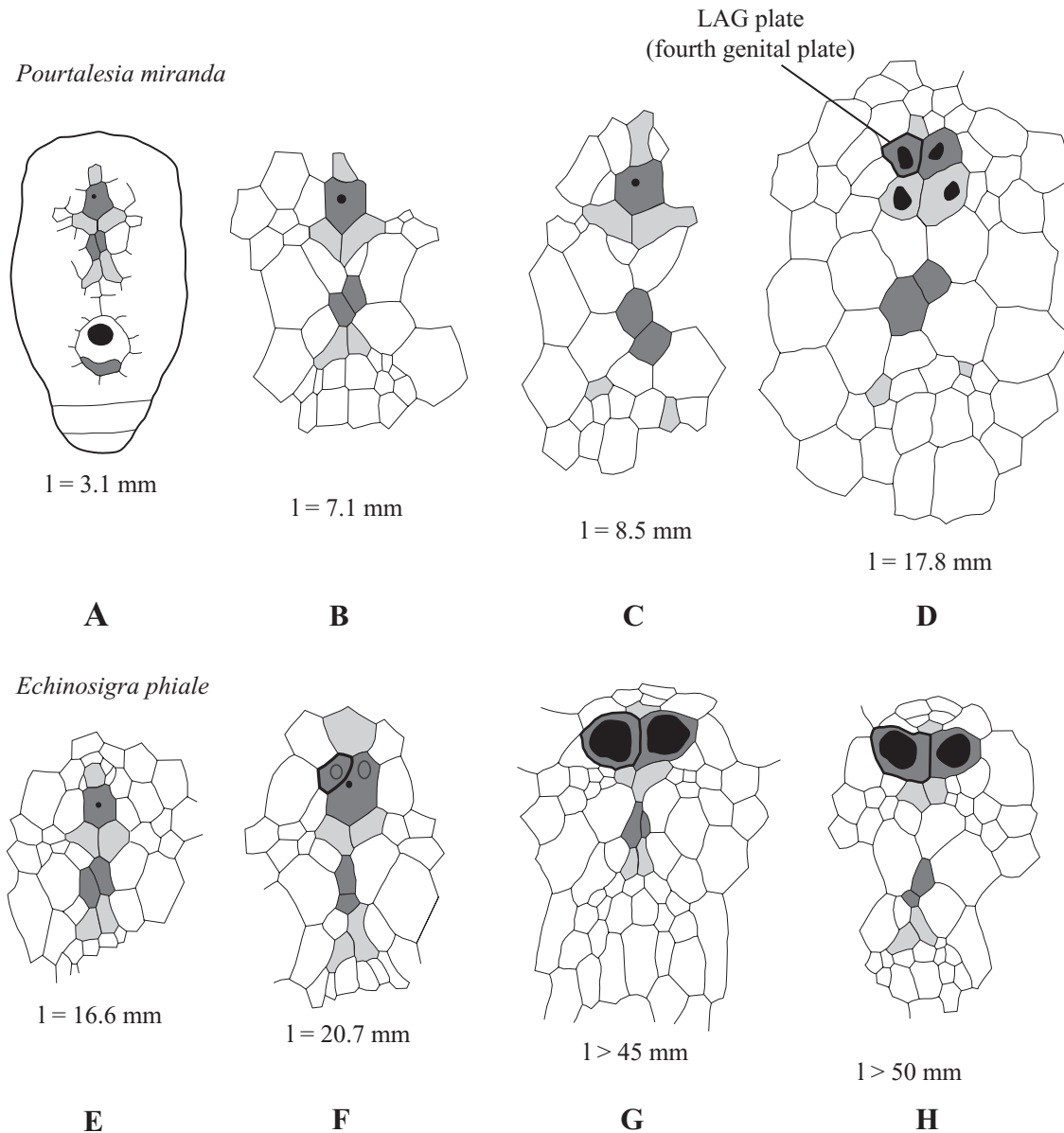


Figure 5. Disruptions of apical architectures and the appearance of the LAG (late-appearing, genital-like) plate during growth of *P. miranda* and *E. phiale*. In the very first stages of the development of *Pourtalesia* and *Echinosisgra*, juveniles have an undisrupted apical architecture, comparable with the plesiomorphic intercalary state. Apical disjunctions occur during subsequent growth (l = length).

rate the posterior ocular plates from the posterior genital plates, as well as the posterior oculars from each other, are achieved.

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 the fourth genital plate.

Therefore, isolation of posterior genitals is attained by disjunctions that occur in a relatively short span of growth in *Pourtalesia*.

The late-appearing, genital-like plate

Arguably the greatest challenge in interpreting plate homologies in the apical systems of pourtalesiids, so far uninvestigated, is the absence in juvenile stages of a plate in the left anterior region of the apical system that would normally be occupied by a genital plate. This plate, the late-appearing, genital-like (LAG) plate, appears relatively late in ontogeny, after the other gonopores have already opened. To determine the details of the processes by which the LAG plate

originates, appropriate stages of development are needed. Survey of the 69 *Pourtalesia* of the BIOGAS sample reveals the phenomenon itself, but does not provide specimens that show an architectural pattern at the precise moment of the appearance of the LAG plate. Instead, this information comes from the specimens of *E. phiale* collected during the INCAL and the BIOGAS programmes. According to David (1990), the genus *Echinostigma* is most closely related to *Pourtalesia*. Because both *Echinostigma* and *Pourtalesia* possess paired plates in the apical portion of interambulacrum 5, these two genera are not only closely related, and are most likely to be sister groups (David, 1985). Apical architectures of both genera are very similar but only two gonopores are present in adults of *Echinostigma*; ocular plates II and IV lack genital openings. As in *Pourtalesia*, juveniles of *Echinostigma* possess a single anterior genital plate, but in the adults, two anterior plates with gonopores develop. In juveniles, the single anterior genital is perforated by hydropores that permit its identification as the madreporic plate.

The juvenile pattern in *Echinostigma* is observed up to a test length of 16.6 mm (Fig. 5E). A specimen 20.7 mm in length represents the exact stage at which gonopores open (Fig. 5F). The last gonopore opens in a plate located on the left anterior edge of the madreporic plate. This is the LAG plate, and is contiguous with, and completely surrounded by, the madreporic plate, the anterior ocular plate, and the plates of the third and fourth growth zones. Notably, the LAG plate is not in contact with the ocular plate, which is situated just posteriorly. However, in larger specimens, the LAG plate enlarges without moving adorally, contacts the aforementioned posterior ocular plate and attains approximately the same size as the madreporic plate (Fig. 5G).

Two important factors of the EAT carry special implications for the origin of the LAG plate. These are: the OPR; and a special, empirically determined property of extraxial elements that shows that they are subject to considerably more evolutionary lability than is commonly observed for axial elements. Accordingly, the ontogenetic behaviour of the LAG plate bearing gonopore 3 exhibits properties of both axial and extraxial elements.

If the LAG plate is considered as axial, it must belong to growth zone III, and consequently to interambulacral column 3a. This axial interpretation would imply a kind of 'locking' of the plate number in that column – once formed, the LAG plate would have to grow without moving adorally, and no new plates would be added to that column. However, the largest specimens (Fig. 5H) show that additional plates are added aborally to half-interambulacrum 3a long after the LAG plate has appeared in the series. These new interambulacral plates are positioned normally in full

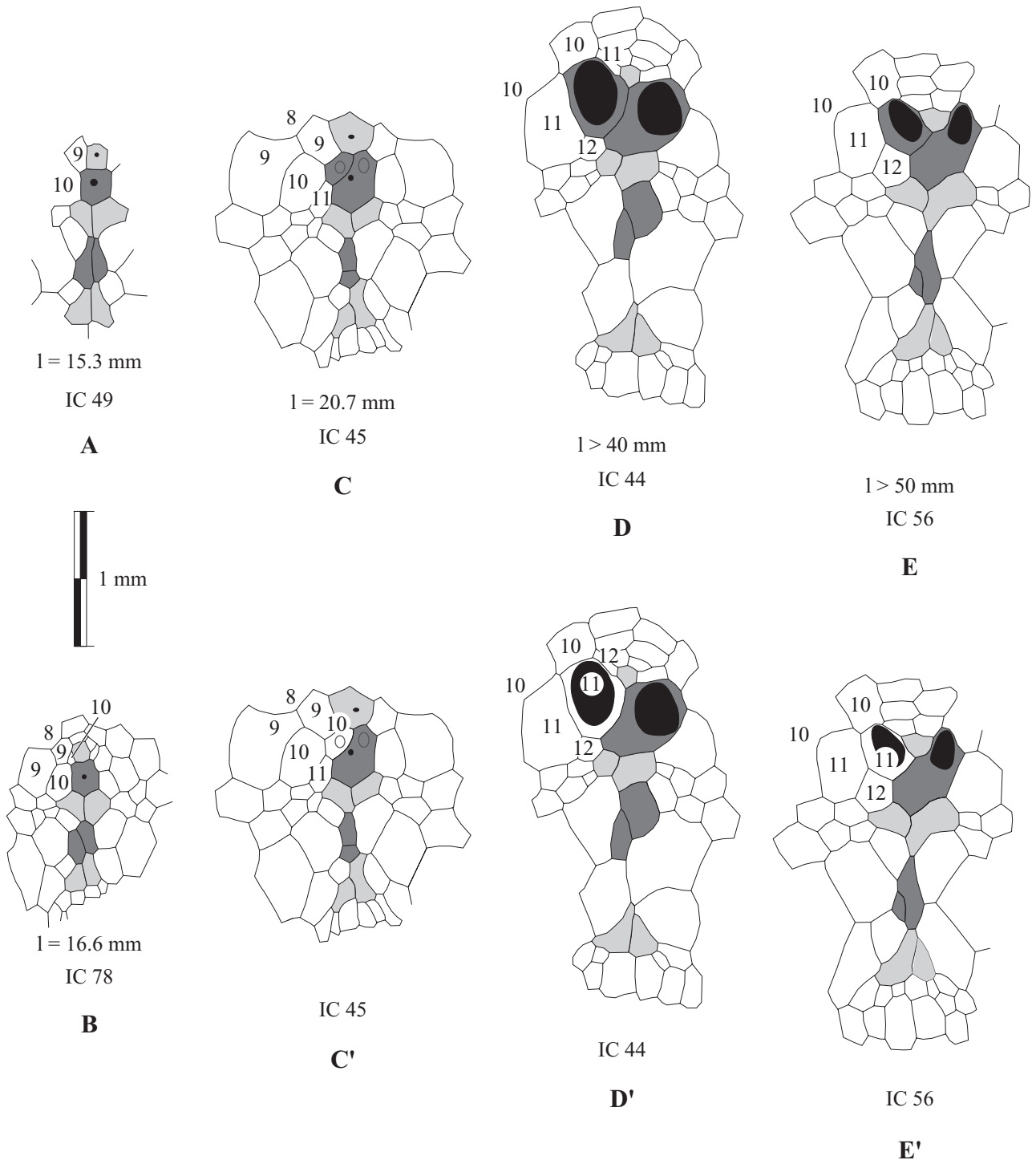
accord with the OPR as well as with respect to the rest of the interambulacrum. In addition, they are connected by their whole width to the adjacent adoral interambulacral plates, thereby isolating the LAG plate, and excluding it from the axial series.

If the LAG plate is considered as extraxial, its sudden appearance would not contradict the EAT because extraxial elements can be formed at any time during growth of echinoids. This is best illustrated by the development of periproctal scales, or by apical pouches in the brooding holasteroid *Antrechinus* (David & Mooi, 1990; Mooi & David, 1993).

In order to test whether the LAG plate should be interpreted as axial or extraxial, we counted the number of plates present in interambulacral columns 3a and 3b in their order of appearance (from the peristome to the apical system). In addition, we checked whether the formation of the LAG plate affects the order of plate alternation between the interambulacral columns. In other words, does the LAG plate fit logically into interambulacral column 3a with respect to the order of plate alternation?

Plate counts were made on 17 specimens of *Echinostigma* ranging from 15.3 mm to 48.4 mm in length. The numeration adopted is the Lovénian label for the interambulacral column (3a for the more anterior column and 3b for the posterior one), followed by the count for the plates present in that column ('3a.n' would therefore be the plate count for column 3a). As already mentioned by David (1987, 1988), *Pourtalesia* and *Echinostigma* are holomeridoplacous. This is a special condition in which the first two interambulacral plates (the plates closest to the peristome) are unpaired. However, because of the alternation of plate formation between the interambulacral columns, each of these plates belongs to a different growth zone. The regular alternation observed in the rest of the interambulacrum suggests that the first interambulacral plate would belong to column 3b (plate notation 3b.1) and the second one to column 3a (plate notation 3a.1).

Plates were counted in two juvenile specimens in which gonopores are not yet open and the LAG plate not yet formed (Fig. 6A, B). The last formed interambulacral plates closest to the oculars are 3a.9/3b.10 in specimen IC 49, which was 15.3 mm long (Fig. 6A). The same plates were 3a.10/3b.10 in specimen IC 78, which was 16.6 mm long (Fig. 6B). Specimen IC 45 displays the precise stage at which gonopores open and possesses two anterior plates pierced by gonopores. This specimen is 20.7 mm long and the last interambulacral plates would be 3a.9/3b.11, if the LAG plate is considered as extraxial (Fig. 6C), and 3a.10/3b.11 if the LAG plate is considered as the last axial interambulacral plate (Fig. 6C'). In larger specimens up to 55 mm in length, plate number increases up to 3a.10/3b.12 or 3a.11/3b.12 when the LAG plate is



Echinostigma phiale

Figure 6. Plate counts on specimens of *E. phiale*. A–E, LAG interpreted as extraxial; C'–E', LAG interpreted as axial. The appearance of the LAG plate close to ocular III separates the last plates formed in columns 3a and 3b, thereby delaying plate formation in column 3a relative to that in column 3b (l = length).

considered as extraxial (Fig. 6D, E), or to 3a.11/3b.12 or 3a.12/3b.12 if it is considered as axial (Fig. 6D', E'). These numbers are relatively stable across the majority of specimens. Therefore, the maximum number of interambulacral plates (n) present in columns 3a/3b switches from between (n/n) and $(n/n + 1)$ according to the axial hypothesis, to between $(n/n + 1)$ and $(n/n + 2)$ following the extraxial hypothesis.

If the LAG plate is axial, then it most logically becomes a part of interambulacral column 3a. Under this hypothesis, there is a maximum difference of one plate between columns 3a and 3b (11 vs. 12) (Fig. 6E'). This can easily be explained by the fact that the last plate of column 3a (3a.12) is not yet formed. This also suggests that the last interambulacral plate has appeared in column 3a. This fits logically with the alternating pattern of plate formation, because the first plate is formed close to the peristome in column 3b. However, the fact that the opening of the gonopore does not stop the addition of new plates constitutes a major argument against the axial hypothesis. If the LAG plate is considered an interambulacral plate, it necessitates two contradictions of major axioms of the EAT: first, it introduces a gonopore to an axial element; and second, it violates the OPR, as this axial element is isolated from its contiguous chain without disturbing the addition or migration of new plates behind the newly formed LAG plate.

By contrast, if the LAG plate is considered to be extraxial, the significant number of specimens displaying the maximum number of 11 plates in column 3a, against 12 in column 3b, does not depart from the 'normal' model of an asymmetric cessation of plate addition according to the formula $(n/n + 1)$ between the adjacent growth zones III and IV. However, some specimens display a difference of two plates between columns 3a and 3b (10 vs. 12). This implies a sudden lag $(n/n + 2)$ in the asymmetric timing of plate formation (Fig. 6E). In addition, comparison of specimens IC 45 and IC 78 suggests that the appearance of the LAG plate severely disrupts the addition of new plates in column 3A. These specimens are close in size with their gonopores not yet open, but whereas specimen IC 45 has two genitals and asymmetric interambulacral plate numbers (3a.9/3b.11), specimen IC 78 has no LAG plate and symmetric interambulacral plate numbers (3a.10/3b.10).

In theory, plate number can differ between interambulacral columns 3a and 3b, without contradicting the OPR. Indeed, interambulacral columns 3a and 3b belong to two different and independent growth zones (zones III and IV) that may produce a different number of plates in their interambulacral columns. Differences can arise especially when these columns are no longer in contact, which is the case when the LAG plate forms and separates the last interambulacral

plates of columns 3a and 3b. Moreover, McNamara (1987, 1990) and David (1985, 1987, 1990) have emphasized the importance of 'sliding' between adjacent plates in spatangoid sea urchins and in *Pourtalesia* – a phenomenon that McNamara terms 'plate translocation'. Plate translocations imply a certain independence of adjacent columns. According to McNamara, plate translocations have been recorded between plates of adjacent ambulacral and interambulacral columns (*Breynia desorii*, *Echinocardium cordatum*), between plates of adjacent interambulacral columns (*Lovenia woodsi*, *Protenaster australis*), between plates of adjacent ambulacral columns (*Pericostmus*, *Faorina*, *Eupatagus*, *Breynia*, *Echinocardium*, *Schizaster*) and between apical plates (*Echinocardium cordatum*, *Micraster coranguinum*). David (1987) has demonstrated that significant translocation occurs between ambulacral plates on the oral side of *P. miranda*. In our study, the different number of plates recorded between interambulacral columns 3a and 3b is not an exception among sea urchins and therefore does not contradict our hypothesis that the LAG plate is of extraxial origin.

In conclusion, the hypothesis that the LAG plate is extraxial remains the most parsimonious one because it does not contradict the OPR and the EAT, and because the perturbation in the number of plates produced in column 3a is easily interpreted as a phenomenon that does not disagree with any of the known ontogenetic patterns of sea urchins in general. For the LAG plate to be extraxial, we have to presume the appearance of an extraxial element close to ocular III that separates the last plates formed in columns 3a and 3b, thereby delaying plate formation in column 3a in comparison with column 3b. This in turn supports our consideration that the LAG plate is genital plate 3.

DISCUSSION

THE OTHER MEMBERS OF THE FAMILY

Our observations of *Pourtalesia* and *Echinosisgra* reveal that they have a highly derived apical system modified by three major phenomena: (1) a series of apical disjunctions that take place during ontogeny; (2) the opening of posterior gonopores in ocular plates; and (3) delayed appearance of genital 3. These features seem to be expressed to varying extents in other members of the family. Our knowledge of apical architectures in other genera comes mainly from the studies of Agassiz and Lovén. However, their interpretations of apical patterns cannot always be supported by the OPR and the growth zone model, requiring us to revisit plate homologies for every genus in light of the new interpretation of *Pourtalesia*.

Agassiz (1881) and Mortensen (1950) described the apical system of *Helgocystis* as well separated into a bivium and a trivium. They interpreted the four plates with gonopores as genital plates, implying that posterior oculars were separated from the rest of the apical system (Fig. 7A). However, the plates situated anteriorly to the posterior oculars are located at a point

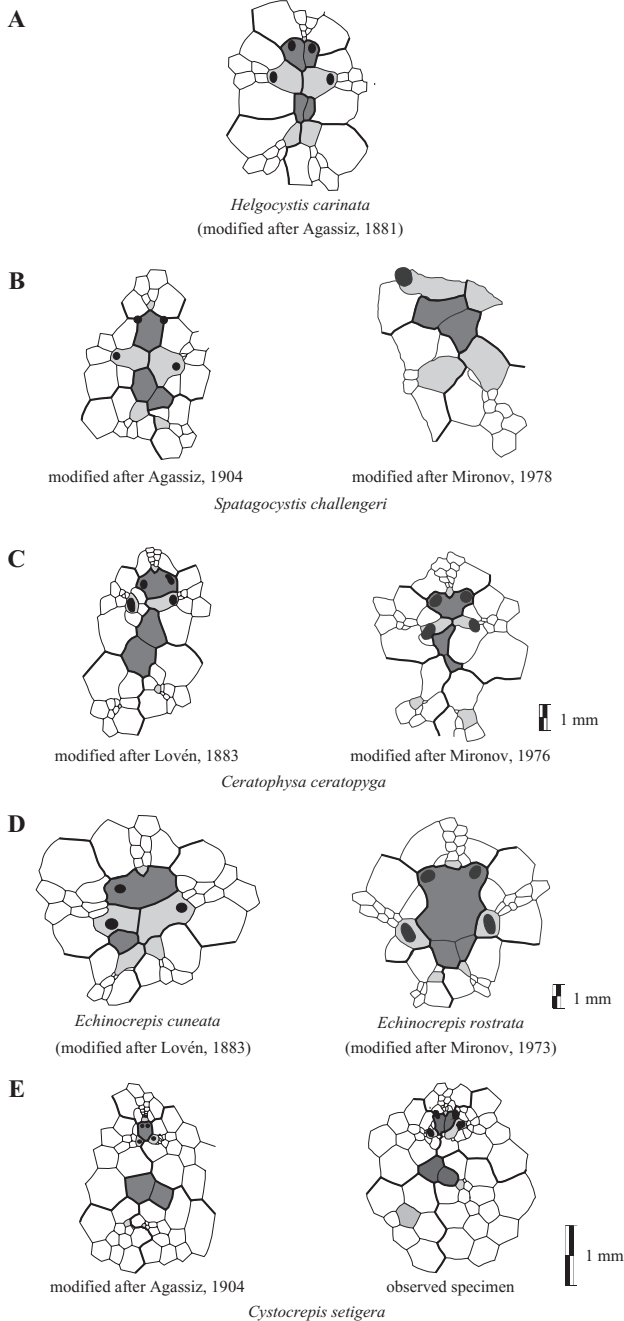


Figure 7. Apical architectures in pourtalesiids. The interpretation of the apical architectures of *Pourtalesia* and *Echinosigra* can be extended to all the other genera of the family.

where four growth zones meet, and should be considered the posterior genitals. Accordingly, the plates that bear the posterior gonopores must be oculars II and IV, as is the case in *Pourtalesia* and *Echinosigra*. Anterior genital plates are not coalescent (Mortensen, 1950), and genital 3 can easily be identified from Agassiz's (1881) drawing. Therefore, the apical system of *Helgocystis* as previously illustrated can be interpreted as a typical intercalary (Fig. 7A), but possessing posterior gonopores in ocular plates.

The apical system of *Spatagocystis* was also described as disjunct (Agassiz, 1904; Mortensen, 1950), with the bivium and trivium separated by additional plates detached from interambulacrum 5. As for *Helgocystis*, we do not consider the apical system to be disjunct, and interpret these additional plates as the posterior genitals. Only one small separation isolates ocular plate I from the rest of the apical system (Fig. 7B). Another specimen described by Mironov (1978) agrees with this interpretation. The apical system of *Spatagocystis* follows the pattern established for *Pourtalesia* and *Echinosigra*, as well as *Helgocystis*, with the posterior gonopores opening in ocular plates. The only additional departures from the more normal pattern are the presence of a single anterior genital and the opening of anterior gonopores directly on genital boundaries. This interpretation is confirmed by Agassiz's (1904) drawing of an internal view of the apical architecture. There is such a large delay in the appearance of genital 3 that the plate is absent into adulthood.

All examined specimens of *Ceratophysa* possess disjunct apical systems. In the specimen collected by the *R/V Challenger*, Lovén (1883) identified six additional plates that he interpreted as 'enclaves' or supernumerary plates detached from interambulacrum 5 (Fig. 7C). These plates display a peculiar pattern because they separate ocular IV from the other apical plates. According to the OPR the additional plates can easily be attributed to growth zone IV, into which they fit logically. By contrast, two plates previously attributed to interambulacrum 4 do not fit into any interambulacral column, and must be interpreted as the posterior, unperforated genitals. Consequently, plates in which posterior gonopores open must be the anterior paired oculars, just as in the other members of the family. Posterior oculars are completely isolated within their respective growth zones, as in the adults of *Pourtalesia* and *Echinosigra* (Fig. 7C). As for *Spatagocystis*, a single genital plate bears the anterior gonopores, suggesting that genital 3 is sufficiently delayed in development that it does not form in *Ceratophysa* either.

Echinocrepis cuneata is the only pourtalesiid that has been described with a non-disjunct apical system (Lovén, 1883; Mortensen, 1950). We follow this inter-

pretation because of the unambiguous contact of posterior oculars with the other anterior apical plates (Fig. 7D). From Lovén's drawing, only one plate can be interpreted as a posterior genital plate. In Mironov's description of *E. rostrata* (Mironov, 1973, 1976), the posterior ocular V is slightly separated from the rest of the apical system and two posterior unperforated genitals can be identified. In both specimens, posterior gonopores open in the anterior paired oculars II and IV, and a single large anterior genital seems to be present. This genital could be genital 2 if it is assumed that this pattern is homologous to that seen in other pourtalesiids.

Among all the members of the family, *Cystocrepis* displays apical architecture closest to *Pourtalesia*. The bivium is separated from the trivium by interambulacral plates as well as by what Agassiz (1904) called additional, intercalated plates. These two isolated plates cannot be assigned to any growth zones, and we interpret them as the two posterior genital plates. Consequently, the plates that bear the posterior gonopores must be the two ocular plates (Fig. 7E). In Agassiz's drawing, both anterior gonopores open in a single plate and genital 3 seems not to have formed. However, observations from a specimen available to us show that there are two anterior genital plates, each of them bearing one of the gonopores. If Agassiz's drawing is assumed to be correct, the expression of genital 3 can only be interpreted as being variable within the species *C. setigera*.

From this overview of the family, it is clear that our procedures for determining homologies in the apical architectures of *Pourtalesia* and *Echinosisgra* can be extended to all the other genera of the family. The most frequently recurring feature shared by these taxa is the opening of posterior gonopores in ocular plates – that is, in axial elements rather than in the extraxial genital plates as in most other echinoids. All the genera possess four gonopores, some species of *Echinosisgra* and *Echinocrepis* excepted. For example, *Echinosisgra phiale* has two gonopores in the anterior genital plates but none in the oculars. In the specimen of *Echinocrepis cuneata* dredged by the *R/V Challenger* (Agassiz, 1881; Lovén, 1883), three gonopores are present: one in each of oculars II and IV, and one in the large anterior genital that we suggest is genital 2.

Apical disjunctions observed in *Pourtalesia* and *Echinosisgra* are expressed to different degrees in other members of the family. Apical disjunctions are absent or minimally expressed in *Helgocystis*, *Spatagocystis* and *Echinocrepis*. Apical systems are more disjunct in *Ceratophysa* and particularly in *Cystocrepis*, which displays a pattern close to that of *Pourtalesia*. These taxa represent an extreme in the degree to which apical disjunctions in the family are expressed.

It has been suggested that genital 3 appears relatively late in the development of *Pourtalesia* and *Echinosisgra*. The absence of this plate in *Spatagocystis*, *Ceratophysa*, *Echinocrepis* and sometimes in *Cystocrepis* can be interpreted as an ultimate expression of the same phenomenon that delays its appearance in *Pourtalesia* and *Echinosisgra*.

THE SISTER-GROUP COMPLEX

The four families Pourtalesiidae, Calymnidae, Plexechinidae and Urechinidae constitute a robust monophyletic group whose ingroup relationships have been firmly set by a cladistic analysis of test features and appendages (Mooi & David, 1996; David & Mooi, 2000). According to this analysis, the unique calymnid species, *Calymne relictata*, is the closest relative to Pourtalesiidae. The Plexechinidae is a robust clade which is sister-group to Calymnidae plus Pourtalesiidae, and the Urechinidae is basal to that entire grouping.

Despite the fact that reduction in gonopore number and disjunctions in the apical system complicate the recognition of ocular and genital plates in members of this clade, ocular and genital plates can be tentatively identified and apical architectures can be clarified using the OPR and the growth zone axioms of the EAT. Therefore, we can recognize patterns that fit more logically into the broad array of morphologies displayed by pourtalesiids than some previous interpretations would otherwise suggest.

The known specimens of *Calymne relictata* display slight disjunction that tends to stretch the posterior part of the apical system, isolating the unperforated posterior genital plates (only two gonopores are present in *Calymne*, on the anterior genitals). Isolated plates have been identified as the unperforated posterior genitals in *Plexechinus cinctus*, *P. hirsutus* and *P. sulcatus* (Mooi & David, 1996; David & Mooi, 2000) (Fig. 8). More extreme architectures arise in plexechinids in which a supplementary disjunction occurs between the anterior paired ocular plates and the anterior genital plates. These sets of plates are always connected in pourtalesiids. Genital 3 is present in some genera of the Urechinidae, but is absent in all representatives of the Plexechinidae. Mooi & David (1996) interpreted this as an apomorphic condition. The late appearance of this plate in *Pourtalesia* and *Echinosisgra*, as well as its absence in *Spatagocystis*, *Echinocrepis* and *Ceratophysa*, shows that the same tendency towards delayed appearance or the total disappearance of the plate is present in all three of the families. In *Calymne*, genital 3 is always present from the first stages of development (test length < 1.5 mm), so that

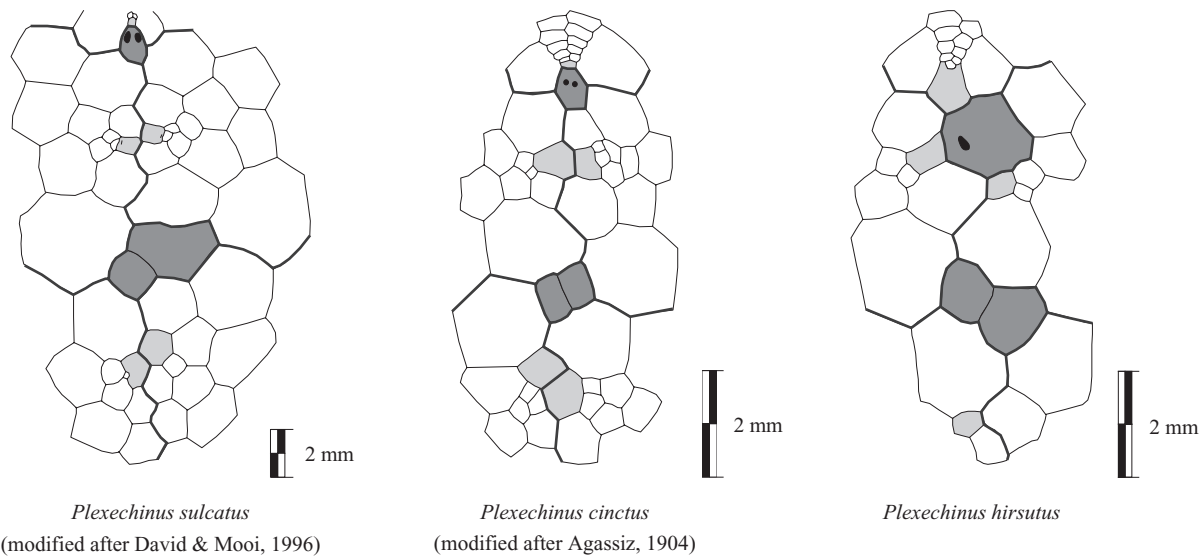


Figure 8. Apical disruptions in three species of plexechinid comparing the absence of genital plate 3 and supplementary disjunctions with the situation in *Pourtalesia*.

its appearance does not seem to be delayed by comparison with other genitals.

The delayed appearance of genital plate 3 is shared by extant holasteroids of different families, but it is expressed to varying degrees among and within these families. Because the failure of this plate to develop occurs independently several times in the different families, the disappearance of the plate is homoplastic. Although this homoplasy cannot be used to support the phylogenetic affinities between the families as suggested by Mooi & David (1996), it does not undermine the hypothesis of relationships they proposed.

The late appearance of genital plate 3 as observed in *Pourtalesia* and *Echinosigra* could be understood as the intermediate stage of a heterochrony that is fully realized only in some species. The plesiomorphic condition is expressed in the stem-group holasteroids in which genital 3 is already present in the earliest stages of development. In plexechinids, the plate is totally absent, and in pourtalesiids (and possibly urechinids) the plate appears very late in ontogeny or not at all. This leads us to suggest that paedomorphosis underlies the disappearance of genital plate 3. More precisely, it is parsimonious to view this as a post-displacement (*sensu* Alberch *et al.*, 1979) because the appearance of a single structure is shifted to a later time in the ontogenetic sequence relative to the pattern observed in more basal groups. Such a heterochronic interpretation of the variations in the expression of genital 3 is tentative, and requires more precise investigation of the ontogenetic patterns in the four holasteroid families.

PALAEONTOLOGICAL COMPARISONS

Using numerous characters other than those from the apical system (David, 1988; Solovjev, 1994), *Galeaster* can be considered the fossil echinoid with the closest affinity to the Pourtalesiidae. A re-interpretation of the apical architecture of *Galeaster* in the light of the EAT clearly supports this relationship.

(1) In *Galeaster sumbaricus* (Poslavskaya, 1949) from the Maastrichtian, posterior gonopores open in genitals following the pattern considered typical for all echinoids (Fig. 9A). Posterior gonopores open astride the boundaries between ocular II and IV and genital plates 1 and 4 in *Galeaster minor* (Poslavskaya, 1949) from the Lower Danian (Fig. 9B). Gonopores open clearly within ocular plates II and IV in *Galeaster dagestanensis* (Poslavskaya & Moskvina, 1960) from the Upper Danian – Montian (Fig. 9C). Solovjev (1994) interpreted this topology as a coalescence between the two posterior genitals and the two anterior, paired ocular plates (as it occurs in the unrelated disasteroids *Metaporinus*, *Tithonia* and *Corthya*). However, his own drawing of the apical system clearly shows distinct, unperforated posterior genitals that fall outside the growth zones. The opening of gonopores in oculars appears to be extremely variable within the five species attributed to the genus (Seunes, 1889; Solovjev, 1994), so that the precise evolutionary pattern among the different species of the genus is difficult to establish. However, the condition of the apical system of *G. minor* suggests a condition in which the posterior gonopores are migrating from the genitals onto the oculars. This event can therefore

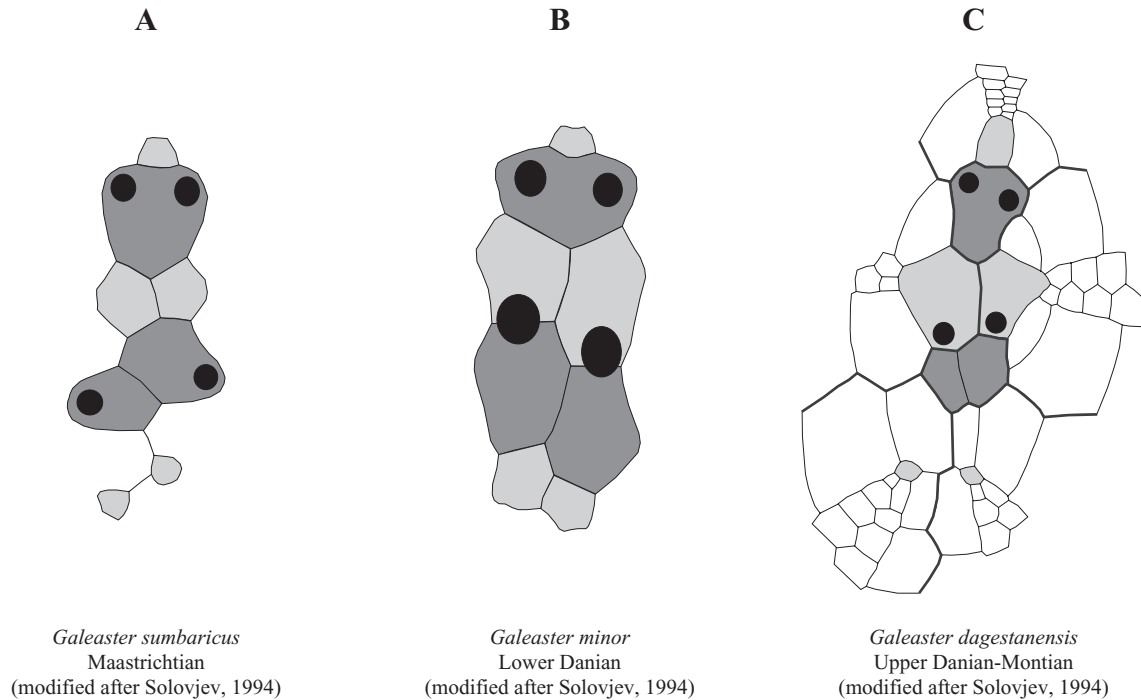


Figure 9. Re-interpretation of the apical architecture of *Galeaster*. The condition of the apical system of *G. minor* suggests a migration of the posterior gonopores from the genitals (*G. sumbaricus*) onto the oculars (*G. dagestanensis*) during the Lower Danian.

be dated to the Early Danian, and indicates a synapomorphy between *Galeaster* and the pourtalesiids. In this respect, *G. minor*, *G. carinatus* (Ravn, 1927) and *G. dagestanensis* can be considered the first representatives of the family, as already suggested by Solovjev (1994).

By this reasoning, the presence of unperforated genital plates in plexechinids, *Calymne* and pourtalesiids must be considered a homoplasy. In pourtalesiids, gonopores do not disappear but move from posterior genitals onto the oculars, whereas in plexechinids they seem to disappear from the posterior genitals without ever migrating onto the oculars. Although only two anterior gonopores are present in *Echinosi-gra phiale*, four exist in the sister species *E. amphora* (Mironov, 1974b), implying that there is a secondary reduction in number in *E. phiale*.

Another indication of the propensity of some holasteroids to have gonopores that open in axial plates can be found in *Guettaria rocardi* (Cotteau, 1889) and in two *Lampadaster* species that display supplementary gonopores in ocular plates II and IV (Lambert, 1896). *Guettaria* is considered to be very close to *Galeaster*, but *Lampadaster* is not (David, 1988).

(2) The double disjunction that isolates the posterior oculars in *Pourtalesia*, *Echinosi-gra* and *Cystocrepis* occurs as early as the Maastrichtian in *Galeaster sumbaricus* (Fig. 9A) (Poslavskaya & Moskvina, 1960;

Solovjev, 1994). Moreover, the pattern seems as variable in this fossil genus as it is between the different extant genera of the Pourtalesiidae. Apical disjunctions are also present in the Lower Palaeocene genera *Basseaster* and *Pomaster* – two taxa considered to be close to urechinids. Therefore, apical disjunctions are already present in the stem group of modern holasteroids, and seem to precede the migration of gonopores onto ocular plates in pourtalesiids.

(3) Only one anterior genital plate can be seen in the four species of *Galeaster* described by Poslavskaya & Moskvina (1960) and Solovjev (1994) from the Late Cretaceous and the Palaeocene of the former USSR, whereas two anterior genitals are distinct in *G. bertrandi* (Seunes, 1889; Smith *et al.*, 1999) from the Maastrichtian (Garumnian?) of the Pyrénées. Therefore, we suggest that genital plate 3 is present in at least one species of *Galeaster*, but may already be absent in others. This could mean that a delay in the appearance of genital 3 may already be occurring in taxa as early as *Galeaster*.

The interpretation we have given to the apical architecture of the Pourtalesiidae seems also to be appropriate to examples from the fossil record. Two of the three architectural peculiarities displayed by pourtalesiid apical systems were already present in their closely related fossils: (1) the migration of gonopores from posterior genitals onto oculars II and IV;

(2) the disjunctions between apical plates. Disjunctions are not as advanced in *Galeaster* as in *Pourtalesia*, but fossil data indicate that the phenomenon is already present at the time of the origin of the family. It cannot be established with certainty whether the disappearance of genital plate 3 was already occurring in the Late Cretaceous – Early Tertiary.

CONCLUSIONS

The comparison of the pourtalesiid apical system with that of other extant as well as extinct holasteroids

shows that apical disjunctions and the late appearance of genital 3 are common features in the entire clade composed of urechinids, plexechinids, calymnids and pourtalesiids. By contrast, the opening of gonopores in ocular plates, and most surprisingly, in axial skeletal elements, is a synapomorphy of pourtalesiids only, but including *Galeaster*.

Apical disjunctions in Pourtalesiidae appear quite late in ontogeny and are completely independent of the migration of the periproct that takes place in the very first stages of post-larval development of irregular echinoids. Therefore, apical disjunctions present in

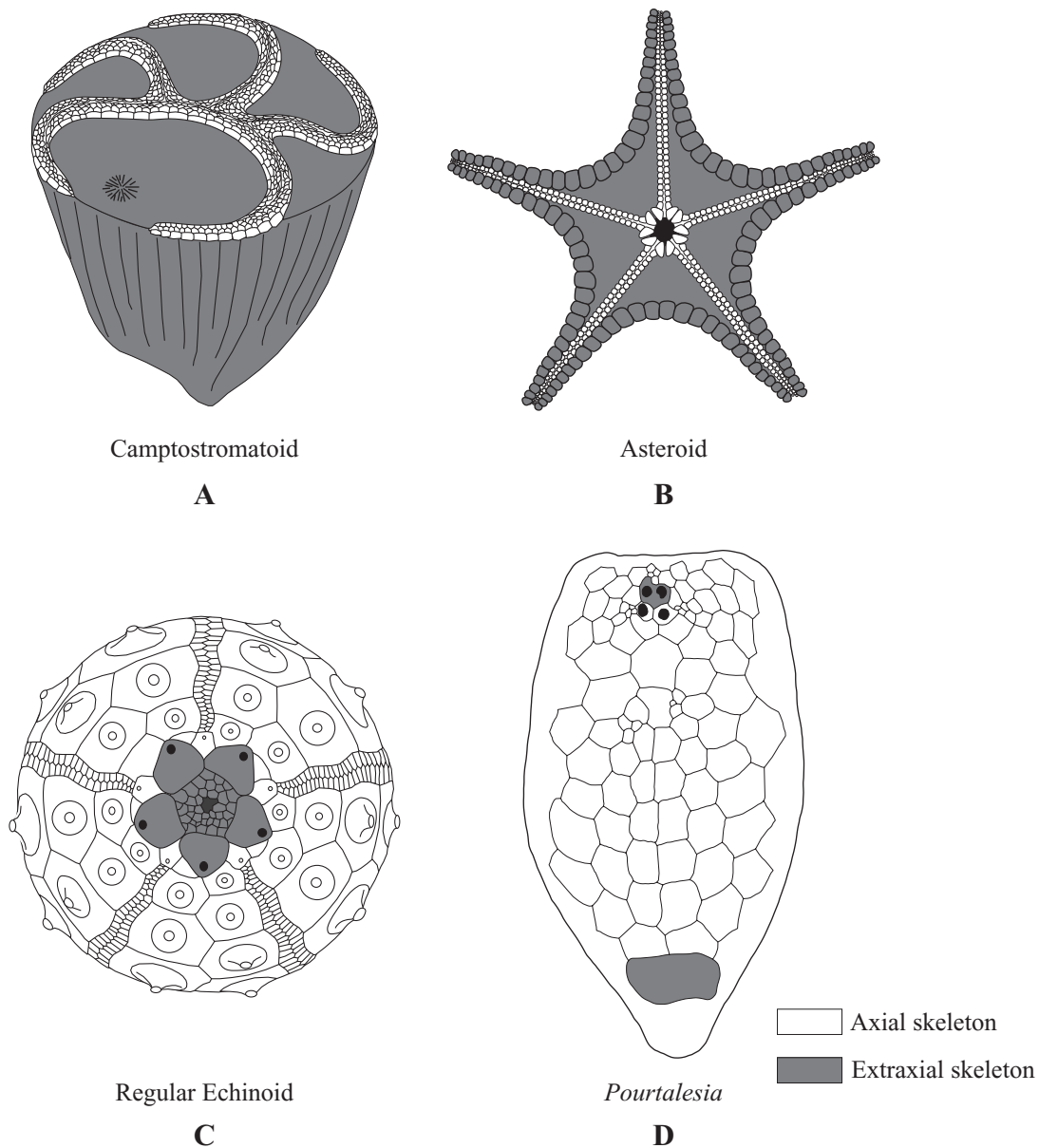


Figure 10. The different proportions of axial and extraxial elements in three classes of echinoderms. The greatest degree of reduction of the extraxial skeleton is found in the echinoids, with an extreme realized in some specimens of *Pourtalesia*.

Pourtalesiidae (as well as in modern holasteroids) can no longer be considered homologous with those found in the Disasteroidea (Jesionek-Szymanska, 1963; Mintz, 1968).

Extraxial and axial elements are present in very different proportions among the major echinoderm clades. For example, in the Palaeozoic camptostromatoids, the majority of the body wall is constructed of extraxial skeleton (Mooi & David, 1998; David & Mooi, 1999). Axial skeleton is represented only by narrow ambulacra (Fig. 10A). In asteroids, the ratio of axial body wall to extraxial increases, but the extraxial part remains the most prominent (Fig. 10B). The greatest degree of reduction of the extraxial skeleton is found in the echinoids in which the extraxial region is restricted to genital and periproctal plates within the apical system (Fig. 10C, D).

In regular sea urchins, genital plates surround the periproctal area so that extraxial elements are grouped together on the adapical side of the test (Fig. 10C). The evolution of the apical system of irregular sea urchins involved a break up of the extraxial entity through displacement of the periproctal area in between the axial growth zones. The rupture between the genital plates and the periproct proceeds by the breaking of the genital circle and by the extreme atrophy of genital 5, which is eventually incorporated into the periproctal area (Gordon, 1926b). The majority of irregular sea urchins retain the reduced number of four genitals. Some irregulars reduce this number again to produce a condition such as that seen in certain holasteroids that lose genital 3. Other irregulars within the order Clypeasteroidea regain a fifth gonopore in interambulacrum 5. Regardless, the presence of an anterior and posterior pair of gonopores is plesiomorphic for the irregular echinoids.

In the context of the reduction of the extraxial part of the body wall, pourtalesiids represent an extreme even within the Echinoidea. Removal of the posterior gonopores from the genitals to the oculars transfers the function of supporting gonopores from the genital plates to the oculars. In other words, the reduction of extraxial skeleton is associated with a loss of function that is now compensated by the *de novo* involvement of axial elements. The extreme is realized in some specimens of *Pourtalesia*, in which posterior genitals also seem to be lacking (Fig. 10D). Genital 2 is the only extraxial element of the apical system that does not undergo any reduction, retaining its function as the bearer of a single gonopore and the hydropores. It is tempting to consider that this last remaining piece of extraxial skeleton in the apical system is retained because it is required to fulfil the function of madreporic plate.

Mooi & David (1997) suggested that the reduction of the extraxial region in echinoderms was an example of

peramorphosis. Extraxial elements are formed in the part of the body wall that is inherited from the larva (David & Mooi, 1996). By contrast, axial elements are formed in the part of the post-metamorphic body wall that comes from the rudiment. The reduction of the extraxial part of the skeleton suggests a more significant development of the rudiment.

David (1990) showed that pourtalesiid diversity is an expression of a global peramorphic process that affects the different characters of the test to varying degrees, and results in a 'mosaic pattern of heterochronies'. The characters of the apical system studied herein are consistent with, and actually support, this general scheme, and it is therefore not surprising that the most extreme reduction of the extraxial part of the skeleton realized in echinoids occurs in Pourtalesiidae.

ACKNOWLEDGEMENT

This paper is a contribution to the theme 'Macroévolution et dynamique de la biodiversité' of UMR CNRS 5561-Biogéosciences.

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