



Evolution

Combining embryology and paleontology: origins of the anterior-posterior axis in echinoids

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Abstract

The tendency of the periproct to move outside the apical system occurred in eight independent sea urchins lineages, but only one succeeded. The origin of the anterior-posterior axis in irregular echinoids results from that successful attempt, and is primarily achieved by eccentricity of the periproct. The mechanism by which this occurs is best understood through synthesis of data from embryology, paleontology, and phylogenetics. In irregular echinoids, the complete escape of the periproct from the apical system (exocyclism) is a consequence of changes in the embryological sequence that governs periproctal eccentricity. The adaptative significance of this change is discussed. *To cite this article: T. Saucède et al., C. R. Palevol 2 (2003).*

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Résumé

Synthèse embryologie – paléontologie : l'origine de l'axe antéro-postérieur chez les oursins. Huit tentatives, phylétiquement indépendantes, de migration du périprocte se sont produites au cours de l'évolution des échinides, une seule a réussi. L'axe antéro-postérieur des échinides irréguliers est le résultat de cette migration réussie du périprocte hors de l'appareil apical (exocyclisme). Une synthèse de données embryologiques, paléontologiques et phylogénétiques permet de cerner le mécanisme impliqué. Les contraintes du développement expliquent pourquoi la migration s'est réalisée huit fois dans la même direction et comment un changement de la séquence embryologique explique l'origine des irréguliers. La signification adaptative de ce changement est discutée. *Pour citer cet article : T. Saucède et al., C. R. Palevol 2 (2003).*

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De nombreux travaux de Stephen Jay Gould insistent sur l'importance des études du développement pour la compréhension des processus et des modalités évolutives [18–21, 24]. Un autre point important de l'œuvre de Gould est le concept de contrainte, c'est-à-dire le poids des structures ancestrales qui influençant le développement, limitent les possibilités évolutives d'un groupe [23]. Dans certains cas, il est possible de s'appuyer à la fois sur des données phylétiques et des données du développement pour démontrer l'existence et l'influence de telles contraintes. Nous en présentons un exemple dans cet article: l'origine de l'axe de symétrie antéro-postérieur chez les échinides irréguliers.

Des études récentes [2–4, 5, 34, 35] proposent une nouvelle lecture des homologies entre régions du corps chez les échinodermes. Ce nouveau système d'homologies – modèle EAT (pour Extraxial-Axial Theory) – distingue deux grands types de squelette : le squelette axial et le squelette extraxial. Selon ce modèle, toute la couronne de l'oursin est axiale, organisée en cinq zones de croissance, tandis que le squelette extraxial est restreint aux plaques génitales et au périprocte (Fig. 1). L'un des événements les plus significatifs de l'histoire évolutive des oursins est l'apparition d'un axe de symétrie bilatérale secondaire dans un groupe très diversifié: les oursins irréguliers. La symétrie bilatérale est associée à la migration du périprocte (dans lequel se situe l'anus) en dehors de l'appareil apical, situé au sommet du test, et se superpose à la symétrie pentaradiée pré-existante. Ce processus — exocyclisme — correspond à un étirement puis à une rupture du squelette extraxial en deux sous-ensembles distincts : (1) les plaques génitales qui restent en position apicale ; (2) le périprocte qui migre vers la bordure du test (et parfois même jusque sur la face orale).

L'exocyclisme ne se manifeste que chez les oursins irréguliers qui forment un groupe monophylétique [43, 44]. Cependant, certains oursins réguliers (ensemble paraphylétique regroupant tous les oursins « non irréguliers ») présentent divers degrés d'excentricité du périprocte au sein de l'appareil apical, mais le périprocte ne quitte ni ne rompt jamais le cercle apical. Chez les oursins réguliers, l'excentricité du périprocte est apparue au moins sept fois indépendamment ; elle

se produit une fois chez les oursins irréguliers, soit en tout huit tentatives indépendantes au cours de l'histoire évolutive des oursins [10, 28, 33, 39]. Dans les huit cas, le périprocte migre toujours dans la même direction : celle de l'interambulacre 5.

Il est donc vraisemblable que l'excentricité du périprocte des oursins réguliers et l'exocyclisme des oursins irréguliers soient liés par des facteurs qui pourraient contraindre le déplacement du périprocte à des modalités d'expression communes. À partir de données anatomiques et ontogénétiques, obtenues à partir de matériel fossile ou tirées de la littérature, nous avons donc essayé de mettre en évidence l'existence éventuelle de contraintes internes influant sur le déplacement du périprocte.

D'après le modèle EAT, la migration du périprocte en dehors du système apical correspond au déplacement d'un élément extraxial au sein d'une région axiale. Les cinq zones de croissance axiales forment des unités de développement ou modules [12] ; or, il n'existe chez les échinodermes aucun exemple d'élément extraxial inséré dans un module axial. On peut donc affirmer que le périprocte migre préférentiellement entre les zones de croissance, plutôt qu'au sein des zones de croissance elles-mêmes. Cela laisse cinq directions possibles de migration, correspondant aux cinq interambulacres.

Le canal du sable et le stolon génital sont situés sous la plaque génitale 2, entre les zones de croissance II et III, dans l'axe de l'interambulacre 2. Ces deux organes internes apparaissent assez tôt dans l'ontogénèse des oursins, à des stades où, chez les oursins irréguliers, le périprocte commence à migrer [7, 41]. Les deux organes représentent donc une contrainte qui rendrait difficile la migration du périprocte en direction de l'interambulacre 2. Il reste alors quatre directions possibles de migration, correspondant aux quatre interambulacres restants (Fig. 2). La probabilité pour que le périprocte migre huit fois indépendamment dans la même direction est alors de $(1/4)^8$, soit une chance sur 65 536. La probabilité pour que le périprocte ait migré huit fois par hasard dans l'interambulacre 5 est donc infime, de sorte qu'il est plus parcimonieux de considérer que d'autres facteurs que le hasard ont contraint la direction de migration.

Les travaux sur le développement des oursins réguliers [14, 16, 17, 38] montrent que la plaque géni-

tale 4 est la dernière génitale à se former et qu'elle apparaît en position excentrée par rapport au cercle formé par les autres génitales (Fig. 3). A ce stade, les plaques génitales présentent un arrangement particulier marqué par une symétrie bilatérale selon un plan passant par l'ambulacre II et l'interambulacre 4 [47]. Cette symétrie bilatérale est ensuite remplacée par la symétrie pentaradiée, lorsque la génitale 4 grandit et vient s'insérer dans le cercle génital. Chez les oursins irréguliers, lorsque la migration du péripacte débute, la symétrie primordiale est encore marquée, de sorte que l'interambulacre 5 est situé en face de l'interambulacre 2 (Fig. 3) [15, 16]. Ainsi, la migration du péripacte débute selon l'axe 2–5 et non pas selon l'axe III–5 qui apparaît à un stade plus tardif. La recherche de facteurs internes pouvant expliquer l'excentricité répétée du péripacte dans la direction 5 doit donc considérer l'axe 2–5, et non pas l'axe III–5 qui concerne les stades ontogénétiques ultérieurs.

Le développement du système génital débute par la formation du stolon génital, situé sous la plaque génitale 2. Celui-ci émet ensuite deux bourgeons qui divergent en arc de cercle, puis se rejoignent pour former l'anneau génital. Les gonades et les gonoductes se forment plus tardivement à partir de l'anneau génital. Chez les oursins réguliers, l'anneau génital encercle le rectum sous les plaques génitales. Chez les oursins irréguliers, le déplacement du péripacte débute avant la fermeture de l'anneau génital [15, 16, 41], de sorte que le rectum se développe en dehors de cet anneau (Fig. 4). Enfin, chez les oursins réguliers à péripacte excentré, le rectum demeure à l'intérieur de l'anneau génital. Ce dernier s'étire et se déforme alors dans la direction de migration du péripacte, mais l'excentricité du péripacte n'empêche ni la formation, ni le fonctionnement des structures génitales (la plaque génitale 5 est perforée et la gonade correspondante est fonctionnelle).

L'anneau génital se forme à un stade ontogénétique où la génitale 2 est encore située en face de l'interambulacre 5. Or, l'anneau génital commence à se former sous la génitale 2, et se ferme dans la direction opposée, c'est-à-dire dans la direction de l'interambulacre 5 (entre les zones de croissance I et V). La dynamique de formation de l'anneau génital détermine donc, dans la direction 5, une zone de moindre résistance pour permettre le passage du péripacte. Cette contrainte du développement permet donc

d'expliquer pourquoi le péripacte migre ou tente de migrer à huit reprises dans la même direction, celle de l'interambulacre 5. Quelles qu'en aient été les raisons adaptatives, l'unique chemin emprunté est une remarquable illustration du poids des contraintes du développement dans l'évolution.

L'observation de matériel fossile montre que, dès le Jurassique moyen, l'excentricité du péripacte apparaît très tôt lors de la croissance des oursins irréguliers, beaucoup plus tôt que chez les oursins réguliers à péripacte excentré [10]. Ceci suggère que, chez les oursins irréguliers du Jurassique moyen, le péripacte se déplace déjà avant la fermeture de l'anneau génital. Nous pensons que la différence fondamentale entre oursins réguliers et irréguliers, à savoir l'exocyclisme, peut alors être expliquée par un simple changement dans la séquence ontogénétique des premiers irréguliers. Une anticipation de la migration du péripacte par rapport à la fermeture de l'anneau génital aurait permis la mise en place de l'exocyclisme chez les premiers oursins irréguliers. L'exocyclisme peut ainsi s'expliquer par un début de migration plus précoce du péripacte, ce qui, dans une interprétation hétérochronique, serait un cas de pré-déplacement [32].

1. Introduction

In numerous and diverse works, Stephen Jay Gould repeatedly advocated the importance of developmental studies to decipher evolutionary patterns or processes [18–20, 21, 24]. Indeed, he and many others have argued that some major events in the evolution of life cannot be properly understood in the absence of data concerning development (e.g., the evolution of jaw bones into middle ear ossicles). The present burgeoning research qualified as falling into the active and exciting field of 'evo-devo' demonstrates vividly the perspicacity and vision typical of many of Gould's views.

Another important theme running throughout Gould's work reflects upon how evolution can only work with what historical contingency yields up to its selective attention. Evolutionary novelty is possible only insofar as there are pre-existing structures to modify, and the trajectories of those modifications can

be restricted, for lack of a better phrase, by what is possible. This obvious and tautological point is nevertheless important to the concept of constraint that was an occasionally contentious part of Gould's heritage [23]. However, difficult it might be to escape some of the clinging philosophical and sociological issues that circulate around the concepts embodied by constraint, there are certainly instances in which phylogenetic and developmental data converge on an intellectually profitable avenue of research that explores the influence and indeed the existence of such constraints. We present just such a case here.

Without too much fear of contradiction, we think we can make the claim that among the most significant events in the evolution of the echinoids is the origin of an axis of secondary bilateral symmetry in a large and important subset of the Echinoidea: the irregular sea urchins. Formally known as the Irregularia, this group includes forms as diverse as the lamp urchins, heart urchins, and sand dollars. The event that most distinguishes these forms from other 'regular' globose echinoids resulted in the establishment of an anterior-posterior axis in the otherwise pentaradial sea urchins. This event in turn corresponded to the migration of the periproct (which contains the anus) outside the apical system at the summit of the test.

As already established [10, 13, 28, 29, 33, 38, 42], and as we will further analyze below, this migration has occurred more than once. However, there remains little or no research into why, over the course of evolution of the entire class Echinoidea, the periproct moved (or at least began to move) out of the apical system in the same direction eight times independently. The aim of this paper is to use information on the early development of echinoids in conjunction with phylogenetics and morphology of fossil forms to explore how the emergence of the Irregularia is deeply rooted in developmental trajectories common to all sea urchins, however they might be modified.

2. Homologies in echinoids

Recent studies [2–4, 5, 34, 35] have proposed a new interpretation of body wall components among echinoderms. This new system (the Extraxial–Axial Theory, or EAT) bases the recognition of homologies on the embryology and on the ontogeny of structures [2, 3,

37]. It identifies two body wall categories in the Echinodermata: axial and extraxial. The identification of these two distinct body wall regions permitted establishment of new homologies pertaining to all echinoderms. In some cases, it also led inexorably to drastic challenges of previous phylogenetic hypotheses [6, 35, 36].

As emphasized in the papers cited above, echinoids are unique among the echinoderms because the entire coronal part of the test consists of axial body wall. The extraxial region is restricted and indeed constricted to the scales present on the periproctal membrane and to the genital plates (Fig. 1). The axial region of the corona is organized into five growth zones that form and continue to grow in accordance with the 'Ocular Plate Rule' (OPR). 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 of the ambulacrum. New ambulacral and interambulacral plates are formed next to the ocular plate. Plates are shifted away from the apical system and the ocular plate as new plates are added between the old plates and the ocular. The end result of the OPR is that the plates in each of the ambulacral and interambulacral columns get older with proximity to the mouth, and younger with proximity to the apical system.

In the irregular echinoids, the pentaradial symmetry of the five growth zones is disturbed by the migration of the periproct out of the circle formed by the genital and ocular plates. This phenomenon is called exocyclism. Exocyclism can be viewed as a stretching and in fact disruption of an echinoid's small remaining extraxial region into two distinct units: (1) genital plates that stay in an apical position; and (2) the periproct and its associated scales that move towards the margin (and in some cases all the way to the oral surface) of the test. The phenomenon appears in fossil forms as early as the Jurassic. It occurs concomitantly with an important evolutionary radiation of the Irregularia, which have since come to constitute about 60% of fossil and extant known species of echinoids as tabulated since their first appearance [29]. After study of their lantern apparatus and of the tooth structure, Smith [43, 44] suggested that the irregular echinoids formed a monophyletic assemblage. Hence, in irregular echinoids, the periproct migration is likely to be an apomorphy that occurred just once.

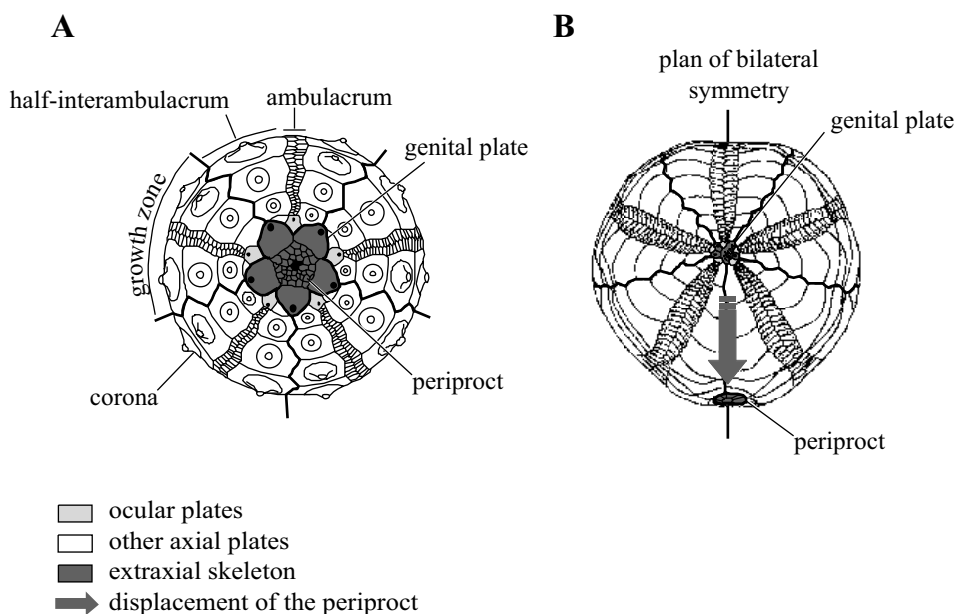


Fig. 1. The EAT recognizes two body wall regions (axial and extraxial) among echinoderms. The echinoid test is constructed almost entirely from axial elements organized into five growth zones. In regular echinoids, the periproct is enclosed within the apical system (A) (after [4]). In irregular echinoids, the periproct has moved out of the apical system (B) (modified after [31]).

Fig. 1. D'après le modèle EAT, le corps des échinodermes comprend deux régions (axiale et extraxiale). Le test des oursins est constitué presque entièrement de squelette axial, organisé en cinq zones de croissance. Chez les oursins réguliers, le péripérocte est enfermé au sein de l'appareil apical (A) (d'après [4]). Chez les oursins irréguliers, le péripérocte a migré en dehors de l'appareil apical (B) (modifié d'après [31]).

3. Eccentricity of the periproct in echinoids

The migration of the periproct to a position completely outside the apical system, or 'true' exocyclism, occurs only in irregular echinoids. However, in the paraphyletic assemblage known as the 'regular' echinoids (which includes the formally designated extant major groups Cidaroida, Echinothurioidea, and the non-irregular Acroechinoidea), some taxa are characterized by varying degrees of eccentricity in the position of the periproct within the apical system. However, in these groups the periproct neither fully leaves nor even disrupts the apical ring formed by the ocular and genital plates.

Examination of the inventory of such 'regular' echinoids with an eccentric periproct reveals that the feature is conspicuous in twelve different genera belonging to seven families: the Pseudodiadematidae (*Pseudodiadema*, *Trochotiar*a), the Acrosaleniididae (*Acrosalenia*, *Monodiadema*), the Hemicidaridae (*Alomma*, *Heterodiadema*), the Phymosomatidae (*Gauthieria*, *Phymosoma*, *Rachiosoma*), the Glypho-

cyphidae (*Glyphocyphus*), the Pedinidae (*Hemipedina*) and the Diadematidae (*Farquharsonia*) [10, 28, 33, 39]. Occurring as they do in only distantly related families, these genera have no close phylogenetic relationships [11, 44]. Therefore, the eccentricity of the periproct has arisen independently at least eight times (seven times in 'regular' echinoids, plus once in irregular echinoids) in the evolutionary history of echinoids. In each case, the periproct always moves in the same direction distally from the centroid of the apical system down interambulacrum 5 (as numbered according to Lovén's system – see [5]). Within the order Cidaroida, Fell [13] and Kier [29] also noticed an 'evolutionary trend' in which the periproct moved towards interambulacrum 5, but the phenomenon is usually only subtly expressed and never as pronounced as in the genera listed above.

An apparent exception to the movement down interambulacrum 5 can be found in the stirodont family Saleniidae, in which the anus is displaced towards ambulacrum I, close to ocular plate I. However, in the Saleniidae, the eccentricity is expressed in a manner

very different from that seen in forms that have displacement towards interambulacrum 5. In saleniids, it is instead an eccentricity of the anus within the periproctal membrane itself – a condition probably related to the existence of a central supplementary plate, the so-called ‘suranal’ plate, and not to the actual position of the entire periproctal complex within the ring formed by the apical plates. In fact, within saleniids, the periproct remains in the center of the apical system itself. The position of ocular plate I in the apical system is also not affected by the movement of the anus within the periproctal membrane. We conclude that this is very different from what might be expected of the kind of eccentricity that affects the entire periproct and not just the anus, and we will consider it no further here.

4. Convergence and constraints

In spite of the independent events leading to the seven different origins of eccentricity in the ‘regular’ echinoids mentioned above, there seems to be a relationship to the strongly expressed exocyclism seen in the Irregularia. It is tempting to think of the eccentric position of the periproct in the ‘regulars’ as an incipient exocyclism that did not advance beyond the condition of mere eccentricity within the apical system. Conversely, the exocyclism of irregular echinoids could be viewed as an extreme case of eccentricity culminating in the rupture of the ring of apical plates, followed by the escape of the periproct from the apical system entirely. In other words, in their topological aspects, all the independent cases of periproctal eccentricity seem to be related through hitherto unexplored underlying factors that constrain the eccentricity to common patterns of expression.

To explain such convergent patterns, several hypotheses involving common internal (developmental) constraints may be formulated. In contrast, external selective or adaptive scenarios could be invoked. Most ‘regular’ echinoids are epifaunal and opportunistic feeders. Irregular echinoids are largely sediment swallowers and infaunal representatives limited to soft bottom environments [8, 46]. Habitat and ecology of regular echinoids are very different from those of irregular echinoids. Invocation of common selective or adaptive factors favoring the convergent evolution of periproctal

eccentricity along a single direction in a subset of ‘regular’ echinoids, as well as in the Irregularia is difficult to support with the available data (but see below). A more promising approach would be to explore the possibility of intrinsic constraints on periproct displacement that might be inferred from ontogenetic and anatomical data already well-known from examination of appropriate material and from the literature. Analysis of these data shows that pathways open to the processes leading to periproctal displacement are in fact strongly limited.

A first set of restrictions can be deduced from the EAT and the OPR-based growth zone model described above. According to the EAT, the coronal part of the echinoid test is built entirely of axial elements organized into five growth zones, each headed by an ocular plate. Each growth zone is therefore a developmental unit, or module in the context [12]. Such a module includes only those axial plates formed in association with the corresponding ocular plate. In all cases of eccentricity in the ‘regular’ echinoids, and in exocyclism of irregular echinoids, the migration of the periproct out of the apical system is indicative of the displacement of an *extraxial* element into a region of *axial* body wall. There are no instances in which *extraxial* elements have inserted themselves within axial modules, and we regard this as an important constraint on the possible number of options open to a migrating periproct: it cannot move distally from the apical system through an axial module. Therefore, the periproct can only move outward between adjacent growth zones. There are five possible pathways for the periproct: along the five boundaries between growth zones. In the parlance of accepted echinoid anatomy, these are represented by the interradial suture which marks the mid-line of each of the five interambulacra. Therefore, the EAT provides an interpretation by which it is easier to see how the periproct is more liable to move down the *interradius* of an interambulacrum than along the *perradius* suture of an ambulacrum, or even along the *adradial* suture that marks the boundary between an ambulacrum and an interambulacrum. This is even easier to comprehend when it is realized that the radial water vessel running along the *perradius* beneath each ambulacrum represents itself an important anatomical constraint that would have to be circumvented in order to facilitate the migration of the periproct down the center of an ambulacrum.

Similarly, other types of internal organs situated immediately beneath genital plate 2 (that is, between growth zones II and III) constitute further anatomical constraints on periproctal displacement. A genital stolon from which the genital system will later develop appears beneath genital 2, at about 2–3 mm length in *P. lividus* [7, 41]. This is a size similar to that attained at the point of onset of periproct migration in irregular echinoids. Therefore, the genital stolon could constitute a hindrance in the movement of the periproct in the direction of interambulacrum 2. We explore other constraints related to the development of the genital stolon and subsequent gonadal elements below.

The stone canal (associated with the axial organ) also forms early in echinoid development, sometimes before the post-metamorphic echinoid achieves a length of 1 mm (for example in *E. cordatum*). The stone canal is set beneath genital plate 2, through which it opens via numerous hydropores [15, 25, 40]. Therefore, two organs, the stone canal and the genital stolon, form early in ontogeny beneath genital 2, each representing a constraint that would make the migration of the periproct difficult to achieve along interambulacrum 2 (that is to say between growth zones II and III).

Once these constraints are taken into account, four interambulacra remain as candidates for the direction of periproctal migration. These four axes constitute the interradii of interambulacra 1, 3, 4 and 5 (Fig. 2). The probability for the periproct to move eight times independently in the same direction is $(1/4)^8$, that is to say, one chance in 65 536. The probability that movement only along the perradius in interambulacrum 5 happened by pure chance is so low that it is more parsimonious to consider that some underlying, causal factor is coming into play to constrain the direction of migration. We are forced to seek additional factors that might influence this movement, and it is appropriate to look at embryological data for these factors.

5. Embryological data and von Ubisch's axis

Studies of the development of several regular echinoids (*Paracentrotus lividus*, *Psammechinus miliaris*, *Echinus microtuberculatus*, and *Arbacia punctulata*) by Gordon [14, 16] and Gosselin and Jangoux [17], show that genital plate 2 is the first genital plate to

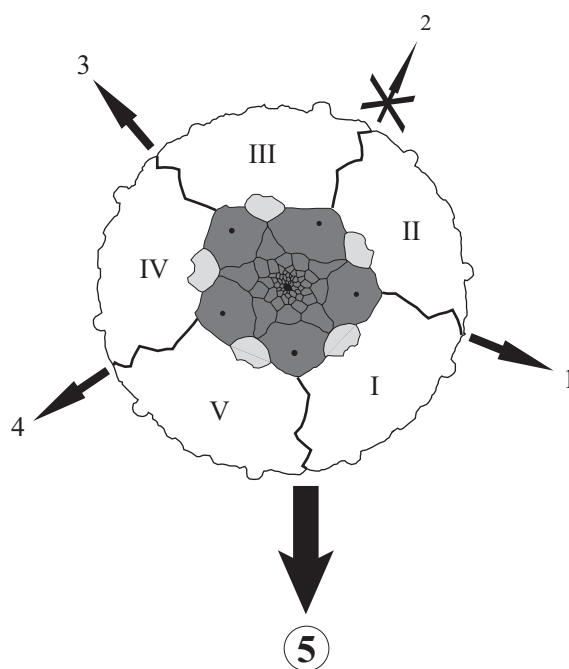


Fig. 2. The four possible theoretical directions in which the periproct could move out of the apical system. In reality, only one direction, along interambulacrum 5, is ever followed and that occurs eight times independently.

Fig. 2. En théorie, le périprocte peut migrer en dehors de l'appareil apical dans quatre directions. En réalité, le périprocte n'emprunte qu'une seule direction huit fois indépendamment, celle de l'interambulacre 5.

appear, whereas genital 4 is the last one to form, just before metamorphosis. The latter plate forms and starts to grow in the posterior part of the larval body, in a distinctly eccentric position relative to the circle formed by the four other genital plates [16]. During metamorphosis, the rudiment evaginates and the larval epithelium retracts towards the future apical area. As a consequence, the elementary genital plates are propelled towards the apical area where they continue to grow until they contact each other. The exception to this overall pattern is genital plate 4, which remains slightly displaced peripherally (Fig. 3). With only minor differences, the same general pattern of genital plate development has been observed in all regular echinoids so far examined [17, 38].

Accordingly, Gordon's observations [14] of the post-larval stage of *Psammechinus miliaris* exemplify the 'tetrameric' pattern of genital plate arrangement, in which genital plate 4 is still excluded from the tetrad formed by the other four genital plates around the

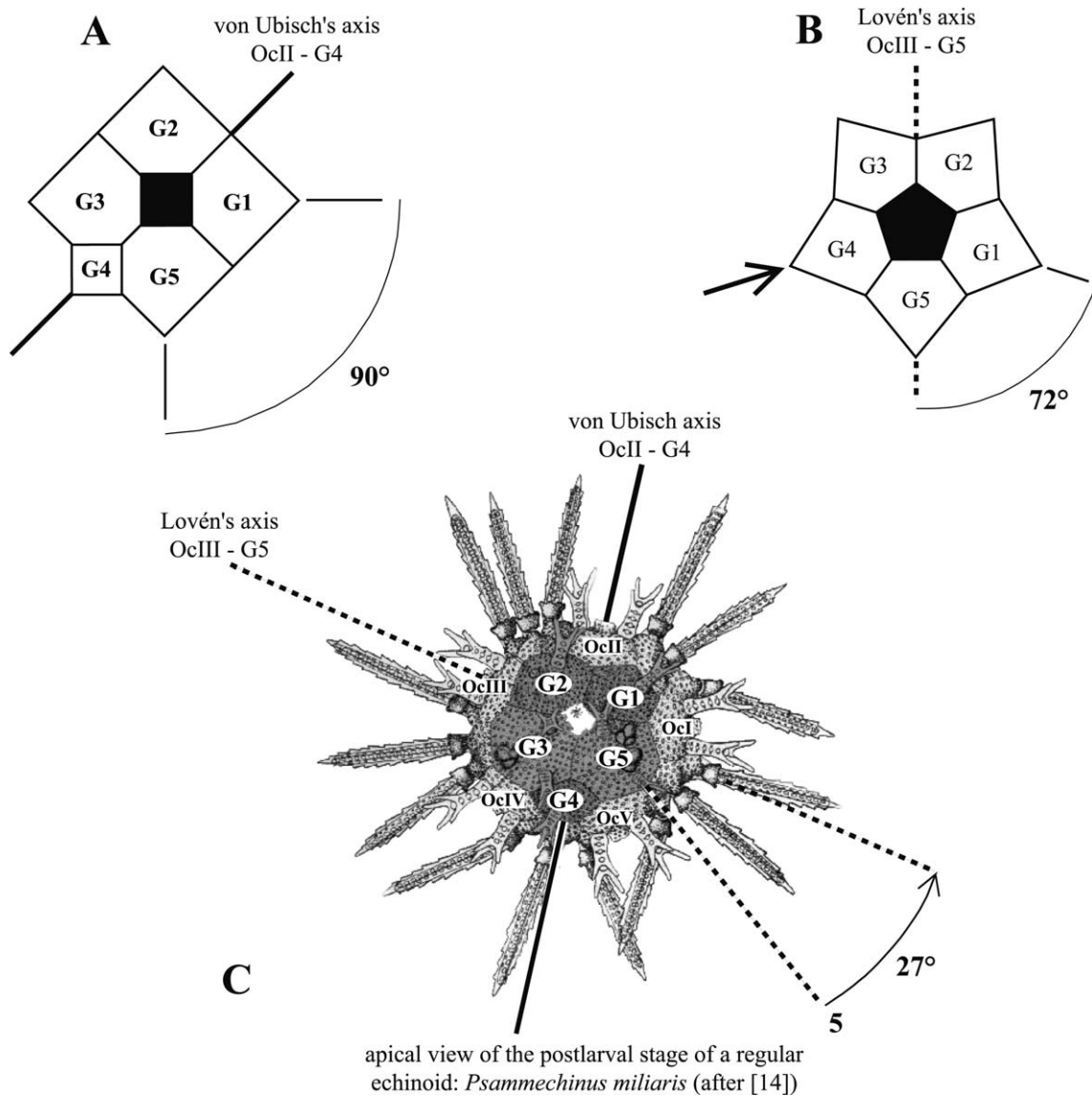


Fig. 3. In early ontogeny, an original cirlet of four genital plates (G1, G2, G3 and G5) with 90° angles (A) becomes a cirlet of five genitals with 72° angles (B). In the initial configuration, ocular plate OcII is diametrically opposite genital G4, thereby defining von Ubisch's axis (A). At this stage, the OcIII–G5 angle is about 207° . The insertion of G4 in the cirlet of the other 4 genitals (G1, G2, G3 and G5) shifts G5 about 27° , coincidentally reducing the OcIII–G5 angle to 180° . OcIII is now opposite G5, defining Lovén's axis (C).

Fig. 3. Au début de l'ontogenèse, un cercle de quatre plaques génitales (G1, G2, G3 et G5) disposées à 90° les unes des autres (A) devient un cercle de cinq génitales disposées à 72° (B). Dans la configuration initiale, la plaque ocellaire OcII fait face à la génitale G4 (A), définissant ainsi l'axe de von Ubisch. À ce stade, l'angle OcIII–G5 est d'environ 207° . L'insertion de G4 dans le cercle des quatre autres génitales (G1, G2, G3 et G5) induit un déplacement de 27° de la plaque G5 et corrélativement une réduction de l'angle OcIII–G5 à 180° . Les plaques OcIII et G5 sont alors face à face, définissant le plan de Lovén (C).

periproctal area (Fig. 3). At this point, the angle (measured clockwise) between axes passing through the centers of ocular plate III and genital plate 5 is 207° . This pattern was first noticed by von Ubisch [47], who remarked that the genital plate arrangement was bilaterally symmetric about a plane passing through ambulacrum II and interambulacrum 4. Von Ubisch named this plane the ‘primordial plane of symmetry’, and the corresponding II-4 axis is now known as ‘von Ubisch’s axis’.

In regular echinoids, this primordial symmetry is rapidly obscured by a pentameric symmetry introduced when genital plate 4 enlarges to become a more equal contributor to the circle of genital plates, between genitals 3 and 5. The late insertion of genital 4 between other genitals consequently induces changes in the symmetry of the apical system. The genital ring is subsequently enlarged, reducing the angle between ocular plate III and genital 5 from 207° to 180° . This then establishes an apparent III-5 axis which has come to be known as Lovén’s axis of symmetry.

In irregular echinoids, the primordial symmetry expressed as von Ubisch’s axis is difficult to discern, in part because of the significant hypertrophy of genital plate 2, and in part because of the early displacement of the periproct [15]. The migration of the periproct in the development of irregular echinoids is initiated at a test length of about 1 mm, as exemplified by Gordon’s [15, 16] work on *Echinocardium cordatum* and *Echinarachnius parma*. Given the timing of formation of the circle of genital plates, interambulacrum 5 is still opposite genital plate 2 when the periproct begins its migration from the apical system (Fig. 3). In adults, interambulacrum 5 actually comes to lie opposite ocular plate III. In other words, owing to the tetrameric pattern displayed by genital plates at the post-larval stage, the direction of periproct displacement starts along the axis through interambulacrum 2 and interambulacrum 5 (direction 2-5), and not along the axis through ambulacrum III and interambulacrum 5 (direction III-5). If we are searching among events in early post-larval development for an explanation of the repetitive eccentricity of the periproct in the direction of interambulacrum 5, we should examine what happens along the primary direction 2-5, and not restrict our analysis to later ontogenetic events along the adult’s anterior-posterior axis (direction III-5).

6. Reconciling Lovén’s and von Ubisch’s planes of symmetry

With great perspicacity, Gordon [16] discussed and compared Lovén’s and von Ubisch’s planes of symmetry (2-5 and III-5 respectively). She stressed the importance of von Ubisch’s primordial plane of symmetry during plate development. In contrast, for her, Lovén’s symmetry masked this primordial symmetry in adults and was therefore “more apparent than real” ([16]: 314). We reach a somewhat different conclusion because in fact, Lovén’s bilateral symmetry of irregular echinoids about the III-5 plane is not in conflict with or any less real than von Ubisch’s primordial plane of symmetry. We point out that von Ubisch’s symmetry corresponds to a post-larval arrangement that causes the genital stolon (in interambulacrum 2) to face the boundary between growth zones I and V (interambulacrum 5). In this way, von Ubisch’s symmetry foreshadows and in some ways actually determines the direction of migration of the periproct along interambulacrum 5. This in turn establishes the future symmetry of adult irregular echinoids about the III-5 plane because by these later ontogenetic stages, genital 4 will have induced the aforementioned changes in geometry of the circle of genital plates. Therefore, von Ubisch’s and Lovén’s axes of symmetry are not in conflict; the latter is part of an ontogenetic trajectory that proceeds seamlessly from the former.

7. The closure of the genital ring

Remarkably exact observations of the embryology of echinoids have existed for more than a century [1, 30]. However, none of these data have ever been applied to the questions raised in the present study. In fact, the movement of the periproct towards interambulacrum 5 is also inimitably tied to the formation of the intestine and rectum, and by the development of the extraxial skeleton. Therefore, any comprehensive explanation for a singular, constrained direction of migration must also be able to inform studies of the concomitant development of the genital system and of the aboral part of the digestive tract, all in conjunction with the migration of the periproct itself.

The development of the genital system of echinoids is initiated by the formation of the genital stolon, a

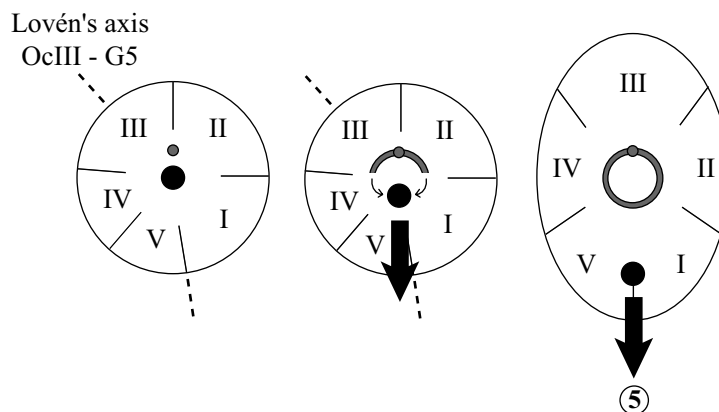


Fig. 4. The closure of the genital ring (gray) determines a weak point in interambulacrum 5, between growth zones I and V. The periproct follows this favored direction (black arrow) and migrates before the closure of the genital ring in irregular echinoids.

Fig. 4. La fermeture de l'anneau génital (en gris) détermine un point de faiblesse dans l'interambulacrum 5, entre les zones de croissance I et V. Le périprocte emprunte cette direction privilégiée (flèche noire) et migre avant la fermeture de l'anneau génital chez les oursins irréguliers.

structure most likely derived from the left somatocoel [25]. The genital stolon gives rise to two buds that curve around in opposite directions and then merge, forming the genital ring (Fig. 4) which, in 'regular' echinoids, encircles the rectum below the genital plates [7, 41]. Later, the gonads will bud from the adoral surface of the ring, while gonoducts will come off in the opposite direction. Then the stolon itself separates from the somatocoel and disappears as the genital ring atrophies. In the adult, the gonads remain connected to each other by the remnants of the genital ring, and the gonoducts finally open through the gonopores on the aboral surface of the test.

The aboral part of the digestive system includes the intestine, the rectum, and the anus. The intestine forms the second loop of the gut, and the rectum corresponds to an uncoiled tube connecting the intestine to the anus [9]. Intestine and rectum form quite late, after the appearance of the periproctal plates, by elongation of the larval intestine. In irregular sea urchins, the periproct's displacement is initiated before the closure of the genital ring [15, 16, 41], and the rectum expands outside the genital ring (Fig. 4). In all 'regular' echinoids with an eccentric periproct, the rectum remains inside the genital ring, but it is likely that this genital ring is stretched in the direction of migration. Nevertheless, genital plate 5 is always perforated, and the corresponding gonad in interambulacrum 5 is func-

tional. In other words, even if the eccentricity of the periproct deforms the apical system, it does not hinder the formation and the functioning of the gonadal structures in interambulacrum 5.

We have noted above that the genital ring forms at a stage at which von Ubisch's primordial axis brings about a condition in which genital plate 2 is opposite interambulacrum 5. Because the formation of the genital ring commences from beneath genital plate 2, it ends on the opposite side of the genital ring in the direction of interambulacrum 5, between growth zones I and V. Therefore, the direction of migration for the periproct that will least interfere with this development of the genital ring is also towards interambulacrum 5. Interambulacrum 5 is therefore the path of least resistance for the movement of the periproct and related viscera because the formation of the genital ring is timed and configured to provide a kind of 'gateway' to this pathway. It is difficult to envision this series of pleiotropies as anything other than a developmental constraint. This constraint helps to explain why the periproct exhibited a tendency to move (7 times among the 'regular' echinoids), or in fact fully migrated (in the Irregularia) only between growth zones I and V. Moreover, it is this concatenation of developmental events that actually made it possible for the Irregularia to adopt a secondary anterior-posterior axis.

8. Integrating geological and developmental time

Observations of specimens of *Heterodiadema libycum* (Upper Cretaceous [Cenomanian] of Morocco), a ‘regular’ echinoid with a very eccentric periproct, show that the stretching of the apical system due to the displacement of the periproct occurs relatively late in the ontogenetic sequence of the post-larva. As Devriès [10] noticed, the eccentricity becomes more and more marked with the size of the specimen. In the largest specimens that we could observe, the periproct lies in an anal sulcus that extends along interambulacrum 5 to the margin of the test. Such a pattern suggests considerable distortion of the genital ring or even partial disruption of that ring.

In the Lower Jurassic, the very earliest echinoids that can be placed in the Irregularia, such as *Plesiechinus hawkinsi* (Sinemurian of Nevada) and *Loriolella ludovicii* (Domerian of Italy), still display the pattern observed in ‘regular’ echinoids, namely that genital plate 5 bears a gonopore. In addition, the eccentricity of the periproct becomes more pronounced as ontogeny progresses [26, 45].

However, as early as the end of Lower Jurassic, genital plate 5 of irregular echinoids is no longer perforated, a condition that can be interpreted as either a loss of the fifth gonad or at very least a loss of a genital connection to genital 5. Moreover, our observations on early juveniles of irregular echinoids from the Jurassic and Cretaceous confirm the precocity of periproct migration noticed by Gordon [15] in her studies of the extant *Echinocardium cordatum*. For example, a specimen of *Pygaster lourdinensis* 8.7 mm long (Middle Jurassic [Bathonian] of western France and the type specimen of Lambert’s collection), as well as a specimen of *Pygaster subtilis* 7.8 mm long (Upper Jurassic [Oxfordian] also from western France and specimen L 8.17A from Lambert collection) display significant periproctal eccentricity at stages that roughly correspond to a size at which we would expect closure of the genital ring. Similar observations have been made on a specimen of *Globator haucockensis* 6.4 mm long (Cretaceous [Albian] of Texas). The smallest Cretaceous specimen we found is a juvenile of *Pygopyrina incisa* 2.9 mm long (from the Lower Cretaceous [Valanginian] of eastern France), which possesses a conspicuous

anal sulcus at a stage in which the genital ring may not yet be closed.

These results indicate that among irregular echinoids as early as Middle Jurassic, the eccentricity of the periproct is initiated very early in ontogeny – even earlier than in the very first irregular echinoids and earlier than in any ‘regular’ echinoids that possess eccentricity. This further suggests that the periproct moves down interambulacrum 5 before closure of the genital ring. Early displacement of the periproct likely suppresses the formation of the fifth gonad, and genital plate 5 remains unperforated. We suggest that an essential difference between ‘regular’ and irregular echinoids, exocyclism, can be explained by a shift in the timing of periproctal migration.

Gould [22] defined heterochrony as “shifts in developmental timing for features already present in ancestors”, stressing the resulting shape (either juvenilized or peramorphic), but refusing to extend the terminology to the rates and timings that themselves cause the shifts. He also raised the problem of the application of heterochronic concepts to paleontological data, especially when the absolute ontogenetic age of a fossil could not be determined. He felt that the relative size of a specimen of a given fossil species was a “false surrogate for developmental stage” [22, 27].

Nevertheless, we consider the early displacement of the periproct in the development of irregular echinoids to represent a shift in the developmental timing of a feature present in an ancestor common to all irregular echinoids. We can only estimate ontogenetic stage by size, leaving open the question of whether apparent precocity of the displacement of the periproct could be interpreted simply as a general decrease in growth rate of irregular echinoids. If this was the case, we should be able to recognize lower growth rates among all irregular echinoids, whether fossil or extant, than in ‘regular’ echinoids. Nothing like that seems to have ever been reported. Therefore, the escape of the periproct before the closure of the genital ring is best interpreted as a time-lag between the initiation of periproctal migration and the closing of the ring. The origin of exocyclism in irregular echinoids can be explained by earlier onset of the migration of the periproct (that is, a shift in the timing of eccentricity). Some (e.g. [32]) would see this type of phenomenon as pre-displacement, or an earlier initiation of morphological development of a specific structure.

9. Radial to bilateral: a scenario for eccentricity

Although embryological data can help to provide a consistent explanation for the mechanism that enables the periproct to move out of the apical system, they do not necessarily tell us what may have been the ecological or adaptive setting for a movement that occurred so many times in the same direction. Fortunately, we know enough about the phylogeny and ecology of echinoids to provide a scenario for the derivation of periproctal eccentricity in general, and an anterior-posterior axis in the Irregularia specifically.

The origin and diversification of irregular echinoids constitute an adaptive radiation corresponding to the colonization of soft bottom environments at the beginning of the Jurassic [29, 43]. In order to obtain sufficient nutrient from the sediments upon which they live, irregular echinoids collect and swallow large numbers of particles, and consequently eject large volumes of fecal material. Some workers argued that the migration of the periproct out of the apical system was necessary to remove the site of fecal discharge from the genital region so as to prevent pollution of reproductive products or hindrance of the spawning of gametes [29, 43]. A similar explanation was invoked by drawing on the need to avoid fouling of the respiratory structures on the aboral surface [44]. A simpler mechanical explanation can be proposed in view of the large amounts of sediment contained in the intestine of actively feeding irregular echinoids. A tendency for migration of the periproct towards the margin of the test could arise from a simple necessity to take advantage of a 'gravitational assist' for the evacuation of large amounts of sediments (De Ridder, personal communication).

Of some relevance to these scenarios is the question of which responses to which selective factors are of most importance to the first irregular echinoids. It would also aid acceptance of the explanation if the embodied concepts were also applicable to the eccentric 'regular' echinoids. One of the most significant features of the more crownward Irregularia is the pronounced, secondary bilateral symmetry. The anterior-posterior axis that demarcates this symmetry is not only anatomical, it is functional in the sense that these irregular echinoids are constrained to move only in a forward direction, with ambulacrum III in the lead. It is worth asking how this relates to the origin of the

posteriorly displaced periproct, not so much in a developmental sense, but in a functional or adaptive sense.

Scenarios for the evolution of the Irregularia indicate that some of the more basal irregulars such as holactypoids were already unselective sediment swallowers. Use of the Aristotle's lantern to scoop up sediment "represents the plesiomorphic condition for the holactypoids" and the "[podial particle picking mechanism] probably did not play a major role in food-gathering in these forms" ([46] : 221). However, with the origin of galeropygoids and other early cassiduloid-like forms, the more crownward irregular echinoids began to employ a highly sophisticated podial particle picking mechanism that greatly enhanced their ability to ingest large amounts of sediment. In cassiduloids, holasteroids and spatangoids, the role of Aristotle's lantern in this process was reduced and indeed lost, thereby reducing the restrictions that jaw elements placed on sediment volume that could be taken in at any given time.

It is equally important to irregular echinoids to keep moving to expose previously unprocessed sediments to the podial particle picking mechanism, thereby ensuring the highest possible access to more nutrient-laden particles. The development of a dominant locomotory direction went hand-in-hand with the need to move the periproct posteriorly where the likelihood of re-ingesting already processed sediments would be minimized. Some of these arguments could be applied to some of the eccentric 'regular' echinoids because these forms might also have benefited from a morphology and behavior that would have avoided ingestion of their own waste material.

However, it was only when forms such as the first 'true' irregulars began to move off hard bottoms and invade shifting sediments that the adjustments in developmental timing within the apical system that produced eccentricity of the periproct triggered a veritable explosion of new forms. Adaptations such as the anterior-posterior axis, anteriorly-placed mouth, single-direction locomotory systems with spines specialized to produce an efficient power-stroke, and a sophisticated podial particle picking mechanism provided continuous access to fresh and abundant supplies of nutrient-poor food. The posteriorly-placed anus worked in concert with these modifications to facilitate elimination of processed sediments. A relatively simple change in developmental timing fueled a diver-

sification into forms as extreme as the highly elongated, bottle-shaped pourtalesiids, and as highly attuned to sediment particle size ranges as the heart urchins and sand dollars.

The fact that the lifestyles of all taxa exhibiting migration of the periproct are different suggests that a single adaptive process is unlikely to explain all observed situations. Whatever the adaptive trigger for periproctal migration in Irregularia might be, the unique pathway open to that migration among echinoids is a vivid illustration of the role played by developmental constraints in evolution. “Evolution is a balance between internal constraint and external pushing to determine whether or not, and how and when, any particular channel of development will be entered” ([20] : 191).

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