Environmental control versus phylogenetic fingerprint in ontogeny: The example of the development of the stalk in the genus Guillecrinus (stalked crinoids, Echinodermata)

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Abstract
The stalk morphology of the deep-sea stalked crinoid Guillecrinus changes a lot from juvenile to adult. As a result of its unusual morphology among the extant crinoids, its taxonomic and phylogenetic affinities remain unsettled. Distinctive morphological changes characterize the various growth stages in stalked crinoids. We conduct and discuss a detailed ontogenetic analysis of the stalk of the two species (Guillecrinus neocaledonicus and G. reunionensis) of this Indo-Pacific genus, which was observed in its environment during submersible dives off New Caledonia. Analyses examined (1) morphological changes, (2) the degree of change in morphology, (3) architectural constraints, and (4) the functional constraints related to environmental factors. The relations between three levels of integration were examined: the ossicle (columnal), the stalk, and the complete individual. The changes in level of organization were estimated. The analysis reveals that the external stalk morphology of Guillecrinus goes from a pronounced xenomorphic type in juveniles, characterized by diversified columnal articulations, which provide the proximal and distal part of the stalk with a considerable degree of flexibility, to a dominant homeomorphic type in adults, characterized by columnal articulations which allow little or no movement. This ontogenetic change through a mosaic of heterochronic developments corresponds with a change in the hydrodynamic environment, from a turbulent to a laminar water flow, and from nutritional constraints. The extensive development of deep ligament fossae in adults and in the distal stalk of juveniles corresponds to a relatively low allocation of energy to the skeleton, rather than a functional necessity. Proximal columnals in juvenile Guillecrinus display characteristics of adult Hyocrinidae. Distal columnals exhibit the typical morphology observed in Bourgueticrinina. Juveniles stages of both proximal and distal columnals show a high degree of specialization (derived characters). Well-supported classifications have typically placed the Bourgueticrinina and the Hyocrinidae in two very dissimilar groups. Specific characteristics from the three very different families Bathycrinidae, Guillecrinidae and Hyocrinidae appear to be expressed either separately (Hyocrinina or Bathycrinina) or together (Guillecrinus). Their expression appears to depend on functional and environmental constraints. The transformation of columnals from juvenile to adult shows the important role of hypermorphic processes. However, no evidence of phylogenetic recapitulation was observed. Does the evidence presented here support or disprove current taxonomic interrelationships? How does morphology relate to ontogeny? Is heterochrony involved?
Introduction

Interest in the study of ontogeny and heterochronic development was revived by the work of Gould (1977). Much research was dedicated to the subject during the following decade (McKinney 1988; McNamara 1995) with an emphasis on phylogenetic reconstruction. However, one of the major consequences of heterochronic processes is the ability to provide phenotypic plasticity during the growth of the individual. This plasticity permits the individual to adapt easily to its environment (Roux et al. 1997). A more global approach, which integrates functional biology with the various interactions that take place during development, has been deemed necessary (Raff 1996; Kupiec and Sonigo 2000).

From this perspective, stalked crinoids, with their capacity for growth and regeneration and their complex skeletal architecture with numerous well-differentiated ossicles, constitute a remarkable subject for ontogenetic analysis (Améziane-Cominardi and Roux 1994, 2003; Roux et al. 1997; David 1998; David and Roux 2000). In similar ecological conditions, phenotypic convergences are frequently observed. The ontogeny of morphological characteristics (morphogenesis) displays convergences (ecophenotypes) or divergences (adaptive radiations). It results from the interaction between genetic potentialities and environmental constraints. It respects architectural constraints. In other words, the phenotype does not necessarily reflect the genotype. In what respect, then, can ontogeny offer an argument in favour of phylogenetic reconstruction?

Stalked crinoids are rheophilic suspension feeders. Their filtration capacity depends on local hydrodynamic conditions. Their stalk must meet certain functional needs (Roux 1987). Phenotypic responses permit either flexibility or rigidity, according to the strength and nature of the current (e.g. whether it is laminar or turbulent). They depend on the frequency of articulations and the extent of their movements. Paraxial ligaments unite the stalk ossicles (columnals) and prevent movement of the articulations when they are resting, by compressing them. When the current exerts pressure (drag and lift) on the filtration fan, which consists of pinnulated arms, the stalk is extended and the articulations gain a greater ability for movement.

The organization of the articulations varies with the taxon. The importance of the genus *Guillecrinus* lies in the wide range of modifications in the pattern of articular facets within the same stalk and also from one ontogenetic stage to the next. Such changes have been observed in the stalks of the genus *Porphyrocrinus*, but its ontogenetic analysis (Roux 1977) was limited due to the lack of sufficiently young specimens. As regards the genus *Guillecrinus*, we now have two young specimens, along with a series of older ones, which permit a more detailed analysis of the ontogeny of the stalk, as discussed here.

Taxonomy, material and methods

The brachial crown (the filtration fan) is linked to the stalk by the aboral cup. The latter is generally made up of two circles of plates (basals and radials), and sometimes a third (infrabasals). New columnals appear at the base of the aboral cup while the stalk is growing.

For a detailed description of the morphology of stalked crinoids, see the general chapters on crinoids in the *Treatise on Invertebrate Paleontology* (Ubaghs et al. 1978) or the recent compilation of living stalked crinoids (Roux et al. 2002).
The genus Guillecrinus

The first specimens of *Guillecrinus* (*G. reunionensis*) were discovered on the bathyal slopes of Réunion Island in the Indian Ocean (Roux 1985) (Figure 1e–h). They differ substantially from other living stalked crinoids in having infrabasals, which appear to be highly developed in one of the specimens. The hypothesis of an affinity with Palaeozoic forms of the subclass Inadunata was suggested. Recently, *G. reunionensis* has been collected in the West Indian Ocean (Mironov and Sorokina 1998). Bourseau et al. (1991) described several specimens of a second species (*G. neocaledonicus*) found during bathyal cruises carried out off New Caledonia (South-West Pacific). None of these specimens shows visible and indisputable infrabasals (Figure 1a–d). This has been interpreted as a tendency towards regression of the infrabasals and cryptodicyclicity. The proximal part of the juvenile stalk (proxistele) is markedly different and disappears in the adult form (Figure 1a, b).

Both species have a crown of five arms, with fine flexible pinnules extending from each. The filtration surface is relatively limited compared with that of specimens of the same size of *Proisocrinus ruberrimus*, a millericrinid stalked crinoid associated with *G. neocaledonicus*, off New Caledonia (Roux 1994). *Guillecrinus* lives on irregular rocky substrates which induce varying hydrodynamic conditions according to individual scale.

The place of the genus *Guillecrinus* among extant crinoids has not yet been established. Recently, Mironov and Sorokina (1998) linked it to the Hyocrinidae. However, it differs from this family in a few characteristics, such as pinnulation, the size and form of the aboral cup, and the external morphology of the stalk. No hyocrinid has infrabasals. Bather (1900) even considered their aboral cup as strictly monocyclic, implying that the infrabasals did not regress and disappear (as in the cryptodicyclic condition) but never appeared at all.

The level of organization of the stalk and the crown of *Guillecrinus* is considered to be the most advanced among post-Palaeozoic stalked crinoids (Améziane-Cominardi and Roux 1994). A marked differentiation in adaptive derived characters seems to mask the phyletic origin of the genus. No fossil is known at this time.

Material studied

The material studied is preserved in the Zoological Collection (Echinoderm Section) at the Muséum national d’Histoire naturelle de Paris (Table I). The specimens of *G. reunionensis* were collected during cruise MD32 of N/O *Marion Dufresne*, off Réunion Island (Guille 1982). The specimens of *G. neocaledonicus* were collected during a series of cruises that explored the Norfolk Ridge and the bathyal slopes off New Caledonia (Richer de Forges 1998). During the latter, *G. neocaledonicus* was observed in situ and as an almost entire juvenile specimen (N3) collected on the CALSUB cruise with the submersible CYANA (Roux 1994).

The need to resolve the problem of the possible existence of infrabasals required dissection of the paratype of *G. reunionensis*, as well as a juvenile (N5) and an adult specimen (N6) of *G. neocaledonicus*. Other skeletal fragments have also been dissected in order to observe their articulations under the scanning electron microscope (SEM). The microphotographs were made at the SEM services in the Muséum d’Histoire naturelle and at the Centre for Interdisciplinary Study in Micro Electronics at the University of Paris VI.
Figure 1. External morphology of the proximal part of the arms of the stalk. (a–d) *Guillecrinus neocaledonicus*: (a) specimen N1, holotype; (b) specimen N2; (c, d) specimen N3, juvenile. (e–h) *G. reunionensis*: (e, f) specimen R2; (g, h) specimen R1, holotype. ba, basals; ib?, pseudo-infrabasals. Scale bars: 1 mm (a, b, e, g, h); 0.5 mm (c, f); 0.2 mm (d).
Analyses and aims

The morphology of the stalk at a given stage of crinoid development is the result of the sum of the ontogenetic stages experienced by the different component columnals (Ameziane-Cominardi and Roux 1994; Roux et al. 1997). New columnals appear just below the aboral cup throughout the animal’s life. The proximal columnals at the adult stage are those which are formed last (the youngest ones), while the distal columnals are older. These distal columnals began their growth in a proximal position at an earlier stage in the animal’s development (Figure 2).

The ontogeny of the whole stalk takes place at a level of integration above that corresponding to each ossicle or articulation. We also observed the level of integration of the whole individual where interactions between the stalk and the crown take place. Particular problems are associated with each level of integration. We attempt to distinguish between the different stages of analysis.

Generally, individual development is reconstructed by means of observing different specimens (either columnals or stalks). While these reconstructions are faithful to real-life specimens, the morphological variability is limited. However, in Guillecrinus, ontogenetic trajectories of columnals vary according to their age and their position on the stalk. Important variations also exist in the growth trajectory at the scale of the individual. In such conditions, only general ontogenetic tendencies are accessible. It is necessary, however, to avoid generalizations and to adopt strict methods of reasoning.

Table I. Inventory and locality data of the material studied.

| Species     | No. | Status       | Cruise | Station | Coordinates         | Depth (m) | Dp  |
|-------------|-----|--------------|--------|---------|---------------------|-----------|-----|
| neocaledonicus | N1  | Holotype     | CALSUB | Plongée 2 | 20°37’S, 67°144E   | 1130      | 4.2 |
| neocaledonicus | N2  | Paratype 1   | CALSUB | Plongée 2 | 20°37’S, 167°144E  | 1130      | 4.2 |
| neocaledonicus | N3  | Paratype 2 juvenile | CALSUB | Plongée 12 | 21°28’S, 166°21’E | 1265      | 1.8 |
| neocaledonicus | N4  | Distal fragment | Biocal | CP 74     | 22°14.06’S, 167°29.01’E | 1300–1476 | –   |
| neocaledonicus | N5  | Juvenile     | Biocal | CP 74     | 22°14.06’S, 167°29.01’E | 1300–1476 | 2.4 |
| neocaledonicus | N6  | Fragment     | Biogeocal | CP 238 | 21°27.64’S, 166°23.41’E | 1260–1300 | 4.8 |
| neocaledonicus | N7  | Fragment     | Biogeocal | CP 238 | 21°27.64’S, 166°23.41’E | 1260–1300 | 3.9 |
| neocaledonicus | N8  | Complete     | Halipro | BT 59     | 24°59’S, 168°42’E | 1312–1520 | 3.7 |
| reunionensis | R1  | Holotype     | MD32   | CP 105    | 20°47.4’S, 55°04.4’E | 1740–1850 | 7.3 |
| reunionensis | R2  | Paratype     | MD32   | CP 105    | 20°47.4’S, 55°04.4’E | 1740–1850 | 5.1 |
| reunionensis | R3  | Distal fragment | MD32   | CP 15     | 21°14.7’S, 56°07.5’E | 1880–1980 | –   |
| reunionensis | R4  | Distal fragment | MD32   | CP 15     | 21°14.7’S, 56°07.5’E | 1880–1980 | –   |
| reunionensis | R5  | Distal fragment | MD32   | CP 68     | 21°12.5’S, 55°00.9’E | 1340–1775 | –   |

Dp, proximal diameter.
The growth (size) and morphogenesis (shape), along with their variation with age, are the three major parameters of heterochronic development (Gould 1977). Growth rates are unknown in *Guillecrinus*, and only relative ages may be estimated. The presence of genital pinnules, described by Mironov and Sorokina (1998), indicate the sexual maturity that distinguishes the adult stage.

A semi-quantitative estimate of the level of organization of specimens suggests a link between ontogeny and a problem of energy allocation (Améziane-Cominardi and Roux 1994; Roux et al. 1997). The level of organization is independent of morphology. Therefore, different shapes may correspond to a similar level of organization.

Morphofunctional analysis reveals an adaptation to the constraints of the physical environment. For rheophilic stalked crinoids, these constraints are mostly linked to hydrodynamics. The best functioning of the articulations in the stalk does not necessarily depend on their level of organization (Roux et al. 1997). A parsimonious use of energy tends to obtain the maximum functioning capacity within a given environment, even when it has a minimal level of organization. Function stalk alternates between flexibility and rigidity. Depending on the development of the filtration fan (the arms and pinnules) and its resistance (drag) to the current, the articulations of the stalk may be extended (increase in flexibility) or compressed (increase in rigidity) (Roux 1987). Analysis of the filtration fan of *Guillecrinus* is the object of a forthcoming study. Here, we only intend to outline some of the major consequences of the arm pattern in relation to the functioning of the stalk.

It is important to distinguish functional units from morphological units, especially at the columnal level of organization. Here, a morphological unit corresponds to one columnal, while a functional unit consists of two halves of adjacent columnals, united by an articulation (Figure 3). A single ossicle may have different articulations at either end and thus be part of two separate functional units. Articular facets are the result of the functional constraints on the articulation through ontogeny. Such interactions between two ossicles could be called co-ontogeny. Depending upon the level of integration examined, different symmetries may appear. For example, a single synarthry, regarded as a functional unit, has one axis of symmetry. A single ossicle with offset synarthries at opposite ends shows two axes of symmetry. The symmetry appears multiradiate when we consider the superposition of articulations along the complete stalk (Figure 3). Thus, the question is raised: why,
among the multiple possibilities of radial symmetries, does the pentamerous pattern predominate?

Ontogeny does not necessarily recapitulate phylogeny, especially when an organism has a high ability to adapt to environmental changes during its development (Roux et al. 1997). The same taxon can develop within various morphogenetic fields. In the absence of a palaeontological record, it is impossible to know whether the historical sequences go towards one morphological pole or the other within these morphogenetic fields. Often extrapolating from the scale of a specimen (ontogeny) to the scale of geological time (phylogeny) may be hazardous and speculative for understanding the evolution of a major taxon. We wish to avoid this trap. We will only refer to those affinities between taxa revealed through the ontogeny of *Guillecrinus*. At first, we shall attempt to situate *Guillecrinus* among present-day stalked crinoids.

Figure 3. Morphological units versus functional units, and symmetries at two levels of integration (ossicle and stalk). (a) A columnal viewed along its proximal/distal axis; (b) symmetry produced by superimposing the proximal and distal fulcral ridges of the columnal in (a); (c) superposition of articular fulcra of all columnals along the stalk; (d) schematic diagram of morphological and functional stalk units and their interactions.
The aim of this study is to provide a detailed example of ontogenetic analysis which comprises: (1) three successive levels of integration, namely the ossicle, the stalk and the individual; (2) their respective levels of organization; and (3) their architectural and functional interactions.

Morphogenesis of the stalk of *Guillecrinus neocaledonicus*

The xenomorphic juvenile stage

One of the paratypes of the species (N3) is a juvenile (Figure 1d). Its stalk consists of 148 columnals. Its preserved length is 13 cm with a proximal diameter of 1.8 mm and a distal diameter of 1.6 mm. The biometrical profile (Figure 4) displays a proxistele distinguished by columnals that are much wider than high (average height 0.2 mm). In the mesistele, columnal heights range from 2 to 2.6 mm, 1.4–1.8 times taller than their diameter. A transitional zone (MI), located between the 70th and 95th columnal, lies at the beginning of the mesistele. It is characterized by a rapid increase in columnal height. The distal end of the stalk is missing. However, the most distal columnals belong to the dististele.

A second juvenile specimen (N5) is slightly older than the first (proximal diameter of 2.4 mm). The proximal part of the proxistele has 25–31 columnals, which are visible externally. At the distal end, the columnals become less pentalobate and more pentagonal. The diameter of the columnals decreases clearly, while their height increases more moderately. This specimen was dissected entirely for the SEM study of articular facets.

![Figure 4. Biometric profiles of the stalk of the juvenile specimens of *Guillecrinus neocaledonicus*. The numbers in circles refer to the symmetry of the articulations (for 5b, 5c, 3’ see Figure 6). Dotted area with the single line defines transitional zone of mesistele; double vertical lines define the entire mesistele.](image-url)
**The proxistele.** In specimen N5, three or four delicate columnals of successively increasing diameter are hidden by the basal ring. The first columnal (Figure 5a) is made up of a layer of undifferentiated stereom, which corresponds to the claustrum, and has a partial and irregular gap in the centre. In the following columnals, five interradial lacunae appear outside of the central lacuna; the five radially orientated extensions of the chambered organ pass throughout the central lacuna (Heinzeller and Welch 1994). These five lacunae progressively connect to the central lacuna and produce a pentalobate lumen at the centre of the claustrum (Figure 5b, c). Such a pentalobate lumen opened in the claustrum is called jugulum in Palaeozoic crinoids (Moore et al. 1968; Ubaghs et al. 1978). Anlages of ligamentary areolae facing the exterior develop at the tips of the star-shaped part of the facets (Figure 5b). These anlages lie on the axis of the basals in an interradial position. The interior of each basal (Figure 11e) has an areola to which one of the five paraxial ligament bundles are attached.

The new columnals develop slightly beyond the base of the aboral cup. Then, their diametrical growth stops when they attain the diameter of the basal ring. Hence, the diameter of the proximal columnals diminishes to the end of the proxistele (Figure 4) so that successive diameters serve as a record of the earlier stages in the growth of the basal diameter of the aboral cup.

In the first columnals, which are externally visible, the articular facets have a central lacuna, which grows into a pentalobate lumen and then becomes subcircular. The five areolae grow and are linked by strips of syzygial stereom (Figure 5c, d). On the outside of each syzygial strip, a symplexial crenular unit with two to five crenulae develops. These, in turn, become articulations which are functional symplexies. In the more distal articulations of the proxistele, the crenularium dominates a central depression which has five areolar extensions (Figure 5f). As the diameter of the central lumen increases, the claustrum tends to disappear.

The proxistele of the smaller paratype (N3) has a similar general morphology. However, the decrease in columnal diameter in the distal part of the proxistele is less moderate and the increase in height is negligible (Figure 4). The possibilities of deepening the areola and the development of the relief of the symplexial crenularium depend on the thickness of the columnals.

**The mesistele and the dististele.** In the juvenile paratype (N3), the principal morphological discontinuity lies between the proxistele and the remainder of the stalk in the M1 transition zone. It is characterized by a stabilization or a slight increase in the diameter and a rapid increase in the height of the columnals (Figure 4). From then on, the changes in the shape of the columnals are more moderate and irregular. The biometric profile of height shows three zones of growth. The most proximal spurt of growth prolongs the transitional zone at the proximal end of the mesistele. The columnals reach their maximum height in the second spurt of growth near the distal end of the mesistele. The more distal spurt of growth in the dististele is characterized by a slight increase in diameter, while the height diminishes markedly.

The articulations remain subpentagonal (Figure 6). They correspond to the pentagonal symplexies present in the first spurt of growth. They have five crenular units with one to two short and regular crenulae, which separate the wide lobes of the areola. These lobes reach the external edge of the facet (Figure 6a). The perilumen is distinguished by a thick framework. In the second spurt of growth, the articular facets remain quite similar. However, the crenularium becomes more irregular and has a syzygial tendency, while
Figure 5. Columnals of the stalk from the juvenile specimen N5, from the most proximal (a) to the distal extremity of the stalk (f). Scale bars: 0.5 mm.
Figure 6. Columnals of the mesistele and dististele of juvenile specimen N3. (a) Columnal 5b; (b, c) columnal 5c; (d) columnal 4; (e) columnal 3; (f) columnal 2 (see their place on the biometric profile on Figure 3). Scale bars: 0.2 mm.
areolar lobes deepen toward the centre (Figure 6b, c). The most distal spurt of growth consists of about 15 columnals. Their articulations develop fewer than five very deep areolar lobes (Figure 6d–f). The perilumen is distinct. It constitutes a pivot, which facilitates the flexibility of the articulation. The interareolar ridges are relatively large and covered by an irregular syzygial crenularium of varying extent. The last articulation is bilaterally symmetrical and forms a quadrangular synarthry (Figure 6f). Its wide fulcral ridge encloses the axial canal. Secondary crests develop somewhat precociously from the outer edge of the areolar pits during the growth of the ossicle. They differ from the primary ridges because they partially separate the areolar depression and never reach the perilumen. They are named subsidiary crests. The morphology of this most distal remaining articulation visible (Figure 6f) suggests that the more distal articulations of this juvenile stage are probably more typical bilateral synarthries.

Discussion. In the young *Guillecrinus* specimens, the scheme of pentaradial symplexies with five areolae is present in both the proxistele and mesistele. Radial symmetries of fewer than five divisions are only present at the end of the dististele. Among them, bilateral symmetry produces a functional synarthry. The hollowing of the areolar lobes into deep ligamentary pits develops in the distal part of the mesistele and in the dististele of the youngest specimen (N3). It begins in the proxistele in the oldest specimen (N5). This hollowing corresponds to an increase in the flexibility of the articulations, which reaches its height in the bilateral and highly evolved synarthries (*sensu* Roux 1977).

The oldest columnals (the most distal ones) have a bilateral or trilateral symmetry. In the later developing, more proximal columnals, the generalized pentaradiate symmetry appears. The five areolar lobes seem to be induced by the organization of the distal side of the aboral cup with its five equal basals. However, the pentaradiate symmetry could also appear in relation to those of the chambered organ.

Adult homeomorphic stalks

The proxistele disappears when the proximal diameter of the stalk is between 2.5 and 3.5 mm. All of the currently known adult specimens of *G. neocaledonicus* have a proximal diameter greater than 3.5 mm and possess a homeomorphic stalk.

Biometric profiles. Variations in the height of the columnals record the different stages in the development of the stalk. The three specimens of the type series show the transformation from a juvenile xenomorphy to an adult homeomorphy (Figure 7). The two adult specimens (N1 and N2) are of a similar size (proximal diameter of about 4.2 mm). However, the holotype (N1) preserves an intermediate pre-adult profile, with subpentagonal proximal columnals. The first 30 or so columnals increase rapidly in height, calling to mind the transitional zone (M1) of the juvenile stage. This zone is much shorter in the adult paratype (N2), in which it consists of fewer than 10 columnals. It is part of a strong and individualized proximal spurt of growth. This, in turn, precedes a return to lower values, similar to those of the holotype, and the height increases once again progressively. The proximal zone of decrease in the diameter of the columnals comprises 20 or so columnals.

The other specimens, whose stalk is complete (or almost), provide complementary information (Figure 8). The biometrical profile of the height of the proximal columnals of the smallest specimen (N8) is intermediate between that of the holotype and that of the
adult paratype. From the distal side, the columnals progressively reach a maximal height. This height then decreases throughout the 30 or so columnals.

The largest specimen (N6) shows a proximal spurt of growth in height, which is both fast and strong. It reaches a value (4.8 mm) greater than that of any other columnals. Then, columnal height falls to 2.5 mm and remains similar until the 75th columnal. The distal part of the profile is similar to that of specimen N8. The other specimen from the same station (N7) is notably younger. The irregularity of its biometrical profile is principally due to abnormally reduced heights between the 63rd and the 96th columnal. It consists of growth cessation or regression of the proximal part of the stalk probably linked to a regenerative phase in the brachial crown. A similar phenomenon is known in the pentacrinid crinoids (Amemiya and Oji 1992; David et al. 1998).

Columnal height diminishes and diameter increases approaching the fixation disc. The increase in diameter (sometimes more than double) can happen quickly in the last 10 columnals (specimen N6) or can be more progressive over 40 or so columnals (specimen N4). Nevertheless, no morphological discontinuity justifies differentiation of a dististele.

**Morphology of articular facets.** The most typical and most frequent articulation (Bourseau et al. 1991) is a pentaradiate syzygy with a circular section and lumen. Its large subtriangular, deep ligamentary depressions do not reach the axial canal (Figure 9f). The interareolar ridges have subparallel edges and a syzygial crenularium, which is usually either irregular or meandriform and is sometimes radial and slightly symplexial. Beyond the external edge and the interareolar axes which support the crenularium, the facet is covered with galleried stereom, characteristic of ligamentary zones. This scheme, always present throughout most of the stalk, varies on both the proximal and distal ends of the stalk.
Proximal facets: at the level of the strong spurt of height increase (the first 10 columnals), the largest specimen (N6) displays more numerous (6–10) deep areolar pits, which are irregular, poorly defined and restricted to the external half of the facets (Figure 9d). However, a pentaradiate symmetry dominates and is emphasized by the radial crenularium. This aspect is more visible on the first columnal (Figure 9a, b). The centrifugal development of the ossicle begins in the five major interareolar zones. It is continued in the secondary interareolar ridges. When the external edge is reached, the stereom circumscribes the future ligamentary pit, and the junction between the different

Figure 8. Biometric profiles of the stalk of the specimens of *Guillecrinus neocaledonicus* which do not belong to the type series. (▲) Fixation disk.
Figure 9. Proximal and median columnals of the adult specimens of *Guillecrinus neocaledonicus*. (a–d) Proximal columnals of the N6 specimen: (a) most proximal columnal, distal facet; (b) same columnal, proximal facet; (c) second columnal, proximal facet; (d) third columnal; (e) one of the proximal columnals of the N7 specimen; (f) most frequent type of columnal in the N7 specimen. Scale bars: 1 mm.
developmental axes is executed on the external surface of the columnal. As a result, the areola divides into as many as 10 small deep ligamentary depressions, which limits the area of each (Figure 9c). The distal facet of the aboral cup bears 10 areolar lobes, where the principal paraxial bundles of ligamentary fibres are anchored (dp in Figure 11d). The articulation between the first and the second columnal shows a strong symmorpherty, and its crenularium is symplexial with crenular units having one or two divisions (Figure 9a). Beyond this, the relief of the crenellae fades and the syzygial character of the crenularium dominates (Figure 9d). At the adult stage, the irregularity of the centrifugal development of the first columnals onward (Figure 9a, b) explains the chaotic aspect of the architecture of the proximal stalk.

In the younger specimen (N7) from the same station, the part of the stalk where the height of the columnals remains relatively low (towards the 50th columnal) has articulations with regular pentaradiate symmetry (Figure 9e). The oval deep ligamentary pits are again restricted to the external half of the facet. The articulations can see-saw on the well-developed perilumen, which facilitates the stalk’s flexibility. The axial canal bears the traces of its pentalobate juvenile stage. The most typical morphology of the articulations is only seen beyond the 100th columnal, when the main part of the growth in height is finally achieved (Figure 9f).

Distal facets: the syzygial crenularium is reinforced, and regular subsidiary crests develop from the external border of the ligamentary depressions (Figure 10a, b). The multiplication of these crests and their extension subdivides the ligamentary depressions and restricts them to the centre of the facet. Towards the distal extremity of the stalk, the successive modifications of the articulations (Figure 10) have been observed in detail on specimen N4, the largest distal fragment collected (Figure 8). The modifications in the articulations are favoured by the growth in the diameter of the columnals. The subsidiary crests appear on the 40 columnals proximal to the fixation disc. Just before the strong growth in diameter of the most distal columnals, most of the facets have 10 crests (five initial crests and five subsidiary crests). Then tetrasyndrommetrical facets appear, first eight crests (four initial crests and four subsidiary crests) (Figure 10d), then 16 crests (four initial crests + four secondary subsidiary crests + eight tertiary crests) in the most distal articulations (Figure 10e). They represent a remnant of the symmetry of the juvenile dististele (Figure 6). For those columnals whose diameter increases, the crests become more narrow in the interior and become larger towards the exterior (Figure 10c, d), while their growth in height has stopped early during their ontogeny. This aspect reveals ontogenetic modifications from the central facet (the younger stage) to the periphery (older stage). The lateral edges of radial crests become more parallel when the columnal height continues to grow near the distal end of the stalk (Figure 10).

The axial and transverse cross-sections of the ossicles of adult specimens allow us to observe the location of the different types of stereom. Columnals with deep ligamentary depressions on the outside are composed for the most part by galleried stereom (α in Figure 11a, b). The labyrinthic stereom is limited to the exterior and under the interareolar ridges (β in Figure 11a, b). Here, the deep pits are the result of a partial hollowing of the ligamentary zone. The distal columnals are mainly made up of a labyrinthic stereom (Figure 11c), while the galleried stereom only covers the central ligamentary depressions. These articulations are no longer functional, and only the reduced ligamentary zone is deepened (the ontogenetic remnant of a younger stage). The wall of the axial canal is irregular and lacunary. This aspect is the result of the growth in diameter of the lumen through the resorption of the perilumen stereom.
Figure 10. Distal columnals of the adult specimens of *Guillecrinus neocaledonicus*. (a–f) Increasingly distal columnals with an increasingly early development of subsidiary crests: (a–d) facets with a pentaradiate symmetry; (e) facet with a four-part symmetry inherited from a juvenile stage similar to that of Figure 5d; (f) facet with bilateral symmetry and with two generations of subsidiary crests, inherited from a juvenile stage similar to that of Figure 5f, note the growth in diameter of the axial canal resulting from resorption of the perilumen stereom of the initial fulcral ridge. Scale bars: 1 mm.
Figure 11. Axial cross-sections of the columnals, and distal end of basals of *Guillecrinus neocaledonicus*. (a–c) Axial cross-sections of specimen N6: (a) columnal 4; (b) columnal 13; (c) distal columnal, showing the growth in diameter of the axial canal by resorption of the perilumen stereom (arrows). (d) Distal facet of a basal of adult specimen N6. (e) Distal facet of a basal of juvenile specimen N5. Dp, ligamentary depression; ca, axial canal; α, galleried stereom; β, labyrinthic stereom. Scale bars: 1 mm (a–c); 0.5 mm (d, e).
Discussion. Two ontogenetical tendencies develop in the adult stalks. (1) From the median stalk with five large deep depressions covering the entire ligamentary area on its proximal side, the last columnals formed multiple deep ligamentary pits restricted to the external part of the articulary facet. These articulations are functional and the galleried stereom dominates the heart of the columnals. (2) Towards the distal end of the stalk, the older columnal facets multiply subsidiary crests during the growth in their diameter. The ligamentary depressions are thus limited to the centre of the facets. The articulations lose their functionality. The labyrinthic stereom tends to dominate the architecture of these columnals.

At the adult stage, generalized of characters expressed solely in the distal part of the young stalks (deep ligamentary depressions, for example) can be observed in the entire stalk. The pentaradiate symplexy and the proxistele of the young stalk disappear. The peculiar articulations of the median stalk, exclusive to the genus *Guillecrinus*, then appear. This type of articulation is unknown in any other living or fossil stalked crinoid.

**Ontogeny of the stalk of *Guillecrinus reunionensis***

**Specimens of the type series**

The type series consists of two specimens from the same station. The holotype (R1) is the oldest specimen (Figure 1g, h). Its stalk is complete. The diameter at the base of the dorsal cup reaches 7.3 mm. The paratype (R2) is a clearly younger specimen (Figure 1e, f). Only the proximal part of the stalk is preserved. Its diameter beneath the dorsal cup is 5.1 mm. The size of these two specimens, and notably that of the holotype, is greater than the size of all known specimens of *G. neocaledonicus*.

**The paratype.** The proximal part of the stalk of the paratype (R2) is preserved over a length of 21.4 cm. The height of the majority of the columnals varies between 2.5 and 4.1 mm. The external morphology (Figure 1e, f), under the basal ring, seems to show five regular ossicles, which are higher than wide and appear to alternate with the basals. Roux (1985) interpreted them as an infrabasal ring. Among all of the specimens of *Guillecrinus* which have been collected since 1985, R2 is the only one with such presumed infrabasals. Dissection of the most proximal stalk and aboral cup of *G. neocaledonicus* has revealed the absence of infrabasals in both the adult and young specimens. A precise verification of the architecture of the dorsal cup of the paratype of *G. reunionensis* was therefore necessary.

The dissection of the proximal stalk and that of the aboral cup of the paratype (R2) also shows the absence of infrabasals. The irregularly star-shaped first columnal (col in Figure 12b) is not visible externally but is masked by the basal ring (ba in Figure 12b). The branches of the star are interareolar zones developed by centrifugal growth that alternate with the basals. This developing ossicle lacks areolar galleried stereom. Its lumen is clearly pentagonal. The second columnal is the first one visible externally (Figure 12c, d). It possesses five deep ligamentary depressions, which are not completely enclosed, particularly on the proximal side (Figure 12c). Externally, what appear to be the separate infrabasals (Figure 11f) are actually the five interareolar zones which are laterally expanded and fused along five externally visible suture lines (Figure 12d). The perilumen of the facets is raised and acts as a pivot, so that the first two articulations provide flexibility to the proximal extremity of the stalk. The axis of each interareolar zone is outlined by syzygial stereom. On the distal facet of the first columnal visible externally, a meandriform syzygial
Figure 12. Proximal and median columnals of *Guillecrinus reunionensis*. (a) Proximal facet of holotype. (b-f) paratype: (b) columnal under the basal circlet, not visible externally; (c) first visible columnal, proximal facet; (d) the same, distal facet; (e) 62nd columnal, proximal facet; (f) 63rd columnal, proximal facet. ra, radials; ba, basals; col, first columnal; s, suture visible externally. Scale bars: 1 mm.
The deep ligamentary depressions vary in size and are located at the outer edge of the facet.

The 13th columnal has six ligamentary depressions. Towards the distal end of the preserved segment, there are up to seven (Figure 12e), before returning to five (Figure 12f). At this place (62th columnal), subsidiary crests are beginning to form within the wider depression.

The biometric profile of columnal diameters (Figure 13) is very similar to that of the holotype of *G. neocaledonicus* (N1), although the values fall faster for the first columnals. The profile of the heights is characterized by two proximal spurts of growth. The second corresponds to a rapid increase in diameter and the acquisition of six deep ligamentary depressions. It precedes a rapid decrease in the height of the columnals up until the extremity of the preserved fragment. This decrease is coupled with a weaker growth in the diameter and a return to the pentaradiate symmetry in the columnals having a minimum height.

Figure 13. Biometric profiles of the stalk of three specimens of *Guillecrinus reunionensis*. (▲) Fixation disk.
The holotype. The holotype (R1) has a long complete stalk (more than 71 cm) with 223 columnals that vary, from 5 to 7 mm in diameter and from 2.3 to 4.5 mm in height. Towards the distal extremity of the stalk, the diameter of the columnals exceeds 11 mm.

The biometric profile of the stalk (Figure 13) is regular. After a rapid decrease in the first columnals, the diameter increases slowly and gradually with an abrupt increase just before the fixation disc. Variations in columnal height are generally similar to those observed in \textit{G. neocaledonicus}, although the increase in height is more gradual and the growth spurts in the distal half of the stalk are absent.

The irregularity in the development of the interareolar zones explains the chaotic aspect of the proximal stalk (Figure 1a). Under the basals, the apparently separate pieces correspond to the first developing columnal and not to a regressing infrabasal circle.

In the proximal half of the stalk, the number of ligamentary depressions on articular facets ranges between six, on the distal facet (towards the 110th columnal), and 10 on the proximal facet. The areolar pits are deep, triangular and regular (Figure 12a). The greater their increase in number, the more they move towards the outside of the facet. A transverse section made 2 mm under a facet of eight deep ligamentary depressions shows a juvenile ontogenetical stage of the columnal with five areolar zones. Even if their number is high, the areolar pits are regularly marked out. The axis of the interareolar zones is always outlined by a thin groove, and syzygial crenulae are absent or reduced (Roux 1985; Mironov and Sorokina 1998). The articulations of the distal half of the stalk have not been examined.

The other distal fragments of the stalk. Three distal stalk fragments that each has a part of the fixation disc come from stations other than that of the type series. One of them (R4) corresponds to a specimen whose size is similar to that of the paratype. However, the most proximal fragment of this specimen is not easily linked to the other fragments. Its position along the stalk is therefore not well established. The columnals of the most distal fragment have been dissociated in order to complete the information provided by the other fragments.

In the most proximal part of the fragment, the articular facets present eight or nine oval deep ligamentary depressions near the external edge. Toward the fixation disc, they become facets with five wide triangular depressions and with a pentagonal lumen. These are located just proximal to the zone of rapid growth in columnal diameter and the reduction in their height. Their syzygial crenularium is more developed than the crenularium of the proximal articulations.

Then, subsidiary crests develop on the external edge (Figure 14a). The perilumen regresses by resorbing stereom as the diameter of the axial canal increases (Figure 14b–d). With the increasing growth in columnal diameter, a new generation of subsidiary crests appears on the most distal articulations (Figure 14e). Crest width is always regular, but the new crests are narrower. The deep ligamentary depressions tend to become confined to the centre of the facet and then disappear (Figure 14f). At the same time, the symmetry is no longer necessarily pentaradiate. It can be either triradial (Figure 14c) or quadriradial (Figure 14e, f), as in \textit{G. neocaledonicus}.

For the two other specimens, the same modifications in the characteristics of the facets are found but subsidiary crests or the multiplication of ligamentary depressions appear at different distances from the fixation disc (Figure 15).

Discussion. The specimen of \textit{G. reunionensis} from the north-eastern Indian Ocean (Mironov and Sorokina 1998) has a proximal diameter of 6.2 mm. As regards its size, this specimen is
Figure 14. Distal columnals of *Guillecrinus reunionensis*. (a–d, f) Specimen R4. (a, b) 15th columnal; (c, d) 11th columnal; (f) 5th columnal; numbering from the fixation disc proximally. (b–d) Growth in the axial canal through resorption of the peripheric stereom. (e) Specimen R5. Scale bars: 1 mm.
situated between the holotype and the paratype. Only the proximal part of the stalk (15 columnals) is preserved. The first columnal is irregular. The diameter of the 15th columnal is 5.3 mm. The proximal maximum height of 5 mm is clearly greater than that of the specimens from Réunion Island. The articulations have 9–10 ligamentary depressions.

The principal ontogenetic tendencies displayed in *G. neocaledonicus* are here expressed along the stalk of the adult specimens of *G. reunionensis*. Besides the size, which is larger in the known specimens of *G. reunionensis*, what are the characteristics which justify the differentiation between the two species? The answer to this question will be given when we have analysed its growth and the heterochronic development.

The examination of the most proximal columnals and their relation to the aboral cup has clearly proved the absence of infrabasals in the two species. The paratype of *G. reunionensis* provides an example of a centrifugal development of the most proximal columnals, which may appear externally as five separate ossicles. In the other adult specimens, the irregularity of this manner of development is responsible for the chaotic architecture of the stalk, which is also found in other crinoids with homeomorphic stalks, most particularly in the Hyocrinidae (Mironov and Sorokina 1998).

Classically, observations on external morphology of the first Palaeozoic crinoids suggested that the monolithic columnal resulted from the fusion of five initial pentamers.
(Bather 1900; Ubaghs et al. 1978). Ours results on detailed columnal ontogeny in *Guillecrinus* conflict with such an evolution and suggest the necessity of a revision of stalk ontogeny in Ordovician crinoids.

**Ontogenetic trajectories**

The general tendencies of ontogenetic trajectories will be treated here by pointing out either the variations due to irregularities in growth, or those resulting from adaptations to particular conditions of the micro-environment in which each individual lives. We reconstruct the trajectories using information provided by the different individuals of each species.

**At the scale of the stalk**

The comparative analysis of the simplified biometric profile of the stalk (Figure 16) shows the development of the mesistele as the proxistele regresses. The dististele remains badly defined by external morphology, although its biometric characterization is accentuated to the remaining parts of the stalk. The schema is different for the height and for the diameter of the columnals, especially in the proximal half of the stalk.

The profiles of the diameters (Figure 16a) show that the zone of the juvenile proxistele is progressively restricted, with growth a smaller proportion of stalk length, yet it does not disappear entirely. The minimum diameter (Dm) is found closer to the dorsal cup. At the same time, the difference between the diameter at the base of the dorsal cup and the minimum diameter strongly increases, especially in *G. reunionensis*. Apart from the largest specimen (the holotype of *G. reunionensis*), the distal increase in columnal diameter from the minimum remains weak until the development of the holdfast.

Columnal height profiles (Figure 16b) show that the transition zone of the proxistele–mesistele (M1) disappears at the end of the juvenile stage. Among the adults, the difference between the minimal height (Hm), situated at the end of the proximal zone, and the proximal and distal maximal heights is accentuated, depending on the size of the specimens. At the same time, proximal maximal height is reached in an increasingly smaller number of columnals. The consequence is an extension of the characteristics of the mesistele to the major part of the stalk as a proxistele becomes unrecognizable.

The columnal which hangs over the fixation disc is visible in the adult (biometric profile), but the progressiveness of the way towards the rest of the stalk increases. On the largest specimen (R3), this progression is the most marked. However, the strong distal growth in the diameter, which affects the rapid changing of the articular facets as they approach the fixation disc, is always confined to the last 5–15 columnals in *G. neocaledonicus*. To external morphology, the juvenile and adult specimens do not present a real individualization of a dististele.

**At the scale of the columnals**

With the great morphological variety in columnal articulations, and their modifications during ontogeny, the analysis at the scale of each ossicle becomes complex. In addition, no specimen displays the transition between the juvenile and the adult stage, which appears to be a period of rapid transformation of the columnals. In other words, three ontogenetic stages can be distinguished. They are the result of a synthesis of observations carried out on
Figure 16. Simplified schemes of the principal modifications in the biometric profiles of \textit{Guillecrinus} stalks during ontogeny. Hm, minimal proximal height; Dc, diameter of the base of the aboral cup; DM, maximum proximal diameter; Dm, minimal proximal diameter; dotted area, proxistele; open area, mesistele; short scattered lines, dististele.
(1) the two juveniles of *G. neocaledonicus*, (2) the adults of the same species, and (3) the adults of *G. reunionensis*. For the former two, the preceding morphological step was deduced from the observed ontogenetic tendencies (Figure 17).

The order of appearance of the columnals. At the juvenile stage of the genus *Guillecrinus*, the columnals can be divided into two groups. In the first, the columnals have a pentaradiate symmetry without marked deep ligamentary depressions. The second consists of the most distal columnals having a symmetry base of two or three and very deep ligamentary depressions. As the oldest columnals are the most distal, the pentaradiate symmetry of the columnals is not initial but secondary, as is the case with pentacrinoid larvae of comatulid crinoids (Lahaye and Jangoux 1987).

From the fixation disc to the proximal stalk, the columnals follow from the oldest to the youngest (Figure 17). At the juvenile stage, the symplexies follow the synarthries. As the diameter increases, the crenular units of pentaradiate symplexies offer an increased number of crenulae. From the young specimens to the oldest ones, the first mature proximal columnals become pentaradiate syzygies and then multiradiate ones. A relationship exists between the generalized deepening of the areolar lobes and the height of the columnals.

![Figure 17. Ontogeny of the columnals in relation to their place within the stalk in Guillecrinus. Horizontal row of columnals represents a succession of columnals along individual stalks; lines connecting columnals of adjacent rows represent a succession of ontogenetic stages with a growth in size. For the axial sections below and to the right each columnal cross-section, the black areas schematize the place and the amplitude of the ligamentary depressions. J, juvenile stage; A, adult stage; J2 and A2, observed stages; J1 and A1, earlier stages deduced from observations on J2 and A2; solid lines, ontogenetic trends of *G. neocaledonicus*; dotted lines, hypothetical relationships with *G. reunionensis*; r, rigid; f, flexible; a, ankylosis. See text for explanations.](image)
However, this generalized deepening of the areolar lobes is as late as the columnal is recent, in the history of the individual.

The axial canal follows the same trajectory, going from a pentalobate section in the columnals with the smallest diameter (first pentaradiate columnals) to a circular one in those with the greatest diameter. In the juvenile *G. neocaledonius*, the most proximal columnals (Figure 5a–d) show the equivalent of a claustrum, at the centre of which, the imprint of the axial pentalobate organization is visible. This claustrum quickly disappears through stereom resorption of the axial lacuna. A secondary lumen develops and produces an irregularly pentalobate axial canal (Figure 5e, f), which then becomes circular (Figure 6). In the adult of both species, the first columnals lack a claustrum. In this case, the axial canal takes its pentalobate or pentagonal form directly.

*The transformation of the columnals after their appearance.* In juveniles, the emerging columnals, which are regular in form and masked by the basal circle, gradually reach morphological maturity via differentiation of the stereom and the axial canal. In the adults, a columnal is highly differentiated as soon as it appears, and its form is very irregular. The morphology of the facet thereby acquired constitutes the point of departure for later ontogenetic transformations. All of the columnals move from a disc to a cylindrical form, the relative thickness of which depends on the growth in diameter and height. The biometric profiles show allometries of growth related to these two parameters.

The ontogenetic profile of the most distal columnals illustrates the consequences of these allometries. At the juvenile stage, they are mainly subjected to a growth in height which favours the deepening of ligamentary depressions. Then, the growth in height slows in favour of a growth in diameter. As a result, the crenulae of the columnal facet multiply. The earlier the growth in height ends, the more the juvenile deep ligamentary depressions become restricted to the centre of the multiradial columnals. This possible ontogenetic record will be destroyed, at least partially, when the diameter of the axial canal increases through resorbing the perilumen stereom. Whatever its initial symmetry may have been (2, 3, 4, 5), the ontogenetic profiles converge towards similar distal articular facets.

The tendency towards multiple deep areolar lobes in the proximal columnals of the largest specimens is favoured by their large initial diameter. Nevertheless, it is disturbed by a very strong proximal spurt of growth in height. If this growth dominates, the columnal remains at a pentaradiate stage, as in the case of the first columnal of the paratype of *G. reunionensis*. A cross-section midway between the two articular facets through a columnal with multiple areolar lobes reveals an initial pentaradiate symmetry. Thus, most of the columnals in the proximal half of the stalk of *G. reunionensis* show that a relative balance between the growth in height and the growth in diameter allows the subdivision of the deep ligamentary depressions during the columnal ontogeny. In *G. neocaledonius*, the stabilization of the diameter to relatively weak values seems to favour the maintenance of the initial pentaradiate symmetry with a maximum development of the large deep ligamentary depressions along the main part of the stalk.

The secondary interareolar ridges are not homologous at the proximal and distal ends of the stalk. In the first case, they develop from the perilumen. In the second case, they develop on the external edge of the facet as subsidiary crests. On the proximal side, the ligamentary pits are restricted to the outside of the facet, which allows the development of a wide perilumen. On the distal side, the perilumen disappears and the precocious development of multiple subsidiary crests prevents the expansion of the ligamentary depressions towards the outer edge. It consists of two ontogenetic profiles of the columnals.
(proximal process and distal ones), which are both different and antagonistic. In *G. reunionensis*, the proximal process largely dominates.

It appears that, due to the limited growth in diameter between the juvenile and preadult stages, the symplexies of the juvenile proxisteles tend to develop a wider perilumen at the adult stage. This tendency is limited proximally in *G. neocaledonicus*, whereas it is widespread except for the most distal zone, in *G. reunionensis*. This widespread appearance of a wider perilumen in *G. reunionensis* is accompanied by a lack of crenularium relief. This could be the consequence of a difference in the ontogenetic trajectory of the columnals between the two species. The discovery of juvenile specimens of *G. reunionensis* could allow us to resolve this problem.

**Growth and heterochronic development**

Each columnal begins its ontogeny with an initial stage that interacts with the basal ring of the aboral cup. This initial stage changes little by little throughout the development of the specimen as the basal ring grows in diameter.

Three types of characteristics are distinguished in the columnals: (1) characteristics relevant to each initial stage, (2) characteristics common to all the initial stages, and (3) characteristics which appear during the ontogenetic development. The first two are analysed at the level of integration of the stalk, the third one at the level of the columnal.

**Growth and relative age**

*Relative age from ontogenic growth curves.* Two quantitative parameters will be used in order to consider relative growth and age in *Guillecrinus*: (1) the maximum proximal diameter of the stalk, Dp, which is always very similar to the basal diameter of the aboral cup and (2) the relative growth rate in height of the first columnals, kH, which is modified progressively from the youngest to the oldest specimens.

The diameter of the base of the aboral cup is the result of the cumulative growth of the basals throughout the life of the individual. It is least dependent on the successive regeneration of arms and radials. It is also little affected by the spurts of growth or accidental events that may cause resorption of stereom in the proximal stalk (David et al. 1998). In fact, the animal is able to regenerate its theca, its crown of arms and its stalk from the single basal ring. Apart from the cases of regeneration (Amemiya and Oji 1992), the maximum proximal diameter of the stalk (Dp) reflects the basal diameter of the aboral cup and is more easily measurable (David 1998). None of the specimens analysed here exhibits any current indication of regeneration.

The relative rate of growth in height of the first columnals (kH) is the most easily quantifiable element of any of the successive aspects of the proximal biometrical profile during stalk ontogeny. In these profiles (Figures 7, 8, 14), it corresponds to the average angle of the slope of the proximal extremity of the curve. It is a parameter which depends on ontogeny. The successive increases in kH (Figure 18a) reveal a morphological modification of the stalk, while those of Dp only depend on the growth in size.

In *G. neocaledonicus*, except for the holotype, the combined variations of the two characters are described by an ontogenic growth curve of the Von Bertallanffy type (Figure 18b), which suggests that kH could be a good indication of relative age. For the same Dp value, the holotype (N1) appears as a variant of rapid juvenile growth rate, and the paratype (N2) appears as an older specimen of normal growth.
For *G. reunionensis*, the paratype (R2) lies (Figure 18b) along the asymptotic growth curve suggested by the six specimens of *G. neocaledonicus*. The holotype (R1) possesses a kH value clearly inferior to that of the paratype (R2). Its proximal diameter, the largest of the specimens known at present, places it outside the growth curve on which R2 lies.

As regards present knowledge, if we maintain the hypothesis that kH is an acceptable index of age, the specimens N1 and R1 would have lived under conditions more favourable to a rapid growth in size than those of other specimens. The two curves in Figure 18b thus appear to delimit a field of variation in growth profiles of *Guillecrinus*, with *G. reunionensis* exhibiting a wider range of variability.

The R1 and R2 specimens came from the same station, and N1 and N2 specimens were collected together. The conditions favourable for faster growth are therefore most likely linked either to a micro-environment, where local hydrodynamics optimizes the capture of nutritive particles, or to juvenile growth during a season of particularly high food supply.

**Multiplication of the columnals.** Another aspect of growth is the rate of appearance of new columnals beneath the aboral cup. The youngest specimen of *G. neocaledonicus* (N3) possesses about 150 columnals (Table II). The longest adult stalks of the same species have about 180 columnals for a young adult (N8) and 165 columnals for the older specimen (N6), i.e. 15–30 columnals more than the juvenile. The holotype of *G. reunionensis* possesses 222 columnals.

### Table II. Average rate of appearance of new columnals in *Guillecrinus*.

|                | G. neocaledonicus | G. reunionensis |
|----------------|-------------------|-----------------|
|                | Juveniles stages  | Adult stage     |                |
| Dp             | 0–1.7             | 1.7–2.4         | 2.9–4.8        | 4.8–7.3         |
| +Ncol          | 150 (+22)         | +13 (+37)       |                |                |
| Tm             | 88                | 28.6            | 6.8            | 14.8            |

Dp, proximal diameter (mm); Ncol, number of columnals (estimated value in parentheses); Tm, average rate of appearance of new columnals (Ncol/Dp). See text for explanations.
In *G. neocaledonicus*, the axial cross-section midway between the two facets of the 13th columnal of the specimen N6 shows (Figure 11b) that it was originated when the basal diameter of the aboral cup was about 2.9 mm. At this juvenile stage, the stalk had 152 (=165−13) columnals (Table III). By joining the distal extremity of the stalk fragment of specimen N5 to a columnal whose proximal part has the same diameter as specimen N3, the number of columnals between these two ontogenic stages is estimated to be 22. The complete specimen N5 would have thus had 172 (=150+22) columnals. Adding the 13 (at least) columnals that appeared between the juvenile stage and the largest adult size (N6) gives at least 185 columnals. The specimen N6 has only 165 columnals. The gap of 20 (=185−165) columnals can be attributed to the possible variation in columnal number in *G. neocaledonicus* adults. The N8 specimen with its 180 columnals falls within this field of variation.

Could the *G. reunionensis* specimens correspond to larger individuals or older stages of *G. neocaledonicus*? We estimate that the young adult of *G. neocaledonicus* (N8) has 185 columnals (+five), to reach the size of the N6 specimen, it must add 37 new columnals, for a growth in the proximal maximal diameter of 2.5 mm, in order to obtain the 222 columnals of *G. reunionensis* holotype. This value more than doubles the maximum average level of new columnals calculated at the adult stage on specimen N6 of *G. neocaledonicus*. However, the rate of increase in new columnals clearly decreases gradually during development (Figure 19), and it is probable that it will be negligible among the older specimens. It is thus unlikely that the *G. reunionensis* specimens fall within the growth pattern of *G. neocaledonicus*. The current state of knowledge favours the distinction of the two species.

Figures 19 and 20 show that the multiplication of columnals varies a lot from one individual to the next. Nevertheless, it appears that the majority of columnals are originated during the juvenile stage, that less than 10% appear at the adult stage and these probably chiefly early on. In the adult, growth in stalk length lessens and is mainly due to growth in columnal height rather than the appearance of new columnals.

**Level of organization of the columnals**

The level of organization of the articular facets of the columnals was catalogued according to seven characteristics: the form of the axial canal, the degree of differentiation in the perilumen, the organization of the stereom, the fractioning of the areola, the deepening of the areolar lobes, the heterogeneity of the radial subsidiary crests, and the importance of the crenular units. The coding of the different levels of organization for each character is indicated in brackets. It is independent of any ontogenetic or phylogenetic succession.

| Specimen | N3 | N5 | N6 | N8 | N6 | N8 | R1 |
|----------|----|----|----|----|----|----|----|
| Dp       | 1.7| 2.4| 2.9| 3.7| 4.8| (4.8)| 7.3|
| Ncol     | 150| 172| 152| 180| 165| (185)| 222|

Dp, proximal diameter (mm); Ncol, number of columnals (estimated value in parentheses).
1. A circular axial canal is considered as having the weakest level of organization (0). The pentaradiate symmetry induces a differentiation which increases from a pentagonal form (1), to a pentalobate (2) and then to five isolated lacunae (3).

2. The perilumen can be absent (0), be weakly differentiated (1) or constitute a sort of axial pivot (2).

3. The stereom of the columnals includes an undifferentiated labyrinthic network (0) whose geometry is independent of the collagen tissue, and a galleried network which defines micro-canals containing paraxial ligamentary fibres (Macurda et al. 1978). The extension of the latter into the articulation raises its level of organization: less than 20% (1), from 20 to 40% (2), from 40 to 60% (3), and more than 60% (4).

4. The degree of fractioning of the areola ranges from two (bilateral synarthry) to 10. Six stages are coded: without fractioning (0), fractioning by two (1), by three or four (2), by five (3), by six, seven or eight (4), and more than eight (5). Taking into account the importance of pentaradiate symmetry in echinoderms, the state of five areolar lobes has been isolated (3). The appearance of distal subsidiary crests in adults is not considered as a true subdivision of areolar lobes.

5. Three stages have been distinguished in the differentiation of areolar depressions depending on the degree of depth and its surface extension (code 0–3). 0 corresponds to the situation without depth.

6. The radial subsidiary crests can all be similar (0) or can be distinguished from each other by their length, which is linked to their slightly late appearance compared to a given state of the columnal development. For example (Figure 16), this appearance of subsidiary crests is very early for a very distal columnal of an adult specimen and the differentiation within the syzgial crenularium is weak (1). For a distal columnal of a juvenile specimen, the appearance is late and the difference in the order of appearance of the crests is greater (3). The intermediate situation is coded (2).

Figure 19. Variations in the level of organization of the columnals during their ontogeny in relation to their position on the stalk at the juvenile stage in Guillecrinus neocaledonicus. Ontogenetic stages of Figure 16 (J1 and J2, juvenile stage; A1 and A2, adult stage). Position on the stalk at the juvenile stage (P, proxistele; M, mesistele; D, dististele). See text for explanations.
Figure 20. Modifications in the profile of the levels of organization of the columnals along the stalk during ontogeny. (a) Guillecrinus neocaledonicus; (b) comparison of adult stages of the two species of Guillecrinus. A, Adult stage (A1 and A2: see Figure 17); J, juvenile stage; Prox. 1, new columnals appearing proximally (proximal vertical axis on Figure 17).
7. The crenular units of the interareolar crests or zones can be either absent (0), or present, but with a reduced importance or a very irregular geometry (1). The juvenile symplexies have crenulae which are highly differentiated and their number grows with the diameter of the columnals: one to two (2), three to four (3), or more than four (4).

The organizational level of each columnal of each specimen, J1, J2, A1 and A2 with J1 and A1 earlier stages deduced from observations on J2 (N2) and A2 (N6), was calculated by addition. For example, the distal columnal of juvenile (J1) is: 0 (character 1) + 2 (character 2) + 0 (character 3) + 1 (character 4) + 2 (character 5) + 3 (character 6) + 2 (character 7) = 10.

The ontogenic profile of the columnals (Figure 17), translated in terms of organizational levels (Figure 19), shows several tendencies. Successive columnals in the proxistele of the juvenile specimens exhibit a rapid increase in their level of organization. The important morphological change in the articulations during the transition to the adult stage occurs with only a slight increase in the level of organization. In the adults, the older the specimen, the more the last columnals appear to maintain a high level of organization from their initial appearance (acceleration). The level of organization of the more distal columnals reaches maximum at the juvenile stage and falls significantly at the adult stage.

The allocation of energy committed to raising the level of organization of each columnal is clearly more important at the juvenile than at the adult stage. During the transition from juvenile to adult, the energy allocated to the growth in volume of already-existing columnals is superior to that allocated to their level of organization. This inversion is at its maximum in the most distal columnals. Energy use required to build the calcite skeleton is economized by deepening of ligament fossae as the columnal volume increases.

**Heterochronies at the level of the columnals**

In the genus *Guillecrinus*, the play of heterochronic development mainly affects four of the columnal characters: the crenularium, the deepening of the areolar lobes, the development of subsidiary crests, and the differentiation of the perilumen. The general form of the columnals derives from allometries, as the diameter and the height increase.

With regard to the stalk of the juvenile specimen of *G. neocaledonicus*, the columnals exhibit a syzygial crenularium stage before developing the symplexial crenularium. The development of the latter accelerates more rapidly when the columnal is recent. The augmentation in the number of the crenulae is not recapitulated by the ontogeny of each columnal. It depends on the increase in the initial diameter of the columnal. At the adult stage, paedomorphosis of crenular units transforms the crenularium to a syzygial form. In *G. reunionensis*, the same process accelerates in the homologous columnals and the crenularium tends to disappear. The crenularium of the distal columnals of both species remains syzygial and relatively weak throughout their ontogeny. It consists of a paedomorphic character compared to the proximal juvenile symplexies of *G. neocaledonicus*.

The extension and deepening of the areolar lobes is accelerated in the dististele of the juvenile stage and then stops somewhat earlier before the adult stage. The relative extension, which is maximal at this stage, is maintained in the more frequent and typical columnals of *G. neocaledonicus* in the adult stage. It is most reduced in the homologous columnals of *G. reunionensis*. The multiplication of areolar lobes, favoured by the initial increase in diameter of the columnals at their appearance, is a hypermorphic process (*sensu* Gould 1977), while their limitation towards the periphery of the facet is a neotenic tendency. These two aspects develop with certain independence in *G. neocaledonicus*. They
are linked by the complementarity of heterochronies in the contrary sense (peramorphosis/paedomorphosis), which acts precociously in *G. reunionensis*.

When they multiply on the most distal columnals at the adult stage, the subsidiary crests which add to the initial interareolar ridges resemble the crenulae of a radial crenularium. Yet, their structure is not homologous. This multiplication, favoured by the growth in the diameter of the facets, may be considered as a hypermorphosis that is all the stronger when the development of the ligamentary depressions ends precociously.

The limitation of the ligamentary pits to the periphery of the facet favours the relative hypermorphosis of the perilumen. However, it is reduced and almost disappears during the ontogeny of the distal columnals due to resorption of stereom associated with growth in the diameter of the axial canal. This process is by no means paedomorphic. In fact, the individualization of the perilumen is, for the most part, the result of the relative development of other characteristics.

At the adult stage, the most marked characteristics that distinguish the two species are those for which the heterochronies are inverse: the fractioning of the areolar zones, their extension, and the individualization of the perilumen. They do not concern the most distal columnals, where subsidiary crests are developing. The differences can also be very weak in the most proximal columnals.

Organizational levels of the stalk

With reference to external morphology criteria, three main morphological stalk types can be classically distinguished (Ubaghs et al. 1978), depending on the degree of the differentiation of three sectors (proxistele, mesistele, dististele) and their component columnals: homeomorphic, xenomorphic and heteromorphic. Homeomorphic stalks are the least differentiated: the height, the diameter and the form of the columnals vary progressively from the proximal to the distal end of the stalk. The adult stalks of *Guillecrinus* illustrate this well. Xenomorphic stalks display rapid or sudden transitions, between the proxistele and the mesistele and between the mesistele and the dististele. The Bourgueticrinina, especially *Bathycrinus* and *Porphyrocrinus*, offer the best examples (Macurda and Meyer 1976; Roux 1977; Duco and Roux 1980). Heteromorphic stalks consist of a succession of segments (noditaxes), each of which is composed of several internodals and a nodal bearing cirri, as in the pentacrinitid crinoids. These morphological types can be combined. Xenomorphy and homeomorphy cohabit in *Guillecrinus*, while homeomorphy and heteromorphy cohabit in *Proisocrinus* (Bourseau et al. 1991; David 1998). From the perspective of the external morphology of the stalk, homeomorphy appears to be the lowest level of organization and xenomorphy the highest.

The image is considerably modified when the diversity of articulation types and their level of organization are taken into account. High levels of organization can be reached in a homeomorphic stalk, like that of *Guillecrinus*. They vary a lot in the xenomorphic stalk of the Bourgueticrinina (Améziane-Cominardi and Roux 1994; Roux et al. 1997). The diversity is weaker in the case of the heteromorphic stalks of the pentacrinitid crinoids, and is weakest in homeomorphic stalks, like those of hyocrinid crinoids.

Throughout the ontogeny of *Guillecrinus*, the global level of organization of the stalk tends to decrease. At the juvenile stage, the strong xenomorphy is accompanied by varying and highly differentiated articulations: pentaradiate symplexies, with or without deep areolar depressions; syzygies with an order of symmetry of three, four or five, and synarthries with deep and wide ligamentary depressions. At the adult stage, homeomorphy
dominates, while the variety of articulations diminishes: the proximal pentaradiate symplexies and distal synarthries disappear, and multiradiate distal syzygies tend to develop from different initial symmetries, and the disappearance.

If the level of organization of the stalk is considered equal to the sum of the level of organization of its component columnals (Figure 20), the result of the modifications during ontogeny is different. In *G. neocaledonicus* (Figure 20a), the level of organization increases from the juvenile to the adult. The same is true for the level of organization of the initial stage of the appearance of columnals. Nevertheless, the level of organization of the distal portion of the stalk decreases from juvenile to adult. In the most proximal part, after a decrease at the end of the juvenile stage, the level of organization increases at the adult stage. Thus, at the adult stage, the level of organization of the stalk seems to be lower in *G. neocaledonicus* than in *G. reunionensis*. During ontogeny, the modifications in the level of organization of the stalk depend thus on the scale of analysis and the elements which are taken into account.

**Heterochronies at the scale of the stalk**

The stalk is the result of the development of all of the columnals. It appears as a mosaic of heterochronies, which ensure its variability and the adaptive response to the changes in the environment.

In *G. neocaledonicus*, the disappearance of the proxistele which has pentaradiate symplexies, in the adult, corresponds to an acceleration in the first part of the ontogenetic process and ends in a generalization of distal characteristics which usually appear later in columnal ontogeny. It consists therefore of a peramorphy and even of a hypermorphy in the final phase.

The multiplication of areolar lobes stretches over the main part of the stalk of *G. reunionensis* apart from the R2 specimen, which retains a juvenile aspect for this characteristic (Figure 15). By contrast, it appears later and always proximally in *G. neocaledonicus* (paedomorphy). The larger extension of the distal zone with multiradial syzygies in *G. reunionensis* compared to *G. neocaledonicus* corresponds to a similar process. On the whole, and on the scale of the stalk, each species is situated at an extremity of a paedomorphy–peramorphy gradient. *G. reunionensis* is the most hypermorphic.

**Interpretations and discussions**

**Functionality of the articulations of the stalk**

The articulations between the columnals can ensure two functions antagonistic separately or at the same time: rigidity or flexibility (Roux 1987). The symplexies of the juvenile proxistele block all movement if the ligaments compress the articulation during the absence of current. When the current flows, the pressure on the crown of arms forces the ligaments to extend and the articulations become mobile. The crenulation of symplexies prevents dislocation of the articulation when the current is strong. An articulation that lacks a symplexial crenularium, but which has an exposed perilumen that serves as a central pivot, ensures the suppleness of the stalk when it is subjected to a very slight extension. In *Guillecrinus*, strong ligamentary fibres restricted to the deep areolar lobes prevent dislocation. The synarthries which have elliptical facets permit the greatest amplitude but limit movements to a single direction perpendicular to the fulcral ridge. The few distal synarthries observed at the juvenile stage have a subcircular and quadrangular section
which ensure the greatest possible flexibility in *Guillecrinus*. The articulations with flat facets, like the multiradial distal syzygies, are no longer functional. They ensure the rigidity and cohesion of the distal stalk above the fixation disc.

At the scale of the stalk, the closer the functional articulations, the greater the potential flexibility. Therefore, in the juvenile proxistele, the limited mobility of each articulation is compensated by the thinness and large numbers. The biometric profiles of the heights of the columnals have thus a functional significance (Figure 15b). The wider spread of the tall columnals at the adult stage corresponds to an increase in the rigidity of the stalk, if it is not compensated for by a wide amplitude in movement at the level of each articulation, as in the juvenile dististele. Apart from the distal extremity, the bending potential is developed in the portions of minimal columnal height. In the juvenile stage, the proxistele and the dististele are potentially the most flexible portions of the stalk, while the mesistele is more rigid.

The in situ observations of *G. neocaledonicus* carried out during the cruise CALSUB (Roux 1994) corroborate our morphofunctional analysis. They allow understanding of phenotypic adaptation to environmental conditions. This species lives on irregular rocky substrata, which are sometimes almost chaotic. The juvenile specimens live in the boundary layer, where the water flow is turbulent. The best adaptation is thus a relatively flexible stalk, which favours the changes in the orientation of the crown of arms and absorbs the variations in the velocity of the current. Growth raises the crown into a zone where the flow is laminar with a more regular velocity and orientation. A relatively rigid stalk is necessary in order to maintain the elevation of the crown.

The crown of *Guillecrinus* possesses five arms with short, flexible pinnules. As the animal grows, these arms lengthen faster than the pinnules. Therefore, the surface covered by the filtration fan decreases during ontogeny relative to the potential surface of the whole filtration cone (Figure 21). The relative resistance of the crown to the current diminishes as well as the source of the force for extending the stalk articulations (Roux 1987), especially in the proximal portion. Under these conditions, the symplexies are poorly adapted to ensure the minimum of proximal stalk flexibility necessary to allow the whole crown to move. They are replaced during ontogeny by articulations that are able to move around a pivot when they are subjected to weak extension or none.

The morphological modification of the stalk during ontogeny clearly reflects the adaptation of each individual to local hydrodynamic constraints. The spatial heterogeneity of such rocky substrata explains the individual adaptive variations to the characteristics of each micro-environment. In the same environment, *Proisocrinus ruberrimus* shows an opposite adaptive compromise (Roux 1994; David 1998). Its arms and pinnules cover the entire surface of the potential filtration cone due to numerous ramifications and a dense and robust pinnulation (Figure 21). The resistance to the current (drag) and the load-bearing (lift) capacity thereby developed ensure the elevation of the crown above the substrate and extend the articulations of the stalk. The pentaradiate and highly crenulated symplexies are maintained at the adult stage throughout the proximal half of the stalk and the height of the columnals remains relatively low. The specimens of *Guillecrinus* and *Proisocrinus* which inhabit the same environment offer an example of strong morphofunctional differentiation linked to opposed adaptive compromises.

**Affinities and phyletic relations**

**Consequences of the absence of infrabasals.** The detailed analysis of the aboral cup, at the juvenile as well as at the adult stage, has shown the absence of infrabasals. Externally, the
regular and highly developed ossicles in the paratype of *G. reunionensis*, which seem to represent infrabasals (Roux 1985), actually correspond to a particular mode of development in the proximal columnals of the adult. The main argument of the hypothesis of a direct phyletic relation between *Guillecrinus* and certain Palaeozoic cladid crinoids is shattered.

Examination of external morphology can therefore be misleading. However, in most fossils, interpretations of aboral cup architecture are founded on external morphology alone. It would therefore be useful to verify the structural details of these supposed infrabasals identified in external morphology in those specimens in which ossicles exhibit an aspect (which is developed or regressed) similar to that observed in *Guillecrinus*.

However, among extant stalked crinoids, the juvenile proxistele of *Guillecrinus* is the single example of early columnal ontogeny showing the appearance of a claustrum with a

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Figure 21. Comparison of the filtration potential of the crown in several extant stalked crinoids.
regular pentalobate jugulum. This seems to recapitulate a succession of ancestral columnal features known in Palaeozoic crinoids (Moore and Jeffords 1968; Moore et al. 1968).

Relationship with the genus *Vityazicrinus*. The monospecific genus *Vityazicrinus*, recently described from a single specimen collected in the depths of the central Pacific (Mironov and Sorokina 1998), shows the closest affinities with the genus *Guillecrinus*. It differs principally in its basal circle, which consists of three rather than five pieces. The absence of a genital pinnule, the weak size (Dp of 3 mm), the differentiation of a proxistele which is continued in a transitional zone with columnals of increasing heights (zone M1 of the mesistele) leads us to interpret the holotype of *V. petrachenkoi* as a juvenile specimen.

At the beginning of the proxistele, the columnals are octagonal. They then become hexagonal. Then, the articulations possess four or five crenular units with one or two crenulae. The articulations at the beginning of the mesistele are highly similar to their counterparts in *Guillecrinus* (Figure 6a). Thus, beginning with the juvenile stage, the four- or five-part symmetry becomes six, then eight, throughout the appearance of new proximal columnals. The development of a proximal multiradial symmetry would be accelerated in *Vityazicrinus* compared to *Guillecrinus*. In any case, according to the original description, the proximal articulations seem to maintain a very low level of organization. They lack the crenularium and other indications which could confirm the existence in symmetrical terms of the external hexagonal or octagonal form of the columnals.

The example of the ontogeny of *Guillecrinus* suggests that, in the adult stage, the morphology of the stalk of *Vityazicrinus* could be very different from that of the juvenile holotype. Only the discovery of adult specimens of *V. petrachenkoi* will allow us to know whether the two genera are different enough in order to be placed in two different families, as suggested by Mironov and Sorokina (1998), or if they can be grouped in a single family (Guillecrinidae), as we believe.

Affinities with the Hyocrinidae. The symplexies, when they are well expressed in the juvenile stage (Figures 5f, 6a), possess crenular units which are identical to those of the stalks of Hyocrinidae (Roux 1980, 2002; Mironov and Sorokina 1998), especially in the genus *Laubiericrinus*, the single hyocrinid genus with a stalk which exhibits a pentaradiate symmetry (Roux 2004).

Although the crown of arms and its pinnulation, as well as the theca are apparently significantly different, *Guillecrinus* and *Vityazicrinus* have been associated with the Hyocrinidae by Mironov and Sorokina (1998). They share with this family sometimes fewer than five basals, a homeomorphic adult stalk, symplexies with crenular units, whose general organization is similar, articular facet symmetry, often greater than five, and a tendency to a hollowing of the ligamentary lobes.

In the Hyocrinidae (Roux 1980, 2002, 2004; Mironov and Sorokina 1998; Roux and Pawson 1999), the functional articulations are all symplexies that become multiradiate syzygies in the distal extremity of the stalk. The characters of the distal mesistele and of the dististele of juvenile *Guillecrinus*, unknown in the Hyocrinidae, are spread in the adults. Only the ontogenetical process which leads to the symplexies is shared between the two groups. In *Guillecrinus*, its expression is limited to the juvenile stage and it will be replaced during growth by the process which results in syzygies with deep and multiple ligamentary depressions.

An extra argument in favour of affinities with the Hyocrinidae is the presence of an early stage of columnal development with the equivalent of a claustrum in the juveniles of
Guillecrinus. Among the extant stalked crinoids, the presence of a claustrum which can be maintained at the interior of the axial canal of the mature columnals (Agassiz 1892; Holland et al. 1991; Roux and Pawson 1999; Roux 2002) is only known in the Hyocrinidae.

Affinities with the Bourgueticrinina. Among the extant crinoids, the type of xenomorphy of the stalk expressed at the juvenile stage in *G. neocaledonicus* was until now only known in the Bourgueticrinina. It evokes that described in the genus *Porphyrocrinus*, although in this case, the pentaradiate symmetry is expressed only in the proxistele (Roux 1977). Similarities of biometrical profile, of the hollowing of the areola and of the morphology of the synarthries are found especially in certain *Bathycrinus* (Macurda and Meyer 1976; Duco and Roux 1981; Roux 1987). However, the proxistele is less developed and the pentaradiate symmetry is absent in the stalk of *Bathycrinus*.

The synarthries, which are bilaterally symmetrical articulations, with an axial fulcral ridge, occur throughout the entire adult stalk in Bourgueticrinina such as *Phrynocrinus* and *Zeuctocrinus* (Donovan and Pawson 1994; Roux 1977). Synarthries have been described in the stalks of the pentacrinoid post-larval stage of comatulids (unstalked crinoids) (Lahaye and Jangoux 1987) and in the juvenile stalk of pentacrinid crinoids (Carpenter 1884; Améziane-Cominardi 1991). However, these articulations have a very low level of and actually correspond to symplesiomorphies (Améziane-Cominardi and Roux 1994). They are therefore not homologous with bourgueticrinid synarthries and not can be used to support a phylogenetic relationship with them as has previously been the case (Rasmussen 1978; Simms 1988).

The juvenile stalk of *Guillecrinus* consists of synarthries (Figure 6f) of a high level of organization with a highly differentiated fulcral ridge, due to the hollowing of deep ligamentary depressions. The same type of articulation with a fulcral ridge enclosing the perilumen and axial canal is found in the mesistele of the Bathycrinidae, in particular in *Bathycrinus* (Macurda and Meyer 1976; Duco and Roux 1981; Roux 1987). This articulation may represent a synapomorphy, linking the Bathycrinidae, Hyocrinidae, *Guillecrinus*, and *Vityazicrinus*. However, a morphofunctional convergence remains possible (Améziane–Cominardi and Roux 2003). A better knowledge of the ontogeny of the Bourgueticrinina, which must include analysis of the juveniles, should clarify the relationship.

An additional argument in favour of affinities with the Bourgueticrinina is that arm pinnulation in *Guillecrinus* is closer to bourgueticrinid than to hyocrinid crinoids.

The origin of fulcral ridges and subsidiary crests. The ontogeny of *Guillecrinus* clarifies the origin of fulcral ridges that are diametrically opposed and separated by the axial canal, and which are found throughout the Bourgueticrinina. They can either (1) derive from a fulcral ridge which includes the axial canal and its perilumen (as in the mesistele synarthries of *Bathycrinus* and in the most distal articulations of juvenile *Guillecrinus*) by the enlargement of the axial canal diameter through resorption of the perilumen stereom, or (2) appear on the outer edge of an areolar depression and never include the axial canal (as in the subsidiary crests of the distal stalk of adult *Guillecrinus*). Synarthries with bilateral symmetry (frequent in the Bourgueticrinina) and multiradiate “synarthries” of all types (dominant in *Guillecrinus*) will therefore exist and must be distinguished from the multiradiate syzygies such as in the distal stalk of Hyocrinidae.

Besides, in *Guillecrinus*, during the ontogeny of a columnal and at the time of its growth in height, no architectural obstacle prevents transformation from a pentaradiate symplexy
to a pentaradiate synarthry with five deep ligamentary depressions. In this case, the interareolar ridges can be derived from the zones which initially support the crenular units. Yet, the development of synarthries can also be direct. In the case of distal columnals of the juvenile stage, they could be derived from a synarthry with a weak level of organization as in those of the pentacrinoid post-larval stage. Within a single stalk, many types of articulation are realized depending on variable processes. The same type of articulation results in ontogenetically different trajectories. In these conditions, the morphological successions during the ontogeny of a columnal or of a stalk do not necessarily reflect evolutionary history (i.e. phylogeny). They could result from various successive environmental changes.

Conclusion

The ontogeny of the *Guillecrinus* stalk, analysed on the scale of the columnal, as well as on the scale of the stalk, brings a wealth of information. The development and organization of the columnals and their articulations along the stalk depend on two major factors (Roux et al. 1997): genetic potential and epigenetic constraints. During its growth, the individual is subjected to changing hydrodynamic conditions which necessitate morphofunctional and architectural adaptations. The large differences between the juvenile stage and the adult stage in *Guillecrinus* are a remarkable demonstration of this. The mosaic-like play of heterochronic development along the stalk ensures the adaptation of the individual to new environmental conditions.

The phenotypic plasticity of the ossicles (morphological units) is, for the most part, a result of the interactions at the level of the articular system (functional units), since mechanical constraints are mostly linked to hydrodynamic conditions. It is limited by the available energy (i.e. the food supply) captured by the crown of arms and by the part which can be allocated to the growth of the skeleton. Each individual, like each columnal, has its own individual history. On the irregular rocky substrata where *Guillecrinus* lives, hydrodynamic conditions are extremely heterogeneous. Differences within this microenvironment are accentuated by seasonal variations in food supply, which create changing levels of nutrition each year, as well as by the possible need to give priority to the allocation of energy to regenerating a partially or totally autotomized crown. The ontogenetic analysis reveals the effects of complex interactions throughout development between the environment and the functional units of the individual at different levels of integration. The successive phenotypic modifications in the stalk of *Guillecrinus* essentially recapitulate the changes in hydrodynamic and nutritional constraints during the growth of an individual. *Guillecrinus* illustrates the great variety of articulation types realized on the same stalk that derives from the same genome.

The first articulations which appear during ontogeny have a bilateral pattern. Then, diverse symmetrical orders appear. The pentaradiate symmetry allows an optimal connection with the circle of five basals, under which the new columnals appear, and dominates the proximal part of the stalk from the juvenile stage onwards. At the adult stage, it can never be expressed or disappear during the ontogeny of a columnal. In fact, this disappearance is the expression of a tendency towards the doubling of each ligamentary unit, according to modalities which permit the expression of each intermediary stage between five and 10 ligament bundles. In a given stage of growth, the stalk appears as a complex mosaic of functional units (co-ontogeny of each half of the columnal on each side of the articulation, see Figure 3). These functional units have each been subjected to a varying play of heterochronic development. On the whole, from the hydrodynamic
perspective, the heterogeneity of the turbulent water layer causes a diversification in the morphologies and the modes of articulation of the columnals in the young *Guillecrinus*, while the laminar water flow, which is more homogeneous and stable, canalizes the ontogeny towards convergences in the adult stage. Thus, only knowledge of the juvenile stage of *G. reunionensis* allows us to confirm the distinction between these two species. Indeed, it is at this stage that the divergences in the ontogenetic trajectory are most likely to be expressed.

Whether they are analysed from the perspective of the level of organization or morphogenesis, the most typical articulations (pentaradiate or multiradiate “synarthries”) are original and confirm a highly peramorphic tendency. They are unknown in palaeontological archives. The absence of infrabasals, which adds to the other characteristics, leads us to abandon the hypothesis, according to which *Guillecrinus* is an ancestral taxon and the direct descendant of Palaeozoic crinoids.

Through the analysis of the juvenile specimens, we have shown the possible affinities of *Guillecrinus* with the Bourgueticrinina and the Hyocrinidae. The highly differentiated derived characteristics upon which the revelation of these affinities is based are not the result of simple convergences. They reveal common potentialities whose partial or more complete expression varies depending on the taxa. It is necessary to add a detailed analysis of the crown of arms and of the theca (in preparation) in order to understand the possible phyletic relations between *Guillecrinus*, the Bathycrinidae and the other Bourgueticrinina. The role of epigenetic constraints should also be further clarified.

However, the results of our analyses clearly show that ontogeny provides constraints to phyletic reconstructions. In the juvenile *Guillecrinus*, the proximal symplexies and the distal synarthries have a high level of organization and of functionality with associated derived characters, which may not be interpreted in terms of plesiomorphy. On the other hand, they suggest possible synapomorphies with Hyocrinidae and Bourgueticrinina. At present, synapomorphies between Hyocrinidae and Bourgueticrinina are unknown. The specific characteristics of the three taxa (Bourgueticrinina, Hyocrinidae, *Guillecrinus*) are either expressed separately (Bourgueticrinina, Hyocrinidae) or together (*Guillecrinus*). Their appearance during ontogeny seems to be mainly controlled by the constraints of the environment, functional interactions and the change in position of a given articulation within the stalk when the number of columnals increases rapidly. However, the hypothesis of such a phylogenetic relationship, previously proposed by us (Améziane-Cominardi and Roux 2003) and confirmed here, is consistent with the first preliminary results on molecular phylogeny of stalked crinoids (Cohen et al. 2004).

The transformation of the columnals from the juvenile to the adult stage is dominated by hypermorphic processes. Among the different modes of heterochronic development, hypermorphosis is traditionally presented as being very favourable to the expression of a recapitulation in phylogeny through ontogeny (Gould 1977). In *Guillecrinus*, such recapitulation does not appear to be a credible hypothesis. On the other hand, our study shows that the succession of observed morphologies results from modifications in epigenetic constraints during growth, which are often closely related to the particularities (heterogeneities) of the ecological niche.

However, there is no argument which allows us to make precise conclusions on the evolutionary path (the historical direction) through geological time, especially not in the manner of a phylogenetic tree. Besides, these conclusions could not be tested in the absence of historical documents (fossils). In addition, the weight of epigenetic factors in phenotypic modifications is such that one must be wary of drawing genetic conclusions (presence or
absence of genes) regarding the expression or lack of phenotypical characteristics and their levels of organization. The wealth of ontogenetic analysis above all provides information on the modalities of the adaptative compromise between the genetic potential and the epigenetic constraints at all scales of observation.

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