Growth patterns of noetiid ligaments: implications of developmental models for the origin of an evolutionary novelty among arcoid bivalves

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Abstract: The dorsal ligaments of arcoid bivalves typically consist of oblique, lamellar and fibrous sheets, alternating along the hinge so that their attachments form characteristic chevron patterns. New elements are added at or near the middle of the pattern, as the ligament grows ventrally and gets longer. Most Palaeozoic arcoids exhibit this growth pattern, which still predominates among their living descendants. Early in the Cretaceous, a novel pattern emerged, with vertical strips of lamellar ligament embedded in grooves in the sheet of fibrous ligament which is attached to each valve. In contrast with the chevron, duplivincular ligament, new elements are added to each end of the noetiid ligament, anteriorly and posteriorly. This distinctive growth pattern is the defining character of the family Noetiidae.

Remarkable variation among individuals within populations of a living limopsid arcoid includes forms with vertical strips of lamellar ligament. These variants suggest how the noetiid growth pattern could have been derived from the duplivincular pattern. Computer simulations show that such patterns can be generated by a reaction–diffusion mechanism of the sort first conceived by Turing (1952, *Philosophical Transactions of the Royal Society, London, Series B*, **237**, 37–72). Moreover, the noetiid growth pattern can simply be derived from the duplivincular pattern by a developmental switch based, for example, on a change in boundary conditions. These results indicate that striking differences in form may arise from modest changes in the developmental process. The evolution of the Noetiidae, members of which are quite disparate in overall shell form, should be reassessed. The derived character on which this family is based may not be uniquely shared, so the group could well be polyphyletic.

Debate arises in different contexts over rates of evolutionary change in form, the magnitude of change that can occur from one generation to the next, and the reliability of characters as indicators of common ancestry. However, these issues all turn on patterns of change that have a common basis. They all depend on degrees of genetically based change that are constrained by what is, or is not, permissible in the course of individual development. Thus, they are different aspects of a single problem.

The bivalve family Noetiidae is supposedly defined by a constellation of shell characters (Newell 1969), but only one of these appears in no other arcoids. Noetiid species vary considerably in size and shell sculpture. They live attached to rocks, nestle in crevices or burrow near the surface in soft sediments, over a fairly wide range of nearshore marine habitats. The family is united by the unique form of the ligament that links the two valves, dorsally (MacNeil 1937). It consists of vertical strips of elastic, lamellar material, embedded in fibrous ligament that is attached to the cardinal area of each valve (Fig. 1). The soft-part anatomy of the noetiids has not been systematically differentiated from that of other arcoids. Consequently, the group is defined by a single, rather striking character.

If the arcoids bearing this distinctive ligament are all descended from a single common ancestor, this trait is the synapomorphy that defines the clade, and the family Noetiidae is soundly based. On the other hand, if ligaments of this kind appeared independently, more than once, the taxon would be polyphyletic. The former alternative is more probable if the derived character represents a

(a)

(b)
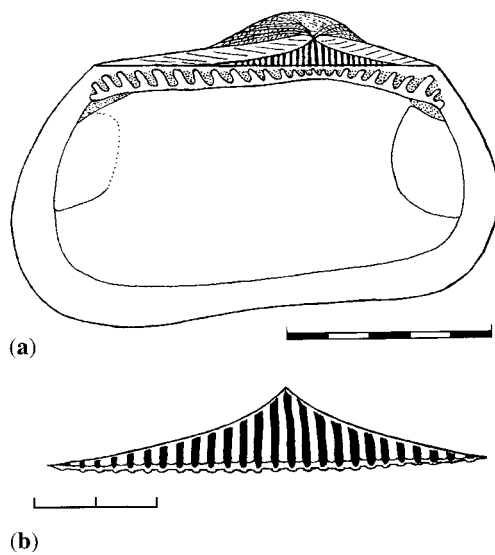
Fig. 1. (a) Left valve of *Striarca lactea* (Linné) showing allometric growth of the ligament, achieved by expansion from a small, triangular area to occupy a large proportion of the cardinal area in the adult shell. Scale bar, 5 mm. **(b)** Enlargement of (a) showing vertical strips of lamellar ligament embedded in fibrous ligament and not directly attached to the shell. Scale bar, 2 mm.

radical departure from the ancestral condition. Multiple origins are more likely if the development of the novel ligament arose as a simple modification of the preexisting mechanism of pattern formation.

In this paper, observations of unusual, naturally occurring ligaments are reported. These lead to a hypothesis for the means by which changes in ligament pattern formation have occurred, among the arcoids. The types of developmental processes by which such patterns can be formed are modelled to determine how novel patterns may have arisen. Finally, the forms of living and extinct noetiids are examined in relation to this analysis.

Growth and form of arcoid ligaments

The typical arcoid ligament consists of multiple sheets of lamellar material, embedded in a sheet of fibrous ligament. This is thinner, but possibly never entirely absent where the lamellar layers are attached, and thicker between them (Waller 1990). Dorsally, away from the region of ligament growth along the mantle isthmus, the brittle fibrous ligament splits as the growing valves diverge. The lamellar ligament is first stretched, exerting tension that causes the valves to spring open when the adductor muscles relax. Then, further dorsally, it

tears as it exceeds its elastic limit (Owen 1959; Trueman 1969). In many burrowing bivalves, this unavoidable breakage of the lamellar ligament occurs at its anterior extremity, immediately below the umbones, where most divergence of earlier growth stages of the shell takes place. In most arcoids, the umbones are located about half-way back along the shell and they grow much more rapidly away from one another. In this case, breakage of the earlier formed dorsal parts of the ligament necessarily occurs along its whole length.

In the majority of living and extinct arcoids, the zones where lamellar ligament is secreted migrate anteriorly and posteriorly away from the umbones, along the mantle isthmus, as the shell grows. The tracks of these zones form two sets of oblique ridges and grooves on the ligamental areas where they are attached. The resulting chevron pattern (Fig. 2a) constitutes the duplivincular ligament that is characteristic of arcoids and many extinct Palaeozoic pteriomorphs (Newell 1937). This ligament has been considered primitive because its materials, with different physical properties, simply alternate rather than being segregated in positions appropriate to their functional roles. It is more appropriate to regard this serial construction as the simplest of several strategies that emerged early in the evolutionary radiation of the bivalves to offset the effects of breakage of the lamellar ligament in animals of increasingly larger size (Thomas 1978).

A number of variants on this general plan have evolved among the arcoids, some of them repeatedly (Fig. 3). The ligament may be more or less asymmetric, depending on the position of the umbones. Where they lie unusually far forward, or towards the rear, the anterior, or occasionally the posterior, series of lamellar sheets has been eliminated. In *Cucullaea*, which is relatively large but has a thin shell, there is generally only one pair of sheets of lamellar ligament, inserted in well-defined grooves at the anterior and posterior extremities of the cardinal area. *Limopsis*, which is small and paedomorphic in several shell characters (Tevesz 1977), likewise has a single pair of lamellar sheets, but here the entire ligament is inserted in a small, triangular pit, near the midpoint of the hinge line. In most arcoids with multiple sheets of lamellar ligament, their width and spacing is remarkably uniform, but in some forms, notably *Arca* itself, the pattern is quite irregular.

Growth and form of the noetiid ligament

The growth pattern of the noetiid ligament (Fig. 2b) departs from those of all other arcoids in two ways. Here, lamellar ligament is inserted in vertical strips, as opposed to forming oblique sheets. This is accomplished by keeping the site of secretion of
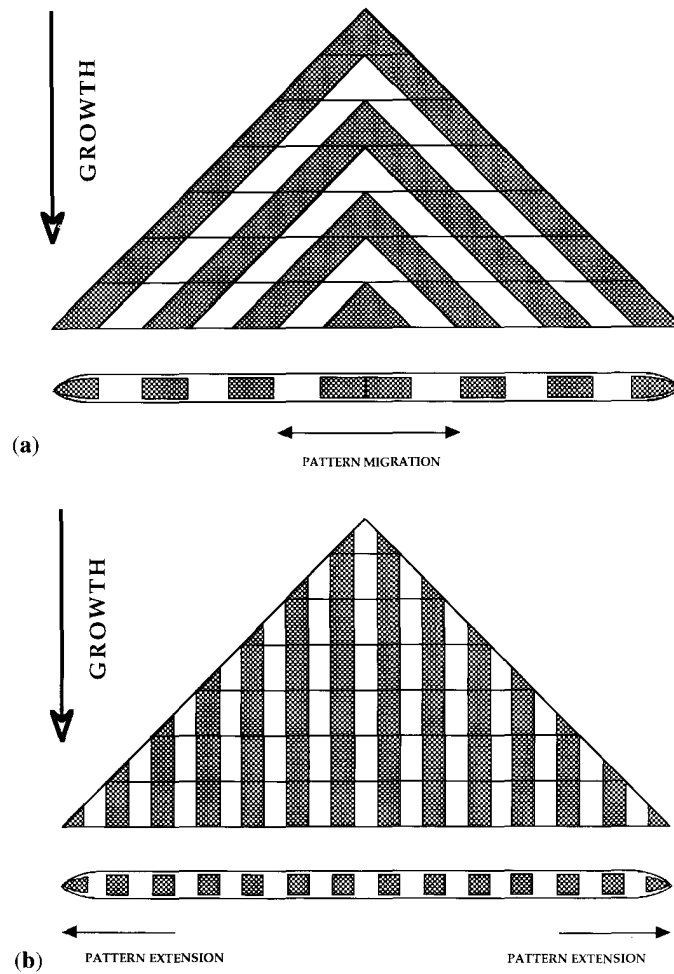
Fig. 2. Growth patterns of: (a) the duplivincular ligament typical of *Anadara*, *Barbatia* and *Glycymeris*; (b) the noetiid ligament. Each diagram shows a sagittal view of the ligament, as it is inserted on the attachment area of either valve, and a dorsal view of the mantle isthmus where new material is secreted.

each lamellar strip fixed, instead of migrating along the hinge axis. Consequently, new elements are added to the pattern at its anterior and posterior extremities, rather than medially beneath the umbones. This innovation evidently required the pattern-forming process responsible for formation of the ligament to be decoupled from that which controls growth of the hinge plate. In other arcoids, growth of the ligament and growth of the row of hinge teeth follow a common pattern. In both cases, new elements are inserted at or near the middle of the set, beneath the umbones.

A remarkable series of specimens of *Limopsis marionensis* Smith from the vicinity of the Falkland Islands suggests how this change in pattern formation may have been accomplished (Fig. 4). The shells are large for this genus, where a maximum dimension of 1–2 cm is usual. Their ligaments exhibit strong positively allometric growth. This is characteristic of many arcoids on account of the inherent weakness of their ligaments (Thomas 1976). The juvenile shells have typical limopsid ligaments with a single pair of anterior and posterior lamellar layers. The adults are quite
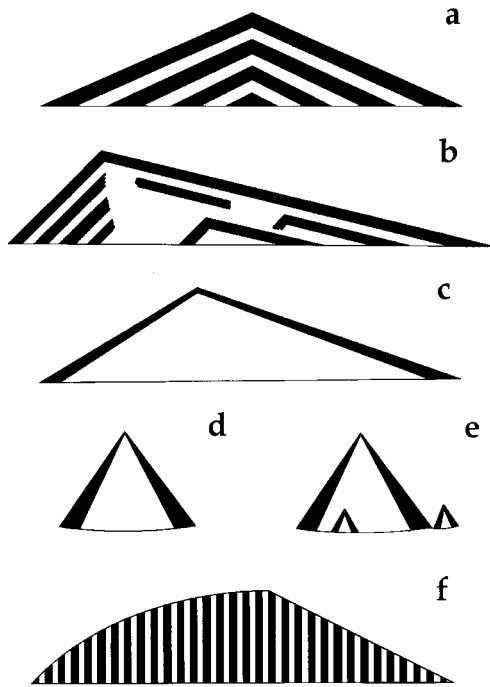
Fig. 3. Representative growth patterns of arcoid ligaments. (**a**) *Glycymeris, Anadara, Barbatia, Parallelodon*; (**b**) *Arca*; (**c**) *Cucullaea*; (**d**) *Limopsis*; (**e**) *Limopsis* variant, not uncommon in some species; (**f**) *Noetia (Eontia)*.

inhibition control the production of lamellar ligament that forms either oblique sheets or vertical strips, depending on the direction in which activation propagates as the shell grows. New elements are added wherever space available between existing zones of activation exceeds a limit that defines the repeat interval of the pattern. If this model is correct, only a single, simple change in instructions to the narrow field of cells constituting the mantle isthmus should be required to change the process from generating one pattern to produce another.

To assess the plausibility of this model, the present authors have developed computer simulations of arcoid and noetiid ligaments, based on growth programs that incorporate its assumptions.

Harmonic bifurcation model

A simple, one-dimensional model treats the mantle isthmus as a finite, expanding space that can accommodate an integral number of waves. This approach employs the kind of morphogenetic rules that were employed by Oster *et al.* (1988) to explain the patterns of cartilage condensation in the

different in form, with varying numbers of more or less irregularly disposed, vertical strips of lamellar ligament. In the most extreme variants, the ligament extends to the extremities of the cardinal area and, apart from its irregularity, the growth pattern is that of a noetiid ligament.

This growth series shows that, after a phase of isometric expansion, the zones of secretion of the initial lamellar components of the ligament stopped migrating anteriorly and posteriorly. As a result, space for the insertion of additional strips of lamellar ligament became available at the anterior and posterior margins of the ligament, rather than medially as in other arcoids. The inferred relationship between this growth pattern and those of actual noetiids is confirmed by the ligaments of living and Cretaceous species of *Striarca*, where lamellar strips can be seen to grow first obliquely and then perpendicular to the hinge line (Fig. 5).
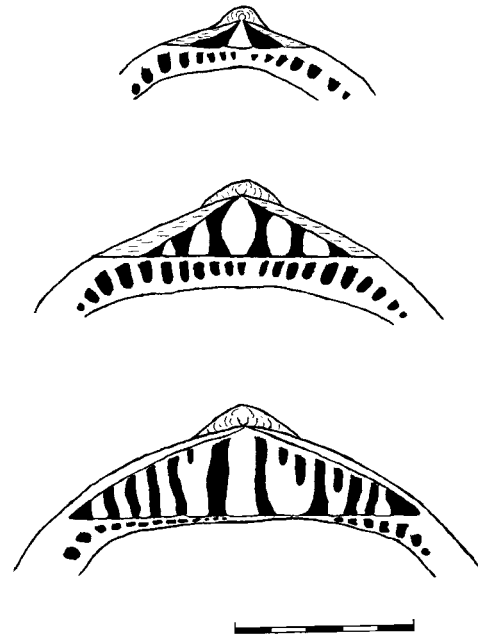
In combination with the regularly spaced chevron patterns of typical arcoid ligaments, these observations suggest a general model for development of the observed patterns. Along the mantle isthmus, alternating zones of activation and

Fig. 4. Ontogeny of the ligament of *Limopsis marionensis* Smith from the South Atlantic, near the Falkland Islands. Scale bar, 1 cm. Specimens from BMNH lots 1964576 and 1964581, 'Discovery' stations 819 and 652, described by Dell (1964), but without reference to this aberrant growth pattern.
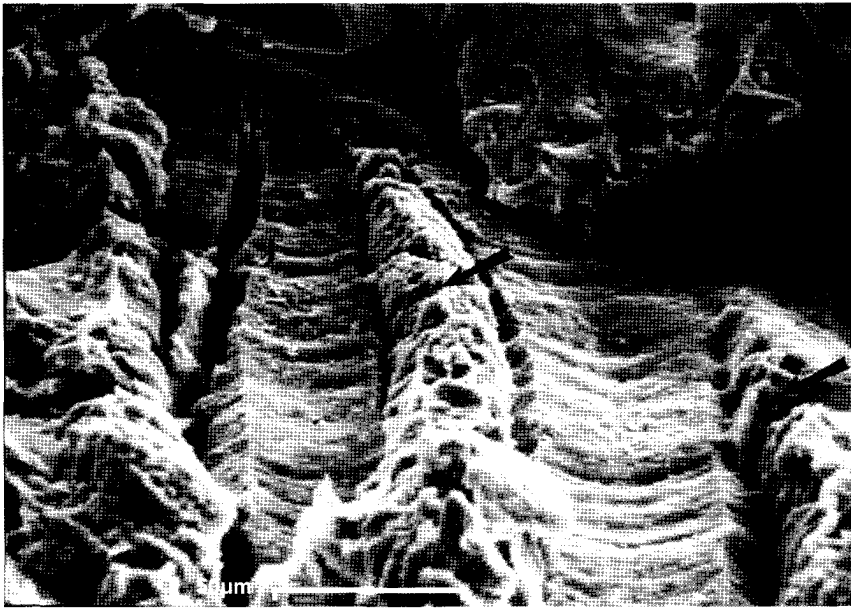
Fig. 5. Scanning electron micrograph of the ligament of *Striarca lactea* (Linné) from the Bay of Naples, Italy. Note strips of lamellar ligament (arrows) inserted in grooves in the fibrous ligament, turning away from the margin of the attachment area to assume a vertical orientation.

development of vertebrate limbs. Here, a sine function represents the net effect of activating and inhibiting processes that control the serial repetition of lamellar sheets as they grow to form a typical chevron ligament (Fig. 6). A threshold value of this function acts as a switch, calling for a change in the type of secretion each time it is passed. The level of the threshold determines the relative widths of the lamellar sheets and the fibrous intervals between them.

As growth increments, δh, are added to the ligament area of height h and length L, then:

$$h' = h + \delta h \text{ and } L' = L + f(\delta h) \quad (1)$$

where $f(\delta h)$ determines the shape of the attachment area (Fig. 7a). At growth stages in which the medial chevron is a new lamellar sheet, the relation between the length of the ligament and the number of alternations is given by:

$$L = 2ma + 2mb + r_{lam} \quad (2)$$

where m is the number of lamellar sheets, a and b are the lengths of the lamellar sheets and fibrous intervals in the plane of the hinge axis, respectively, and r_{lam} is the length of the newly developing lamellar sheet in the same plane (Fig. 7b). Likewise, when the medial chevron is a new fibrous interval, then:

$$L = 2(m + 1)a + 2mb + r_{fib} \quad (3)$$

where r_{fib} is the length of the newly developing fibrous interval. New elements are added to the pattern when:

$$r_{lam} = 2a \text{ or } r_{fib} = 2b \quad (4)$$

These relationships define the proportions of the triangular ligamental area as a whole and they maintain the constant widths and spacing of the elements of the growth pattern.

A computer program incorporating these principles, written by Luke Kiskaddon, produces simple graphic simulations of the growth patterns of arcoid ligaments. At each step in the process, the preexisting pattern serves as a template for the next growth increment. An instruction corresponding to $f(\delta h)$ controls the rate of anterior and posterior migration of the zones of secretion of lamellar and fibrous material. This variable determines the angle of the chevrons and hence the shape of the ligament's attachment area (see Equation 1 and Figs 3 and 7). The introduction of new medial increments is controlled by a sine function and by a limiting value that triggers the switch and sets the relative magnitudes of a and b (Fig. 8a).

The same model produces noetiid growth patterns if the zones of secretion of the two types of ligamental material remain fixed, producing strips that expand vertically downwards once they are established (Fig. 8b). Here, the sine function
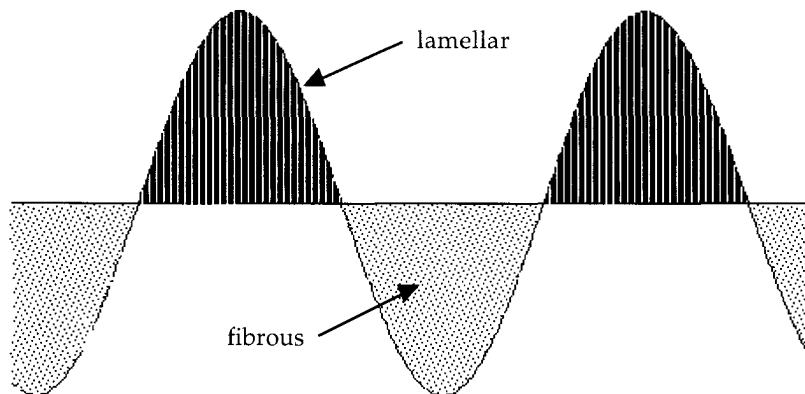
Fig. 6. Simple harmonic, sine wave model for control of secretion of lamellar and fibrous ligament along the mantle isthmus by arcoid bivalves.

governs the introduction of new elements at the anterior and posterior margins of the ligament, rather than medially. Thus, two simple changes in a program written to simulate typical arcoid ligaments are sufficient to convert it to generate noetiid growth patterns. Actually, one change would suffice if both programs were modified in such a way as to prompt the introduction of new elements wherever the available space exceeds a limiting value. This is what one would predict if a set of morphogens controls activation and inhibition uniformly along the length of the mantle isthmus.

These models confirm that quite simple changes in instructions are sufficient to derive a noetiid ligament from a developmental system originally programmed to produce the chevron patterns of typical arcoids. These simulations represent the outcomes of development in this system appropriately. However, they do not incorporate the dynamics of diffusing morphogens, or cell migration, that are generally inferred to control the process of pattern formation. A more realistic approach to this problem is to employ a Turing model (Turing 1952) that simulates the kinetics of the reactions that may be involved in development. Models of this kind have been used extensively by Meinhardt (1984, 1998) and Meinhardt & Klingler (1987) to simulate the development of colour patterns observed in molluscan shells. Some of these patterns are very similar, but not quite identical in form or regularity, to those that are involved here.

Reaction–diffusion model

The harmonic bifurcation model simulates interaction of a sine function with the growth of a

bounded domain – the ligamental attachment area – as a mechanism that could generate the spatial patterns of arcoid ligaments. However, it does not account for the origin of the oscillating signal represented by the sine function. A model that has commonly been invoked to explain pattern formation of this sort involves the interaction of a short-range 'activator' and an 'inhibitor' with effects that extend over a greater distance. Turing (1952) first showed theoretically that such a system could spontaneously generate heterogeneous concentrations of reacting chemicals which could, in principle, lead to biological pattern formation. The stable, steady state patterns of morphogens predicted by Turing (1952) have yet to be documented in living systems, but they have been produced experimentally in chemical systems (Castets *et al.* 1990; Ouyang & Swinney 1991), confirming the feasibility of such models.

Turing models are based on the supposition that at least one of the reactants is migrating through the system by diffusion and that there is an autocatalytic step in a linked set of reactions. The concentration of one of the reactants triggers a specific developmental process when it exceeds a certain threshold. Fixed patterns, such as the segmentation of arthropod limbs (Meinhardt 1984), can be modelled by standing waves in such a system. Migrating colour patterns of molluscan shells (Meinhardt & Klingler 1987) and stripes of growing angelfish (Painter *et al.* 1999) are simulated by waves which move through time, due to growth of the domains where these patterns occur. The patterns generated by Turing models depend on diffusion rates, the kinetics of the reactions involved, the size and shape of their domain of activity, and whether or not the reactants can diffuse across the boundaries of the domain.

Models involving cell movement in response to mechanochemical cues have also been invoked to explain spatial pattern formation. Most of these models also involve a mechanism involving short-range activation and long-range inhibition (Murray 1993). The two sorts of models are sufficiently similar mathematically that many developmental patterns can equally well be represented by either one of them. Consequently, one of the simplest types of Turing models has been used here to simulate the growth patterns of arcoid ligaments.

The Schnakenberg (1979) [and see Murray (1993)] model is based on a hypothetical set of three reactions:

$$X \rightleftharpoons A, \quad 2X + Y \longrightarrow 3X, \quad B \longrightarrow Y \quad (5)$$
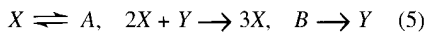
Applying the law of mass action simultaneously to these reactions, production of the activator, X, and the inhibitor, Y, occurs at rates $k_2a - k_1u + k_3u^2v$ and $k_4b - k_3u^2v$, respectively. The variables u, v, a and b are the concentrations of X, Y, A and B, respectively, and k_1, k_2, k_3 and k_4 are rate constants. The simplifying assumption that A and B occur in abundance is made, so that their concentrations may be approximated by constants. Then, the Schnakenberg model takes the form:

$$\frac{\delta u}{\delta t} = \gamma(a - u + u^2v) + \nabla^2u \quad (6)$$

and

$$\frac{\delta v}{\delta t} = \gamma(b - u^2v) + d\nabla^2v \quad (7)$$
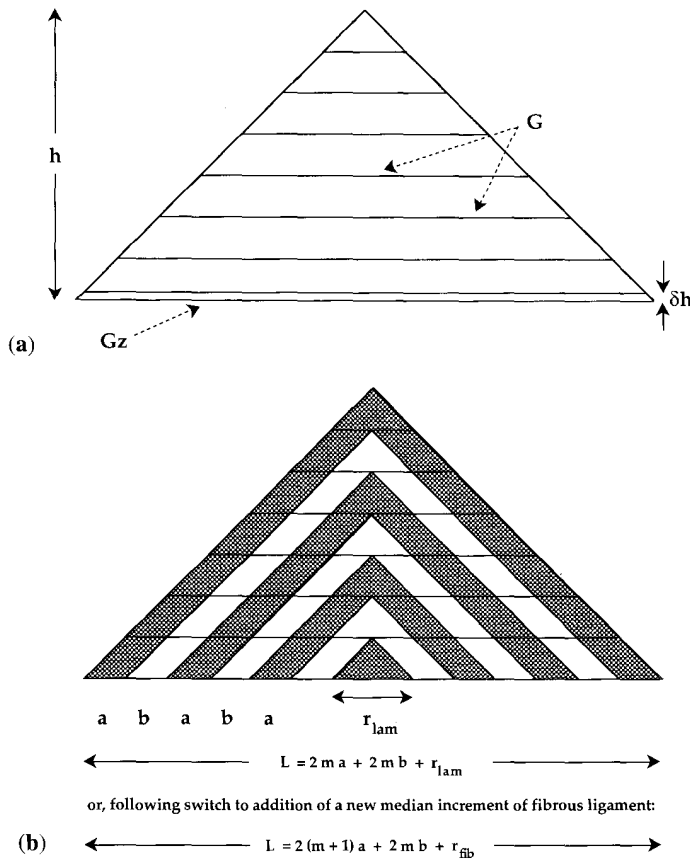
Fig. 7. Parameters of a growing duplivincular ligament. Gz, zone of secretion at the mantle isthmus; G, growth lines; h, height of ligamental attachment area; δh, height of a growth increment; L, length of ligamental attachment area; a and b, lengths of sheets of lamellar and fibrous material, respectively, in the plane of the mantle isthmus; r_{fib} and r_{lam}, length of the latest fibrous or lamellar element, respectively, being added to the pattern; m, number of pairs of ligament elements.
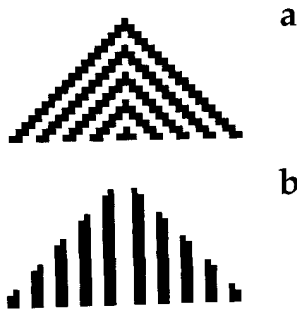
Fig. 8. Simulated growth patterns of: (**a**) the duplivincular or chevron ligament; (**b**) the noetiid ligament; (a) and (b) generated by two variants of a computer model written by Luke Kiskaddon. New elements are added to the pattern whenever the length of the latest median element (a) or distal elements (b) reaches a limiting value.

The last term in each equation models diffusion and the system has been rescaled so as to be nondimensional, reducing the number of constant parameters to four (a, b, γ and d). Here, γ is a function of the size of the ligament relative to the strength of the reaction terms (Murray 1993) and d is the ratio of the diffusion coefficients of the activator and inhibitor, X and Y, respectively.

The boundary conditions for this system take the form:

$$(1 - \theta_L)u_n + \theta_L(u - u_f) = 0$$

$$(1 - \theta_R)u_n + \theta_R(u - u_f) = 0$$

$$(1 - \theta_L)v_n + \theta_L(v - v_f) = 0$$

$$(1 - \theta_R)v_n + \theta_R(v - v_f) = 0$$

where u_n and v_n are the derivatives of u and v, respectively, normal to the domain boundary; they account for the flow of chemicals in and out of the domain of activity. θ_L, θ_R, u_f and v_f are constants. The subscripts R and L denote right- and left-hand boundaries of the model domain, corresponding to the anterior and posterior margins of the ligament. By choosing different values for these constants, different boundary conditions can be set. For example, when $\theta_L = \theta_R = 1$, then u and v take the fixed values u_f and v_f, respectively, on the boundaries. Alternatively, if $\theta_L = \theta_R = 0$, there is no chemical flux across the boundary, which is considered to be impermeable. In this model, growth is represented by increasing x along a one-dimensional interval equivalent to the length of the ligament, from its midpoint, at any time, t (Fig. 9). Initial conditions are given by:

$$u(\underline{x}, 0) = u_0(\underline{x}) \text{ and } v(\underline{x}, 0) = v_0(\underline{x}).$$

To simulate patterns of ligament growth on the expanding domain x_t, appropriate parameters must be set. With $a = 0.1$ and $b = 0.9$, the model yields the homogeneous steady state $u_s = 1.0$, $v_s = 0.9$. This is stable in the absence of diffusion. Standard linear stability analysis is then used to select values of d and γ at which this steady state gives way to linear instability, producing periodic concentrations of the reactants in the presence of diffusion. The number of sinusoidal peaks formed in the domain of ligament growth is determined by the values of the parameters [see Murray (1993) for full details]. In this analysis, the value of d is set at ten and γ is increased until the uniform steady state becomes unstable. At this point, γ is fixed and an exponentially increasing function is selected to define domain growth, representing the allometric growth of the ligamental area. Changes in the spatial pattern of chemical concentrations can now be simulated as this domain expands over time.

In this system, the growth pattern is determined by the boundary conditions and γ prescribes the number of cycles corresponding to alternations between the secretion of lamellar and fibrous ligament material. If $v = 0.7$ at the domain boundaries, and let $u_n = 0$ at these boundaries, the model simulates the symmetrical, chevron growth pattern of typical arcoid ligaments. With $\gamma = 29$, a growth pattern with one anterior and one posterior sheet of lamellar ligament is represented (Fig. 9a). This corresponds to the ligaments of most juvenile arcoids and to the adults of species with a single pair of lamellar sheets, such as *Cucullaea* and normal forms of the paedomorphic genus *Limopsis*. With $\gamma = 185$, the model simulates the characteristic growth pattern of a classic, symmetrical duplivincular ligament (Fig. 9b).

All that is necessary to switch this system to the developmental pattern of a noetiid ligament is a change in boundary conditions. With $v = 0.7$ at $x = 0$, instead of at the expanding margin of the domain, the extremities of the ligamental area are no longer fixed boundaries that anchor the growth pattern. Now, the pattern originates below the umbo and new lamellar elements are added at the distal margins of the ligament. Without any other change in the underlying system, the pattern simulating alternate lamellar and fibrous elements runs perpendicular to the hinge axis, like the ligaments of noetiids (Fig. 9c). Furthermore, by adjusting the concentration of the activator, X, to $u = 1.4$ at the expanding margin, on the right (Fig. 9d), it is possible to simulate the transition from one or more oblique lamellar chevrons, running parallel to the margin of the ligament, to vertical strips as seen in the ontogeny of *Limopsis marionensis* (Fig. 4) and in the early growth stages of the noetiid ligament in some species of *Striarca* (Fig. 5).

This interpretation of the models implies that the

a

b

c

d
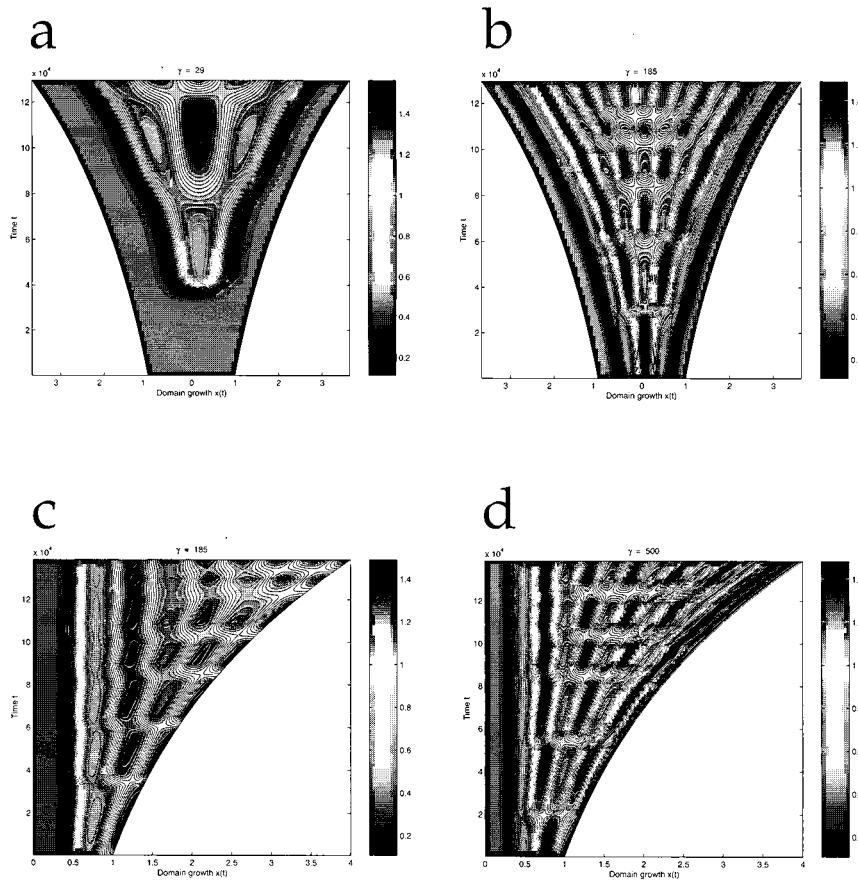
Fig. 9. Schnakenberg models simulating the growth patterns of arcoid ligaments. Colour spectrum represents the concentration, u, of the activator. Limiting values of u model control over the periodic insertion of sheets of lamellar ligament. (**a**) Juvenile of any arcoid with a duplivincular ligament, or adult *Limopsis*. (**b**) Duplivincular ligament of *Glycymeris*, *Anadara*, *Idonearca* or *Grammatodon*. These two simulations represent different stages of development under the same model, with $v = 0.7$ at the domain boundaries and with $u_n = 0$ at these boundaries. (**c**) One side of a noetiid ligament, simulated with $v = 0.7$ and $u_n = 0$ along $x = 0$, and with $v_n = 0$ at the expanding, distal margin of the ligament. (**d**) Model of an intermediate growth pattern. Strips of lamellar ligament first run parallel to the margin of the attachment area, then turn to run perpendicular to the hinge axis. Here, $v = 0.7$ along $x = 0$, and $u = 1.4$ along the distal margin, otherwise with zero flux.

concentration of the inhibitor, v, is fixed at the extremities of the ligament in typical arcoids, which is consistent with their growth patterns. It is less clear how the concentration of this morphogen might be fixed half-way along the mantle isthmus, as required to simulate the noetiid pattern. This may reflect the establishment of a pattern that itself serves as a template for the subsequent distribution of morphogens, except where growth permits the introduction of new elements. This calls for exploration of the possibility that a change in one of the rate-determining variables, rather than the

boundary conditions, may serve as a developmental switch in this system (J. Hutchinson, pers. comm.).

Discussion

The models developed in this work show that what might have seemed to be rather fundamental differences in growth pattern, between the ligaments of typical arcoids and those of noetiids, may be controlled by little more than a relatively simple developmental switch. Shifting the site of addition of new elements to the pattern, from near the

midpoint of the ligament to its extremities, requires only a change in boundary conditions of the expanding morphogenetic field where growth increments are added to the ligament. Consequently, the possibility that this evolutionary innovation emerged independently in more than one lineage must be taken seriously.

The noetiids are quite disparate in shell form, including even the disposition of the ligament. The genera assigned by MacNeil (1938) and Newell (1969) to the Noetiinae, including *Noetia* and *Eontia*, seem to constitute a cohesive group. They are generally characterized by quite strongly opisthogyrate umbones, broad primary ribs and crenulate interior margins. In this group, the ligament extends over much of the cardinal area, including all the space that is available anterior to the umbones (MacNeil 1938). Most of these animals are or were shallow burrowers, broadly comparable in shell form and mode of life with the arcid *Anadara*. Widely distributed today, from temperate to tropical latitudes, this group includes the earliest recorded noetiid, from the early Cretaceous (Aptian) of Lebanon.

The genera placed in the Striarcinae are more varied. This subfamily is defined primarily by the restriction of its ligament to a triangular area, directly below the umbones, which tend to be more nearly orthogyrate than those of other noetiids. In *Striarca*, a conservative genus that appeared very late in Cretaceous and is widely distributed today, the ligament is inserted in a shallow embayment on each cardinal area. Its growth is commonly allometric, so that it occupies an increasingly large proportion of the cardinal area in later ontogeny (Oliver & Cosel 1992). In contrast, the ligaments of other genera occupy small, deep resilifers on cardinal areas that may be broad, as in *Arcopsis*, or very much constricted, as in *Ovalarca*. In this subfamily, some genera have fine radial ribs while in others the exterior surface is marked only by concentric growth lines. The form, number and angular disposition of the hinge teeth are very varied. In short, it is by no means certain that the members of this group share a common ancestry with one another or with members of the Noetiinae.

A third subfamily, the Trinacriinae, consists of three extinct genera with a limited temporal and geographic distribution. This may well be a natural group, as MacNeil (1937) has shown. These are tiny forms, most of them shaped more like *Corbula* than an arcoid, but with taxodont hinges and vertically laminated ligaments. Interestingly, in different species and genera, these ligaments range from occupying a narrowly confined pit to extending over the entire anterior part of an expanded cardinal area (MacNeil 1937).

It is now apparent that none of the shell characters by which the family Noetiidae has been distinguished and subdivided is exempt from pervasive homoplasy. The phylogenetic relationships of these and other arcoids need to be reassessed. Arcoid shells are relatively simple structures, so evolutionary reversals (Stanley 1972) and convergence are not unexpected. Consequently, future attempts to infer true phylogenetic relationships within this group will require the careful integration of morphological, stratigraphic and biogeographical data.

Conclusions

The analysis developed here shows how the strikingly distinctive form of the ligament that characterizes the noetiids is related, in terms of plausible underlying developmental processes, to the duplivincular ligaments of more typical arcoids from which it evolved. Models indicate that the novel growth pattern of the noetiid ligament can be derived as a result of one or two very simple changes in the regulation of development of a typical arcoid ligament. The adaptive significance of this shift has not yet been determined. However, the strength and mechanical function of the noetiid ligament are comparable, in general terms, to those of more typical arcoid ligaments, such as that from which it evolved (Thomas 1978). Furthermore, extreme variants in a living species of *Limopsis* develop a ligament that is incipiently convergent in form with that of the noetiids.

Together, these observations suggest that bivalves with 'noetiid' ligaments are not necessarily monophyletic. The implications of this analysis for evolutionary systematics are quite provocative. The evolution of growth patterns which appear to be quite disparate, but are based on a common developmental process, may require no more genetic divergence than more subtle character shifts. What seem to be 'major' characters, assumed to be of great evolutionary significance, are not necessarily less labile or more constrained than characters like details of shell sculpture that are commonly supposed to be of more local (lower taxonomic level) significance. Consequently, growth processes must be taken into full account whenever a character is used to determine phylogenetic relationships.

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