new plant, may be linked to the very regular pattern of lateral branch departure. In view of this evidence, it is interesting to consider once again what type of xylem existed in plants like the trimerophytes *Pertica* and *Trimerophyton*, which also show a regular pattern of lateral branch departure.

In summary, the new plant, while resembling known Lower Devonian plants in general morphology, is more complex anatomically but can be logically derived from them. Further, it suggests that appendicular structures or leaves were already being differentiated at that time, even though morphologically they still were much divided and non-laminate.

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Recurrent patterns of natural selection in a population of Darwin's finches

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The adaptive significance of morphological traits can be assessed by measuring and identifying the forces of selection acting on them. Boag and Grant[1] documented directional selection in a small population of Darwin's medium ground finches, *Geospiza fortis*, on I. Daphne Major, Galápagos, in 1977. Large beak and body size were favoured at a time of diminishing food supply and high adult mortality. We show here that in two subsequent periods of moderate to high adult mortality (1980 and 1982), the population was subject to the same selection. We have used a recently developed technique[2] to ascertain the targets of direct selection. Beak depth and body weight were commonly under direct selection to increase but, surprisingly, beak width was directly selected to decrease, over all three periods of mortality. The results have implications for our understanding of evolutionary change in morphological traits of Darwin's finches[3–6].

We consider three 18-month periods of adult disappearance, mainly due to mortality[1,3], between June 1976 and December 1982 (Table 1). Each period was associated with a year of low rainfall (Table 1). Less than 5% of adult mortality occurred in the remaining 24 months (January 1978–June 1979 and January–June 1981). Only adults (at least 1 year old) which had been ringed and measured before the periods of high mortality are included in the analyses. Survival of ringed and measured birds was assessed by a detailed census at the end of each period[1,3]. Seed abundance was estimated at this time by counting seeds on plants and in the soil in 50 randomly placed quadrats[1,3]. Four characters (body weight in grams, and beak length, beak depth and beak width in millimetres) have been measured by different observers in a consistent fashion[3,4]. The characters are

highly and significantly positively correlated[4–6]. Before each analysis, data were log$_e$-transformed and then standardized to have zero mean and unit variance.

Table 2 shows the vectors of directional selection differentials (s) and the directional selection gradients (β)[2] associated with mortality in each of the three periods. A selection differential is the difference between the mean value of the character before and after selection, here measured in standard deviation units. The selection gradient comprises the partial regression coefficients of relative fitness (survival) on each character. Relative fitnesses are obtained by dividing absolute fitnesses (0 or 1) by the mean absolute fitness[2], that is, the proportion surviving. Thus, each partial regression coefficient measures intensity of selection acting directly on each character, apart from phenotypic responses due to selection on other correlated and measured characters[2]. After 1978 the ages of birds were known, so we repeated the analysis separately for each age cohort to test for age-specific effects (Table 3).

For all characters and periods, selection differentials are significantly positive, or they are not significantly different from zero: survivors are often larger than those individuals that disappear (Tables 2, 3). The most intense selection in this direction was in 1976–77, when the lowest number of individuals (15%) survived (Table 2). The selection gradients indicate that increases in all measured characters are due almost entirely to selection on beak depth and/or body weight (or to selection on an unmeasured character with which these are highly correlated). Beak length is usually not a target of direct selection, but it increases as a correlated response to selection on beak depth and/or body weight. The partial regressions of relative fitness on beak width are usually negative and often significant: this result was not expected in view of the net increases in the sizes of all traits in 1976–77. Thus, beak shape, as well as size, is subject to selection.

In each of the three periods of mortality, partial regression coefficients of relative fitness on beak depth and body weight are positive and partial regression coefficients of relative fitness on beak width are negative (Tables 2, 3). When the selection over the 1977 drought is divided into three consecutive 6-month periods, this pattern is observed within each period (Table 4). It is also observed when selection on each sex is analysed separately[5].

The repeatedly observed direct selection favouring a small beak width was often intense. It was sufficient to counteract strong selection favouring large beak depth and/or body weight in the 1978 cohort in both 1979–80 and 1981–82, resulting in small selection differentials for all characters, but not in the pre-1976 cohort in 1981–82 (Table 3).

Selection events can be interpreted in terms of feeding conditions. Seed supplies decline during a drought[1], but hard seeds are proportionally common (Table 1). Only the larger individuals can crack these seeds[1,7,8]. Among these large individuals, efficiency at cracking the woody *Tribulus* fruits is a positive function of beak size[7]. Selection for large beak and body size associated with starvation has previously been related to the superior seed handling ability of large individuals[1]. The demonstration here that beak depth is a direct target of selection strengthens this interpretation.

A plausible hypothesis for the selection to decrease beak width is that a relatively narrow beak is favoured in the specialized feeding on *Tribulus* fruits: individuals crack the fruits by placing the side of the beak across a corner and twisting[7]. *Tribulus* is an important food for *G. fortis* during droughts because it remains common (Table 1) and, unlike *Opuntia*, is not defended or consumed by the cactus ground finch, *Geospiza scandens*, the only other common finch on the island. *Tribulus cistoides* may have been introduced to the Galapagos in the past 450 yr[7,9]. If so, the directional selection pressures on beak width that we have detected are relatively new.

This study has shown that selection repeatedly favours individuals with large beak depth and/or body weight in recurring drought conditions. It has also uncovered an unsuspected

Table 1 Selection periods, population sizes before and after each selection period, and seed biomass at the end of drought years (g per 50 m^2)

Drought year	Period studied	Rainfall (mm)	Population sizes Before	Population sizes After	Small seeds	Seed abundance *Opuntia echios*	Seed abundance *Tribulus cistoides*
1977	June 1976 to December 1977	24.0	1,200	200	1.2	13.6	117.9
1980	June 1979 to December 1980	53.5	260	210	1.7	184.2	130.6
1982	June 1981 to December 1982	51.1	200	150	0.5	21.0	38.6

Seeds are divided into miscellaneous small seeds, and a medium-size seed (*Opuntia*) and a large seed (*Tribulus*), both of which require significant force to crack and cannot be handled by all the finches[1,7,8]. All rain fell in January–May of each period.

Table 2 Standardized selection differentials (s) and standardized selection gradients (β) for periods of mortality

	1976–77 s	1976–77 $\beta \pm$ s.e.	1979–80 s	1979–80 $\beta \pm$ s.e.	1981–82 s	1981–82 $\beta \pm$ s.e.
Weight (g)	0.62	0.51 ± 0.14	0.05	0.08 ± 0.06	0.15	0.13 ± 0.08
Beak length (mm)	0.49	0.17 ± 0.18	0.02	−0.04 ± 0.07	0.13	0.06 ± 0.09
Beak depth (mm)	0.60	0.79 ± 0.23	0.03	0.13 ± 0.10	0.12	0.17 ± 0.12
Beak width (mm)	0.49	−0.47 ± 0.21	0.01	−0.14 ± 0.09	0.08	−0.20 ± 0.12
R^2		0.09		0.02		0.06
Sample size		640		192		197
Proportion surviving		0.15		0.78		0.65

All values lie between −1 and 1. Sample sizes refer to birds alive at the beginning of each period. Significance of selection differentials was assessed by *t*-tests comparing survivors with those who disappeared. Significant R^2 values, partial regression coefficients and selection differentials are underlined ($P < 0.05$).

Table 3 Standardized selection differentials (s) and standardized selection gradients (β) for two cohorts over the 1980 and 1982 drought periods

	1979–80 Pre-1976 s	1979–80 Pre-1976 $\beta \pm$ s.e.	1979–80 1978 s	1979–80 1978 $\beta \pm$ s.e.	1981–82 Pre-1976 s	1981–82 Pre-1976 $\beta \pm$ s.e.	1981–82 1978, 1979 s	1981–82 1978, 1979 $\beta \pm$ s.e.
Weight (g)	0.03	0.05 ± 0.08	0.11	0.06 ± 0.08	0.24	0.07 ± 0.12	0.08	0.15 ± 0.09
Beak length (mm)	−0.10	−0.20 ± 0.09	0.11	0.08 ± 0.09	0.28	0.16 ± 0.14	0.02	0.01 ± 0.11
Beak depth (mm)	−0.05	0.03 ± 0.12	0.12	0.37 ± 0.15	0.27	0.16 ± 0.19	0.01	0.16 ± 0.15
Beak width (mm)	−0.04	0.05 ± 0.11	0.05	−0.39 ± 0.15	0.24	−0.09 ± 0.19	−0.04	−0.29 ± 0.15
R^2		0.08		0.11		0.15		0.05
Sample size		92		100		85		112
Proportion surviving		0.84		0.73		0.64		0.67

'Pre-1976' includes all birds hatched in 1975 or earlier. For the 1982 drought period the 17 birds hatched in 1979 are included with the 1978 cohort. Significant values ($P < 0.05$) are underlined.

Table 4 Standardized selection differentials (s) and standardized selection gradients (β) over the drought of 1977, divided into three consecutive periods

	June–December 1976 s	June–December 1976 $\beta \pm$ s.e.	December 1976 to June 1977 s	December 1976 to June 1977 $\beta \pm$ s.e.	June–December 1977 s	June–December 1977 $\beta \pm$ s.e.
Weight (g)	0.05	0.03 ± 0.04	0.28	0.23 ± 0.08	0.28	0.29 ± 0.12
Beak length (mm)	0.06	−0.01 ± 0.05	0.21	−0.17 ± 0.10	0.22	−0.04 ± 0.14
Beak depth (mm)	0.08	0.19 ± 0.07	0.30	0.43 ± 0.13	0.23	0.19 ± 0.19
Beak width (mm)	0.04	−0.15 ± 0.06	0.24	−0.19 ± 0.12	0.21	−0.14 ± 0.17
R^2		0.02		0.09		0.09
Sample size		640		442		194
Proportion surviving		0.69		0.44		0.50

The periods were defined by the times at which a census of surviving finches was taken. The data were not re-standardized from the first selection period. Significant values ($P < 0.05$) are underlined.

opposing selection in favour of small beak width. Given the high heritabilities of these characters[4,10], there is a strong potential for microevolutionary change between generations. The potential is realized[4], but only to a small degree for two reasons. First, there is a high positive genetic correlation, estimated to be between 0.9 and 1.0 (refs 4, 6), between the two beak traits that are selected in opposite directions. Second, net selection

on beak depth and body weight over a whole life cycle is probably small because of opposing selection pressures at other stages of the life cycle, most notably in association with juvenile mortality: small individuals have a selective advantage over large individuals in their first 2–10 months, apparently for metabolic reasons[3].

Results of the study support an adaptive interpretation given

to beak size and shape in this population of Darwin's finches[6,11-13].

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Functions of the canal system in the rotaliid foraminifer, *Heterostegina depressa*

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Advanced fossil and living rotaliacean foraminifera are characterized by canal systems located within the walls of their plurilocular calcareous tests. Although these canals were described in detail during the nineteenth century[1-4], their biological functions have remained obscure. A study of the Recent nummulitid, *Heterostegina depressa*, has now illuminated the role of the canal system and allowed us to interpret similar structures seen in related foraminifera of Tertiary age. It proves to be a structure of fundamental importance for locomotion, growth, excretion, reproduction and protection.

Although foraminiferal tests are characterized by a multiplicity of shapes, wall structures and construction materials, in only a few taxa do we understand their functional roles well enough to demonstrate relationships to feeding methods or environments (substrates)[5,6]. The only group in which structural features can be explained as convergent adaptations to special modes of life are the larger symbiont-bearing benthic foraminifera (that is, members of the Miliolacea and Rotaliina). The transparency of the test wall and the high ratio of surface area to volume in those with flattened tests, provide the morphological basis for a highly advantageous algal–foraminiferal symbiosis[7-9]. We have examined the canal system within the symbiont-bearing Recent nummulitid, *H. depressa*, in which the test walls replace the primary aperture seen in other foraminifera.

H. depressa d'Orbigny inhabits the warm, shallow, nutrient-poor seas of the tropics and subtropics, where the light flux is relatively uniform throughout the year. This species exhibits marked physiological and morphological trimorphism: gamonts are up to 4 mm in diameter, while agamonts are up to 20 mm and schizonts up to 3 mm across. Although laboratory cultures[10] in which all three forms reproduced were a prerequisite for this investigation, specimens from the sea around Hawaii were also used.

In most multilocular foraminifera, successive chambers are connected by a single foramen, the last-formed chamber opening into the surrounding medium through the terminal foramen (aperture). Many species of rotaliid foraminifera have canal systems of different kinds within the chamber walls, and in genera such as *Operculina* these canals allows communication between the undivided chamber cavities and the lateral surfaces of the test. The subdivided chamber cavities (chamberlets) of *Heterostegina* communicate with the lateral surfaces in a similar manner. Nummulitids also have a three-dimensional network of canals (continuous with the rest of the canal system) within the thickened peripheral keel (marginal cord), and this opens into the ambient seawater.

It is known that nummulitids do not usually have true primary or secondary apertures[11], and few, if any, type descriptions of *Heterostegina* species establish their presence. This is not surprising, since the canaliculate marginal cord together with the canals of the chamber and chamberlet walls serve as an effective substitute. We have, however, observed apertures of various shapes and sizes in at least some individuals (see ref. 12).

The morphology of the canal system has recently been investigated by optical and scanning electron microscopy, and its genesis explained; it has also been used taxonomically[9,11,13,14]. The canal system permits the extrusion of pseudopodia from any point of the marginal cord, even when protoplasm has been retracted from the peripheral chambers. We regard this as its primary function, since it provides the animal with a physiological radial symmetry. In foraminifera lacking a canaliculate marginal cord, pseudopodia emerge only from a single point in the test (the aperture), and then only if the protoplasm has not been retracted from the last chamber. As the extrusion of pseudopodia is the primary function of the aperture in other groups of foraminifera, it seems likely that its secondary functions are also taken over by the canal system in the Nummulitidae. That this is so is demonstrated here for the first time.

In *H. depressa*, the terminal openings of the canals in the marginal cord function as a multitude of small primary apertures and extrude protoplasm which forms the template for the new chamber (Fig. 1). Although this process has been described previously[12], only since it was recorded on film[15] has the significance of the canal system been appreciated. Nummulitids such as *H. depressa*, *Heterocyclina tuberculata* Hottinger and *Operculina ammonoides* (Schröter) would probably be unable to construct large chambers with only a single exit for protoplasm.

H. depressa is nourished by photosynthates obtained from symbiotic algae contained within the cell, and by the continuous digestion of a proportion of the total population of symbionts[16]. Digestion occurs throughout the test, and waste products are transported by the protoplasm from older to younger chambers. Eventually, they are excreted through the openings in the marginal cord on the terminal chamber (Fig. 2) and through the aperture where this exists. The canal system thus provides for the removal of waste matter.
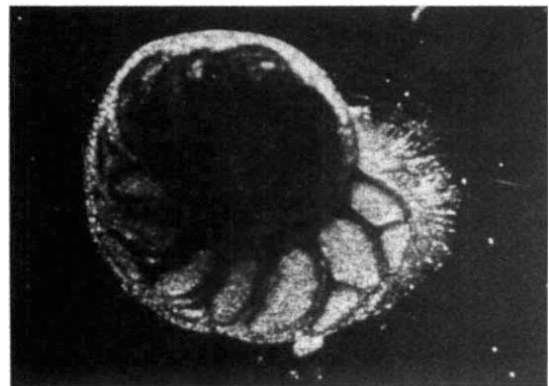

Fig. 1 Process of chamber formation in *H. depressa*. Protoplasmic filaments in large numbers emerge from the canals of the marginal cord of the youngest chamber in order to construct the template of a new chamber. Size of specimen 900 μm.