

# THE ORDOVICIAN TRILOBITE *CAROLINITES*, A TEST CASE FOR MICROEVOLUTION IN A MACROFOSSIL LINEAGE

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**ABSTRACT.** We use geometric morphometrics to test a claim that the Ordovician trilobite *Carolinites* exhibits gradualistic evolution. We follow a previously proposed definition of gradualism, and define the criteria an ideal microevolutionary case study should satisfy. We consider the Lower–Middle Ordovician succession at Ibex, western Utah to meet these criteria. We discovered examples of: (1) morphometric characters which fluctuate with little or no net change; (2) characters which show abrupt ‘step’ change; (3) characters which show transitional change through intermediate states. Examples belonging to (2) and (3) exhibit reversals. The transitional characters were tested against a null hypothesis of symmetrical random walk. The tests indicated that they were not changing under sustained directional selection. Two alternative interpretations are possible. (1) The characters are responding to random causes (genetic drift or rapidly fluctuating selection pressures) or to causes that interact in so complex a way that they appear random. This observation may be applicable to most claimed cases of gradualistic evolution in the literature. (2) Sampling was at too poor a resolution to allow meaningful testing against the random walk. If so, then this situation is likely to apply in most evolutionary case studies involving Palaeozoic macrofossils.

**KEY WORDS:** microevolution, gradualism, pelagic trilobite, geometrical morphometrics.

THE Devonian trilobite *Phacops* provided one of the first fully worked field examples which recognised the role of allopatric speciation, and later punctuated equilibrium, as a dominant evolutionary mode (Eldredge 1971; Eldredge and Gould 1972). Conversely, Sheldon (1987, 1996) used a different set of Ordovician trilobites as a demonstration of gradualistic evolution in several co-occurring lineages. Morphologically complex and numerically abundant fossils are best suited as ‘natural experiments’ in evolutionary tempo and mode, and trilobites are clearly suitable subjects, and ones that have been historically very important in the debate. However, in spite of the body of literature generated by the debate over punctuated equilibrium versus gradualism the number of quantitatively-based, closely stratigraphically-controlled field examples among macrofossils in general remains surprisingly low (see Geary 1995 for review). It is almost entirely the province of microfossils, especially planktonic foraminiferans, to provide quantitative support for gradualistic change (Malmgren and Berggren 1987; Wei and Kennett 1988; Kucera and Malmgren 1998). On the other hand, old ‘case histories’ like the Jurassic bivalve *Gryphaea* have been reworked repeatedly (Hallam 1982; Johnson 1999). Macrofossil examples are time-consuming to collect and prepare, and their field occurrence is often open to criticism of non-sequence, or other forms of stratigraphical incompleteness. New, critically appraised and field-controlled examples remain at a premium.

It has become generally accepted since the review of Johnson (1982) that punctuation/stasis records are the norm among shallow marine benthic faunas. However, the numbers of quantitative studies in support of such assumptions are not numerous. Generally speaking, stasis is assumed to have occurred, and endurance of Linnean taxa is taken as a proxy for morphological conservatism. As Gould and others have pointed out, this is probably why zonal biostratigraphy works (Gould and Eldredge 1986; Levinton 1988, p. 383). Sheldon’s case studies were considered exceptional, and he has sought to relate his observations to a hypothesis that stasis is typical of fluctuating, comparatively stressed shelf habitats, whereas gradualistic change might be more typical of deeper water and more predictable habitats (Sheldon 1996). However,

this particular example is not free of the criticism that the observed changes might be parallel ecophenotypic responses to a progressively oxygen-starved basin.

The Lower–Middle Ordovician trilobite genus *Carolinites* has been the subject of intense study over the last four years. Field occurrence and experimental studies on its eyes show that it was probably epipelagic in life (Fortey 1975a; McCormick and Fortey 1998). One species, *C. genacinaca* Ross, 1951, has been shown by a quantitative study to be morphologically indistinguishable over a global distribution spanning the Ordovician palaeoequator (McCormick and Fortey 1999); it may be the most widely distributed trilobite. Twenty-five years ago the second author suggested that a *Carolinites* stratophenetic series including the transition *C. genacinaca nevadensis* (now *tasmaniensis*) – *C. genacinaca genacinaca* (now *genacinaca*) in the Valhallfonna Formation of Spitsbergen might be a rare example of gradualistic change in a rock section otherwise dominated by stasis (Fortey 1975b). Some quantitative data on the width of the fixed cheeks were presented in support of this idea. The same sequence of species has subsequently been recognised in localities as far apart as the Great Basin of the western United States, and Australia. An examination of this alleged stratophenetic sequence using more quantitative analysis provides a more critical test of a microevolutionary scenario. Here we present what we consider to be an exemplary case history for the quantitative examination of a comparable sequence of *Carolinites* species in the Ibex area, Utah, western United States. There is further evidence that the microevolutionary sequence recorded is globally distributed, and thus is free of the criticisms of local ecophenotypic response.

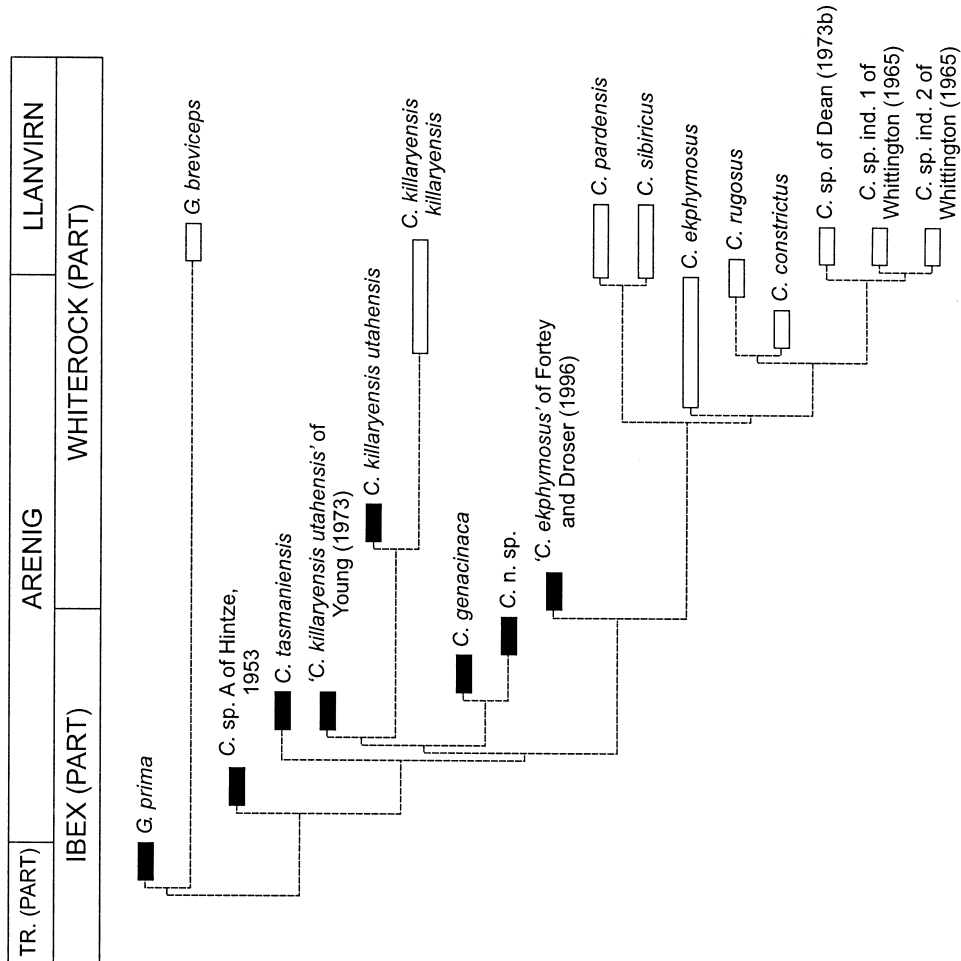
#### RECOGNITION OF GRADUALISM VERSUS PUNCTUATION FROM FIELD EXAMPLES

##### *Definitions*

An unequivocal definition of gradualistic change proves to be rather difficult (Roopnarine *et al.* 1999). We are compelled to make certain assumptions. In the first place, using fossils, we are obliged to treat preserved morphology as a surrogate for species characters. Any *ad hoc* assumption that soft parts record a ‘true’ specific change not reflected in the exoskeleton is beyond proof or disproof. Second, we do not rely on change in a single character, but rely instead on summarising the changes in the whole gestalt by the selection of suitable landmarks. It is possible for some morphological characters to show gradual change of one kind or another while others, ostensibly the true species indicators, behave discontinuously. Third, trilobites depart from the ideal in that we have to treat silicified cranidia, pygidia and free cheeks separately. Therefore we cannot test linkage of characters between these different sclerites.

We also have to establish that the species chosen for study can independently be shown to be phylogenetically coherent. We have carried out a phylogenetic analysis of *Carolinites* and its likely direct ancestor *Goniophrys*. This is not part of the scope of the present paper, but a summary most-parsimonious cladogram is presented (Text-fig. 1) to show that the clade under study (highlighted) is recognised independent of stratigraphy as a closely related suite of taxa. This is important to disprove any claim that end members of the stratophenetic series under examination might be other than the closest-related members of the genus described.

Clearly, the end members of a gradualistic or punctuational series have to be distinctive enough to be recognisable as distinct ‘species’: the examples under discussion involve several features of the exoskeleton, and are not problematic in this regard. As an intelligent and workable definition of gradualism we adopt the formulation of Levinton (1983, p. 115) and infer that gradualistic evolution is occurring when ‘change up a geological section is monotonic and when periods of character stasis do not preclude phyletic divergence of two morphs sufficiently different to be recognised as distinct “species”’. It is not possible to demand of any example an indefinite refinability of sampling horizons, since this will inevitably be limited by the availability of possible samples, time averaging of the samples, and the precision with which characters of ancient fossils can be measured. What we can convey is that the samples between a first and last sample of the earlier and later species, respectively, are consistent, or not, with gradualistic change between them. As Fortey (1985) observed, sufficient prior expectation of the ubiquity of punctuated stasis can accommodate an indefinite number of intermediate ‘steps’. What we analyse, therefore, are the temporal trends in a series of characters of cranidia, pygidia and free cheeks, to see if they conform, or do



TEXT-FIG. 1. Suggested phylogeny of the well-known species of *Goniophrys* and *Carolinites*. TR, Tremadoc. The species considered in this paper are shown in black.

not conform to a series of inter-grading morphological trends consistent with population-level transition between end members.

*Ideal field section*

Field examples of microevolution are vulnerable to several criticisms which can be circumvented by careful choice of the experimental situation in the field.

1. Thick rock sequence. Condensed sections are more likely to conceal non-sequences and other cryptic breaks which may, even if gradualism applies, introduce artefactual punctations by virtue of non-preservation of intermediate populations. In the Ordovician, for example, thin platform successions such as that of Estonia have sharply delimited concurrent range biozones which are truncated by discontinuity surfaces; excellent for stratigraphy but poor for microevolutionary study. Therefore, thick but continuously fossiliferous sedimentary sequences are preferred.
2. Confacial rock sequence. Change in sedimentary regime or biofacies up-section may serve to confuse

ecophenotypic shifts with 'true' evolutionary change. Thus, the examples of gradualistic change studied by Sheldon (1987) occur through a basinal succession which becomes progressively graptolitic (Bettley 1999) and arguably less oxygenated. While it remains eminently possible that any morphological changes recorded are indeed speciations, the example loses impact in that the changes could be claimed as responses to shifting environment, especially since parallel pygidial changes happen in different lineages. A continuously confacial section is preferred.

3. Sampling abundance. Comparatively large samples are necessary to describe adequately the variation within populations. These are time consuming to collect and prepare from most 'crack-out' preservasions. Silicified faunas offer the possibility of retrieving large numbers of sclerites in a preservation style which allows objective measurement. Ideally such preservation should be present throughout the confacial section.

4. Correlation. A test section should offer several other taxa or phyla for objective biostratigraphical correlation with other rock sections. One should not use the hypothetical evolutionary example as the only means of correlation, or circular arguments result.

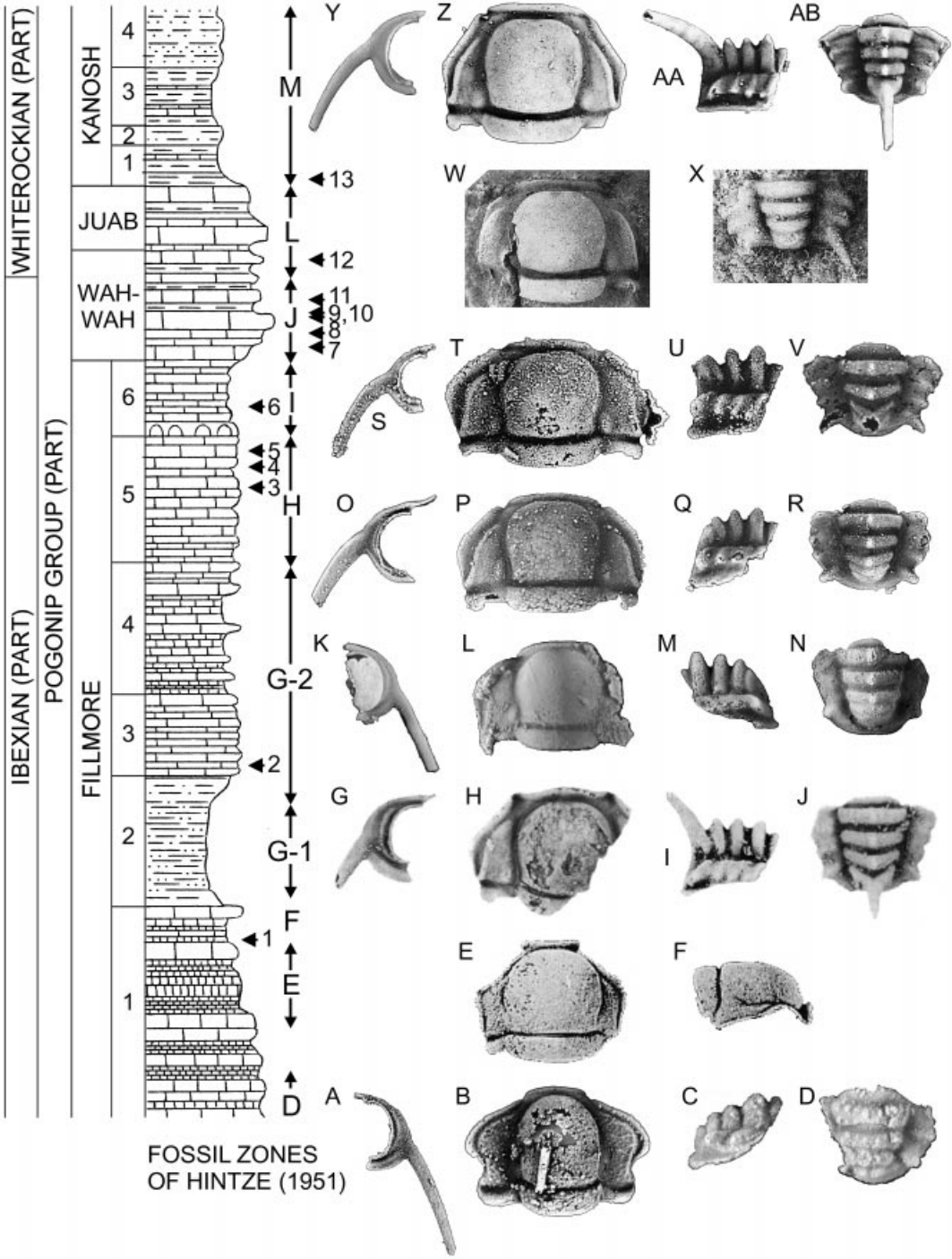
In summary, an ideal test case comprises a thick sedimentary sequence, without obvious breaks, accumulated in a constant palaeoenvironmental setting, yielding fossils of several groups, and yielding silicified faunas at a number of closely spaced horizons.

#### THE IBEXIAN–WHITEROCKIAN SECTION AT IBEX, WESTERN UTAH

The Ibexian–Whiterockian section through the Fillmore, Wahwah, Juab and Kanosh formations in the Confusion Range, Ibex, western Utah is the closest Palaeozoic approach to the ideal test case that we know of. It has been known for fifty years and yielded many of the specimens for Hintze's (1953) classic study of silicified lower Ordovician trilobites. Recently (Ross *et al.* 1997), Ibex has been made type section for the lower Ordovician Ibexian Series, and the co-occurrence of trilobites, conodonts, brachiopods and graptolites has been documented. These various faunas allow for international correlation with other

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TEXT-FIG. 2. Composite stratigraphical section for the Ibex area, Millard County, Utah, showing horizons from which the numbered samples were collected, and representative specimens. The letters adjacent to the geological column refer to the fossil zones of Hintze (1951). Members within the Fillmore Formation are: 1, basal ledge-forming limestone member; 2, slope-forming shaly siltstone member; 3, light-grey ledge-forming member; 4, brown slope and ledge member; 5, calcarenite member; 6, *Calathium* calcisiltite member. Members within the Kanosh Shale Formation are: 1, lower olive shale and calcarenite member; 2, silty limestone member; 3, upper olive shale and calcarenite member; 4, sandstone and shale member (the topmost calcisiltite member is not shown). A–D, *Goniophrys prima*, sample 1. A, dorsal view of right free cheek lacking visual surface, BM It26547;  $\times 7$ . B, dorsal view of cranium, BM It26548;  $\times 7$ . C–D, lateral and dorsal views of pygidium, BM It26549; both  $\times 9$ . E–F, dorsal and lateral views of cranium of *Carolinites* sp. A, sample 2, reproduced from Hintze (1953, pl. 20); both  $\times 5$ . G–J, '*Carolinites killaryensis utahensis*' of Young, sample 3, reproduced from Young (1973, pl. 1). G, dorsal view of left free cheek lacking visual surface;  $\times 3$ . H, dorsal view of cranium;  $\times 5$ . I–J, lateral and dorsal views of pygidium with damaged terminal spine; both  $\times 4$ . K–N, *Carolinites tasmaniensis*, sample 4. K, dorsal view of right free cheek with visual surface, BM It26550;  $\times 6$ . L, dorsal view of cranium, BM It26551;  $\times 7$ . M–N, lateral and dorsal views of pygidium, BM It26552; both  $\times 7$ . O–R, *Carolinites genacinaca*, sample 7. O, dorsal view of left free cheek lacking visual surface, AMNH FI45944;  $\times 5$ . P, dorsal view of cranium, AMNH FI45945;  $\times 6$ . Q–R, lateral and dorsal views of pygidium, AMNH FI45946; both  $\times 7$ . S–V, *Carolinites* sp. nov, sample 9. S, dorsal view of left free cheek, USNM 498179;  $\times 5$ . T, dorsal view of cranium, USNM 498180;  $\times 4.5$ . U–V, lateral and dorsal views of pygidium, USNM 498181; both  $\times 6$ . W–X, *Carolinites ekphyomus* of Fortey and Droser, sample 12, reproduced from Fortey and Droser (figs 14–13, 14–17). W, dorsal view of cranium;  $\times 6$ . X, dorsal view of pygidium;  $\times 9$ . Y–AB, *Carolinites killaryensis utahensis*, sample 13. Y, dorsal view of left free cheek lacking visual surface, BM It26553;  $\times 7$ . Z, dorsal view of cranium, BM It26247;  $\times 7$ . AA–AB, lateral and dorsal views of pygidium with slightly damaged terminal spine, BM It26248; both  $\times 9$ . Geological column redrawn after Hintze (1973).



sections. Strata are almost continuously exposed, and the field relations between different horizons are evident. The relevant part of the section for this paper is over 600 m thick and comprises muddy bedded limestones and subordinate graptolitic shales which represent a uniform open shelf setting throughout the study interval. Individual genera of presumed benthic trilobites, such as *Lachnostoma*, *Goniotelina* and *Protospresbynileus*, range through the succession, as an indicator of facies uniformity. There is thus probably continuous confacial deposition. Silicification of trilobites at certain horizons permits the recovery of large reference collections. *Carolinites* is not present in all collections, and its abundance in those collections where it does occur is variable (see below). The fact that sampling levels include a number of horizons within an interval representing the range zones of single common species of trilobites (*Ptyocephalus declivita*, *Lachnostoma latucelsum*) is a measure of the fine temporal scale of sampling. Although the unique qualities of these sections have been apparent for some time this paper is the first to exploit their potentialities as a field laboratory for microevolutionary change.

Fieldwork was undertaken in the Ibex area during the summers of 1996 and 1997. Bulk samples were taken from horizons where silicified fossils could be seen on bed surfaces. In the main, these fossiliferous horizons form lags in the topmost few centimetres of the massive limestone beds. The rocks were dissolved in 10 per cent acetic acid. The resulting insoluble residues were picked and sorted under a binocular microscope.

The samples yielding *Goniophrys* and *Carolinites* are as follows, in ascending stratigraphical order from 1 to 13 (Text-fig. 2):

1. Fillmore Formation, approximately 52.7 m above the base of Hintze's (1951, 1953) Section G. Ibex Series, Hintze's Zone F (= *Rossaspis superciliosa* Zone; Ross *et al.* 1997). This sample probably equates with Hintze's (1951) sample G-5. Four cranidia, two free cheeks and two pygidia.
2. The single cranidium of *Carolinites* sp. A illustrated by Hintze (1953, pl. 20, figs 2A-C) from his sample D-11. Ibex Series, Fillmore Formation, Hintze's Zone G-2 (= *Protopliomerella contracta* Zone; Ross *et al.* 1997).
3. Two cranidia (one small, one large) one free cheek and one pygidium illustrated by Young (1973, pl. 1, figs 18-20, 23-24, 28-31) from a level about 179.3 m above the base of Hintze's Section H corresponding to the latter's sample H-20. Ibex Series, Fillmore Formation, Zone H (= *Trigonocerca typica* Zone; Ross *et al.* 1997). No new material to add to that illustrated by Young was discovered during this study.
4. Fillmore Formation, approximately 147.2 m above the base of Hintze's Section H. Ibex Series, Hintze's Zone H (= *Trigonocerca typica* Zone). This sample probably corresponds to Hintze's (1951) sample H-23. Eleven cranidia, 13 free cheeks and eight pygidia.
5. Fillmore Formation, approximately 160 m above the base of Section H. Ibex Series, Zone H. The sample probably equates with Hintze's sample H-24. Two cranidia, one free cheek and one pygidium.
6. Fillmore Formation, approximately 192 m above the base of Section H. Ibex Series, Hintze's Zone I (= *Presbynileus ibexensis* Zone; Ross *et al.* 1997). Probably corresponds to Hintze's sample H-28. Eight cranidia, two free cheeks and five pygidia.
7. Wahwah Formation, 1.5 m above the base of Section J. Ibex Series, Zone J (= *Pseudocybele nasuta* Zone; Ross *et al.* 1997). This is Hintze's sample J-2 (L. F. Hintze, pers. comm. 1997). Thirty cranidia, eight free cheeks and 11 pygidia.
8. Wahwah Formation, 11.6 m above the base of Section J. Ibex Series, Zone J. This is Hintze's sample J-8 (L. F. Hintze, pers. comm. 1997). Twenty-nine cranidia, two free cheeks and nine pygidia.
9. Wahwah Formation, approximately 27.6 m above the base of Section J. Ibex Series, Zone J. This may equate with Hintze's sample J-13. Forty cranidia, 39 free cheeks and 28 pygidia.
10. Wahwah Formation, approximately 29.3 m above the base of Section J. Ibex Series, Zone J. Four cranidia, eight free cheeks and 14 pygidia.
11. Wahwah Formation, approximately 40.2 m above the base of Section J. Ibex Series, Zone J. Four cranidia and five free cheeks.
12. Two cranidia (one small, one large) and one pygidium illustrated by Fortey and Droser (1996, figs 14.6, 14.13, 14.17) from the Wahwah Formation at a level in Section J, 6.4 m above the prominent shell bed composed almost entirely of disarticulated valves of *Hesperonomiella minor* (Cooper). Basal Whiterock Series, *Psephosthenaspis microspinosa* Subzone of Fortey and Droser. The material at this level is crack-out, not silicified. No new material to add to that illustrated by Fortey and Droser was discovered during this study.
13. Kanosh Formation, float material at the base of Section K-South. Whiterock Series, Zone M (*Pseudoolenoides*

*dilectus* Zone; Fortey and Droser 1996). This probably corresponds to Hintze's sample K-1. Thirty-five cranidia, 20 free cheeks and 21 pygidia.

#### CAROLINITES STRATOPHENETIC SERIES IN SPITSBERGEN AND IBEX

Fortey's (1975*b*) suggestion of gradualistic evolution in *Carolinites* was primarily based on cranidial proportions in the succession of species in the Arenig–Llanvirn Valhallfonna Formation of Spitsbergen. Fortey noted that the stratigraphically earliest form in the Spitsbergen succession, *Carolinites genacinaca nevadensis* (reassigned to *C. tasmaniensis* Etheridge, 1919 by Jell and Stait 1985), is characterised by possession of small bacculae (the raised processes on the inner margins of the fixed cheeks adjacent to the glabella) which barely indent the base of the glabella, relatively narrow fixed cheeks, a free cheek with a prominent inflated band parallel with the base of the visual surface ('subocular band'), and a straight genal spine which originates close to the posterior of the free cheek. The pygidium tapers only slightly posteriorly and has two clearly defined axial rings. Fortey stated that the succeeding form *C. genacinaca genacinaca* (= *C. genacinaca* Ross, 1951 after the reassessment by Jell and Stait 1985) has slightly larger bacculae which noticeably indent the base of the glabella, slightly wider fixed cheeks, a free cheek which lacks a subocular band and which has a curved, broad-based genal spine originating close to the mid-point of the free cheek, and a pygidium with three clearly-defined axial rings bearing small median tubercles. Fortey noted that stratigraphically early populations of this species have characters that are intermediate between it and the preceding species, including a vestigial subocular band and the absence of median tubercles on the pygidium.

Fortey described two diverging lineages arising from *C. genacinaca*. One lineage comprises, in ascending sequence, *C. ekphymosus* Fortey, 1975, *C. rugosus* Fortey, 1975 and *C. sibiricus* Chugaeva, 1964. *C. ekphymosus* is characterised by possession of narrower fixed cheeks and more inflated bacculae than earlier forms. Its pygidium is similar to *C. genacinaca* but lacks median tubercles, tapers less posteriorly, and has a bisected terminal piece. The two succeeding species continue the trend of narrowing of the fixed cheek and inflation of the bacculae, and have shorter genal spines than earlier forms. The alternative lineage is from *C. genacinaca* to *C. killaryensis killaryensis* (Stubblefield, 1950) which has very wide fixed cheeks, and a rapidly tapering pygidium which bears a terminal spine (Fortey 1975*b*).

At Ibex, the series of telephinid species begins stratigraphically earlier than in Spitsbergen, so that the probable ancestral species, *Goniophrys prima* Ross, 1951 is present. The series also ends earlier, so that *C. rugosus* and *C. sibiricus* are not represented. Forms that have been referred to *C. ekphymosus* and *C. killaryensis* are present, but they are not identical to their namesakes in the Valhallfonna Formation, as will be described below. Two lineages are considered to be represented by *Carolinites* at Ibex (and are represented in Text-fig. 1) for reasons that will become apparent. The stratigraphical range of *Carolinites* at Ibex crosses the Ibexian–Whiterockian boundary.

We have recovered the form referred by Hintze (1953) to *Goniophrys prima* from our sample 1 (Text-fig. 2A–D). As Hintze pointed out, the axial furrows in Ibex specimens are shallow near the base of the glabella. This feature is lacking from Ross's (1951) type material from the Garden City Formation, suggesting that the Ibex form is slightly derived with respect to the Garden City one. Hintze's (1953) *Carolinites* sp. A is the stratigraphically earliest known *Carolinites*, coming from Hintze's shelly fossil Zone G-2 at Ibex (= *Protopliomerella contracta* Zone of Ross *et al.* 1997) (Text-fig. 2E–F). It is not known from elsewhere, and no new material was discovered during this study. As Hintze stated, the cranidium, which is the only sclerite known, appears to be intermediate between *Goniophrys prima* and subsequent species of *Carolinites*. Hintze's single specimen of this species constitutes our sample 2.

*C. tasmaniensis* occurs in Hintze's (1953) Zone H (= *Trigonocerca typica* Zone; Ross *et al.* 1997). Typical features described by Fortey (1975*b*) for this species in Spitsbergen are displayed by specimens from our sample 4 (Text-fig. 2K–N). The anterior of the glabella is rounded and relatively small bacculae are developed which barely indent the base of the glabella. The free cheek has a pronounced subocular band. The genal spine is more or less straight, thin and tubular, and originates relatively far back on the free cheek. Pygidia display three well-defined axial rings and a fourth fainter one, and have moderately developed median tubercles, a feature lacking in Fortey's Spitsbergen *tasmaniensis*. Apart from Ibex and

Spitsbergen, the species is also known from approximately contemporaneous rocks of Tasmania (Jell and Stait 1985) and Alberta (Dean 1989). McCormick and Fortey (1999) tentatively suggested that a small cranidium illustrated by Pillet (1988) from the Arenig of France might belong either in this species or in *C. genacinaca*.

*C. genacinaca* occurs in zones I and J of Hintze (= *Presbynileus ibexensis* and *Pseudocybele nasuta* zones of Ross *et al.* 1997). The typical morphology is well represented by our sample 7 (Text-fig. 2O–R). The glabella tends to be more quadrate than in *C. tasmaniensis*, with a slight anterior median sulcus. The bacculae noticeably indent the base of the glabella. The genal spine is broad-based, rather blade-like and curved, and originates near the middle point of the free cheek, farther forwards than in *tasmaniensis*. The free cheek has no subocular band. The pygidium has four clearly developed axial rings which bear median tubercles. *C. genacinaca* was possibly the most widely distributed of all non-agnostidean trilobites. Apart from Ibex, it is known from broadly contemporaneous strata in north-east Utah, Alberta, east Greenland, Spitsbergen, Siberia, Kazakhstan, China and Australia (McCormick and Fortey 1999).

Specimens from our sample 6 exhibit characters apparently intermediate between *C. tasmaniensis* and *C. genacinaca*. The glabella may have an antero-medial sulcus like *genacinaca*, but the bacculae do not indent the base of the glabella. The genal spine is broad-based and originates relatively far forward on the free cheek, as in *genacinaca*, but the free cheek also has a pronounced subocular band, as in *tasmaniensis*. Fortey (1975*b*) noted similar intermediate populations in Spitsbergen (see above).

We recovered specimens assignable to a new species which succeeds *C. genacinaca* in Zone J during the course of this study. The morphology is exhibited well by specimens from our sample 9 (Text-fig. 2s–v). The cranidium and free cheeks are very similar to those of *C. genacinaca*. The pygidium is markedly different however. The postero-lateral lobes on the pleural regions are more produced as seen in dorsal view (this is demonstrated morphometrically later in the paper). The first and second (posteriormost) axial rings are noticeably produced postero-dorsally (best seen in lateral view; Text-fig. 2U) and the median tubercles are more pronounced. This morphology has not been reported from any locality outside of Ibex.

Fortey and Droser (1996) illustrated rare specimens recovered from the upper part of the Wahwah Formation (basal Whiterockian, Zone L of Hintze 1953; *Psephosthenaspis* Zone, *P. microspinosa* Subzone of Fortey and Droser) reproduced in Text-figure 2w–x. They referred this material to *C. ekphymosus* on the basis of its cranial proportions and the possession of a rugose sculpture on the fixed cheek. Fortey and Droser called attention to the markedly produced postero-lateral lobes on the pleural field of the pygidium. They conjectured that such lobes may have originally been present in *C. ekphymosus* pygidia from Spitsbergen but were not preserved, or alternatively may only have been present in smaller growth stages (the illustrated pygidium is about 1.3 mm in length). This material constitutes our sample 12. This morphology is not known from elsewhere.

Young (1973) illustrated two cranidia (one small, one large), a free cheek and a pygidium from a sample in Hintze's Zone H, which he referred to *C. killaryensis utahensis* Hintze, 1953. Hintze's type material is from lower Whiterockian rocks, much higher in the succession (Zone M, sample 13 in this paper). Young's illustrations of his larger cranidium, free cheek and pygidium are reproduced in Text-figure 2G–J. The cranidium looks rather similar to *C. tasmaniensis* (compare Text-fig. 2L), particularly in the relative width of the fixed cheek and size of the bacculae. Note that the specimen illustrated by Young seems to be tilted slightly anterior-up and so is not a true dorsal view. It is possible that this cranidium belongs in *C. tasmaniensis*. Young's free cheek is much wider and more robust than those of type *C. killaryensis utahensis*, has a genal spine which originates much farther back (this is demonstrated morphometrically later in the paper), and bears a pronounced subocular band which free cheeks from the type horizon lack (compare Text-fig. 2G with the much more delicate free cheek from sample 13; Text-fig. 2Y). There is a real possibility that this free cheek belongs in *C. tasmaniensis*. Young's pygidium bears a terminal spine and thus seems more closely related to *C. killaryensis utahensis* than to *C. tasmaniensis*. It is, therefore, possible that at least two species are represented in Young's material, one of them being *C. tasmaniensis* and the other a species bearing a terminal spine on the pygidium, although the fact that no unequivocal *C. tasmaniensis* pygidia were recovered from this horizon either by Young or by us argues against this. Either way, the discovery of a pygidium with a terminal spine in Zone H strongly suggests that



*C. killaryensis utahensis* in Zone M is not derived from the *Carolinites* species which occur in zones I and J, but rather belongs to a separate lineage probably originating in Zone H, as reflected by the phylogenetic hypothesis shown in Text-figure 1. Young's Zone H material forms our sample 3.

Hintze (1953) erected *C. killaryensis utahensis* for the form he recovered from the basal Whiterockian strata of Zone M (*Pseudoolenoides dilectus* Zone). Hintze allied this form with *killaryensis*, at that time known only from lower or middle Ordovician limestones within the Leenane Grits at Killary Harbour, Co. Galway (Stubblefield 1950), on the basis of the shared possession of a terminal spine on the pygidium. *C. killaryensis utahensis* differs from *C. killaryensis killaryensis* in having considerably narrower fixed cheeks and smaller bacculae, as well as smaller lens facets in its eye. This species is abundant at the base of the Kanosh Formation, which forms our sample 13. The species is not definitely known from elsewhere, although *C. popovkiensis* Balashova, 1961 from the Arenig of the Baltic area, has similar cranidial proportions and may be referable to it. The same is true for the unnamed form described by Dean (1973a) from the Arenig of Turkey.

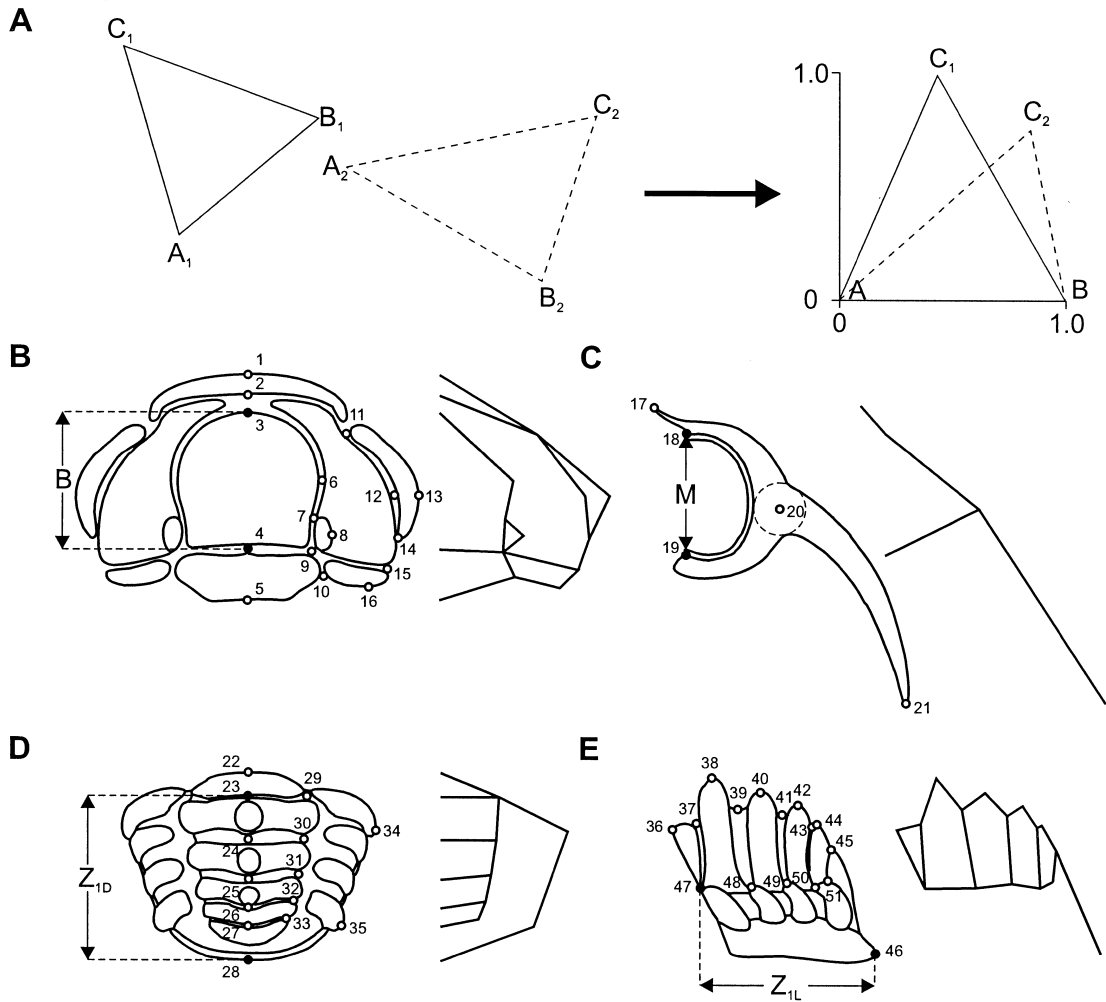
## MORPHOMETRIC METHODS

### *Method*

In this study, we use a technique from geometrical morphometrics to visualise the variation within and among samples, and to highlight particular characters which we then study using univariate methods. Geometrical morphometrics is the term applied to a broad range of methods of shape analysis which share the characteristic of using Cartesian co-ordinates of biological structures in two- or three-dimensions to describe morphology. This approach allows us to capture the shape of an organism much more completely, and to illustrate that shape much more informatively, than a matrix of linear measurements can ever do. A particular strength of the geometrical approach is that differences between forms, represented by homologous sets of landmarks, can be illustrated pictorially. In more 'traditional' methods, which usually involve calculating some distance metric between sets of linear measurements (e.g. hierarchical cluster analysis) or a matrix rotation (e.g. principle components analysis), the original form can rarely be recovered from the data, and the results of the analysis usually do not relate to the original morphology in any simple-to-visualise way.

The technique we use is that of two-point shape co-ordinates, sometimes referred to as Bookstein co-ordinates. This method is a very simple way to factor size and rotation out of landmark configurations so that they can be directly compared (Text-fig. 3A). The shape of interest is placed within a co-ordinate system and represented by a constellation of landmarks, each of which is located on a biological structure. Two of the landmarks are chosen to define a baseline, and the whole configuration is rigidly rotated, translated and scaled so that one end of the baseline lies at (0, 0) and the other end lies at (1, 0) (in a two-dimensional study). The recalculated co-ordinates of the remaining landmarks are referred to as 'shape co-ordinates'. Comparison among a group of specimens is greatly facilitated if the shape co-ordinates for each specimen are connected together by lines to make a 'polygonal figure', which is a sort of simplified representation of the original form. The shape co-ordinates can be analysed using univariate or multivariate techniques. If univariate statistics are to be used on individual landmarks, it is important to choose the baseline carefully. In symmetrical or nearly symmetrical forms, it is probably best to choose a baseline that approximates the midline of the shape (Bookstein 1991). In non-symmetrical shapes, it is probably best to choose a baseline at some distance from the region of greatest variation.

A total of 51 landmarks were used to describe the shapes of cranidia, free cheeks and pygidia in *Carolinites* (Text-fig. 3B-E). Landmarks were chosen so as to describe the shapes of the sclerites as completely as possible. Great care was taken to ensure that the landmarks used were biologically homologous across all samples. For pygidia, both dorsal and lateral views were used, because each view gives potentially important information that cannot be obtained from the other. The landmarks include a mixture of types. For example landmark 9 is very well constrained, placed as it is at the confluence of three furrows on the cranidium. This is the best type of landmark to use. Almost as good are landmarks placed at



TEXT-FIG. 3. Morphometric analysis of *Goniophrys* and *Carolinites*. A, Calculation of shape co-ordinates. Landmarks A and B define the baseline. B, cranium in dorsal view showing landmarks and resultant polygonal figure. The example shown is a small cranium of *Carolinites* (e.g. McCormick and Fortey 1999, fig. 3.6). *Goniophrys* lacks bacculae so that landmarks 7–9 coincide (e.g. Text-fig. 2B). *Carolinites* crania greater than about 1.3 mm in sagittal length lack a preglabellar field, so that landmarks 2 and 3 coincide (e.g. Text-fig. 2L). C, free cheek in dorsal view. D–E, pygidium in dorsal and lateral views respectively. In each case the landmarks used to define the baseline in the shape co-ordinate calculation are shown in black. Note that the shape co-ordinates and polygonal figures are rotated into an intuitive orientation. In the case of crania, free cheeks and pygidia in dorsal view, the calculated shape co-ordinates are rotated 90 degrees clockwise so that the baseline parallels the long axis of the page. For pygidia in lateral view, the shape co-ordinates are rotated 20 degrees clockwise to approximate life orientation. The linear measurements B, M and  $Z_{1D}$  are after Shaw (1957).

the extremities of structures (e.g. landmarks 11, 14, 17, 21 and 35, and many of the landmarks on the pygidium which are placed at extremities of furrows) and landmarks placed at the intersection between the sagittal axis and a furrow (e.g. landmarks 2, 4 and 5). Landmarks that mark the widest points on gently curving structures (e.g. landmarks 6 and 13) are generally considered poorest because they are ill constrained in one co-ordinate.

We particularly wanted to quantify the location of attachment of the genal spine to the free cheek in *Carolinites*, as this has been an important character in systematic and evolutionary hypotheses (see above). However this region is somewhat lacking in obvious structures to use as landmarks (Text-fig. 2). We overcame the problem by using a simple geometrical construction suggested by Bookstein (1991, pp. 80–83). A circle was defined whose circumference just touched the two geniculations where the genal spine meets the main body of the free cheek, and the break in slope just below the base of the visual surface. This third point is not obscured when the visual surface is preserved in place. Landmark 20 is positioned at the centre of this circle (Text-fig. 3c). This type of landmark is called a ‘triple point’ landmark. McCormick and Fortey (1999) used a repetition experiment to show that the error in locating this landmark is extremely small.

The poorest landmarks in the analysis are probably 7 and 8, which mark the anterior and lateral extremities of the bacculae (Text-fig. 3B). This is because these locations are marked only by a subtle break in slope, so that they are sometimes difficult to define accurately. However, it was felt necessary to include some measure of baccule size since this character has also been used in taxonomy and in evolutionary arguments.

Visual inspection of the available cranidia and pygidia suggests that they are symmetrical about the sagittal axis, at least in so far as the landmarks describe them. McCormick and Fortey (1999) demonstrated that this is indeed the case in specimens from sample 7 (called the ‘benchmark sample’ in that paper). On this basis, it was assumed that it made no difference whether left or right halves of specimens were used for morphometrics. For operational purposes, the right half of cranidia and pygidia were used unless damaged, in which case the left half was measured and the co-ordinates reflected across the sagittal axis. McCormick and Fortey (1999) further demonstrated that left and right free cheeks from sample 7 could be considered to be mirror images of each other. On this basis, all available free cheeks were measured, and the co-ordinates of left free cheeks were reflected so that they could be compared with right free cheeks.

Specimens were carefully painted black, mounted on wooden toothpicks, and lightly coated with ammonium chloride. They were imaged using a video camera connected via a framegrabber to a microcomputer. More than one imaging system was used during the course of the study, so at each imaging session a picture of 2-mm-square graph paper was also obtained so that the scale and spatial resolution characteristics of the images could be determined. Cranidia and pygidia were imaged in dorsal orientation. For cranidia, this is achieved when the occipital furrow is vertical and the dorsal surface of the glabella is horizontal. For pygidia, dorsal orientation is achieved when the first (anterior-most) axial ring is vertical and the pleural surface is horizontal. Pygidia were also imaged in lateral view. This is achieved by orientating them in dorsal view, then rotating them 90 degrees about the sagittal axis. Free cheeks were imaged while resting on a horizontal surface. Measurements were made on a total of 372 sclerites from the 13 samples, this total including 170 cranidia, 101 free cheeks and 101 pygidia.

The co-ordinates of the landmarks were recorded in two dimensions from the images using WinDig software (Lovy 1995). The data were stored and manipulated using Lotus 1-2-3 (release 5.01). The landmark configurations were aligned and the shape co-ordinate calculation performed using GRF-ND (Slice 1994). The polygonal figures shown in Text-figures 4, 6, 9 and 11 were generated using the ‘R’ statistical package (version 0.64.2).

#### *Estimation of measurement error*

Measurement error was assessed by repeatedly measuring one specimen 20 times from 20 separate images, over a period of about 20 days. A cranidium from sample 7 was used. The specimen was reoriented from scratch for each image. Shape co-ordinates for the 20 repetitions were calculated using the SC algorithm of GRF-ND, with a baseline defined by landmarks 3 and 4 (Text-fig. 3B). Variation in individual shape co-ordinates over the 20 repetitions was observed to approximate the normal distribution. The greatest variation was found in the x shape co-ordinate of landmark 13. The total range of this variation over 20 repetitions was approximately 7.9 per cent of the baseline length (equating to about 0.16 mm on the approximately 3.0-mm-long cranidium). The standard deviation was about 1.9 per cent (equating to about 0.06 mm). Note that because the two-point shape co-ordinate method does not spread the variance across

all landmarks (as most Procrustes methods do) variances in off-baseline landmarks obtained with this method are usually much greater than variances found using Procrustes fits.

When the same experiment was performed on a pygidium from the same sample, with a baseline defined by landmarks 23 and 28 (Text-fig. 3D) greatest variation was in the x shape co-ordinate of landmark 35. The total range was approximately 4.8 per cent of baseline length (equating to about 0.08 mm on the approximately 2.0-mm-long pygidium). The standard deviation was about 1.3 per cent of baseline length (about 0.02 mm).

A similar experiment was carried out on a single free cheek from sample seven to quantify variability in the measured location of the calculated landmark 20 (Text-fig. 3C). When shape co-ordinates were calculated using a baseline defined by landmarks 18 and 19, it was found that the total variation in the x shape co-ordinate for landmark 20 over 20 repetitions was approximately 3.6 per cent of baseline length (equating to about 0.07 mm on a free cheek whose length, measured between landmarks 17 and 19, is about 2.5 mm). The total variation in the y shape co-ordinate for the same landmark was approximately 2.5 per cent of baseline length (about 0.05 mm). The standard deviations in the x- and y-directions were 0.8 and 0.9 per cent respectively (equating to approximately 0.02 mm).

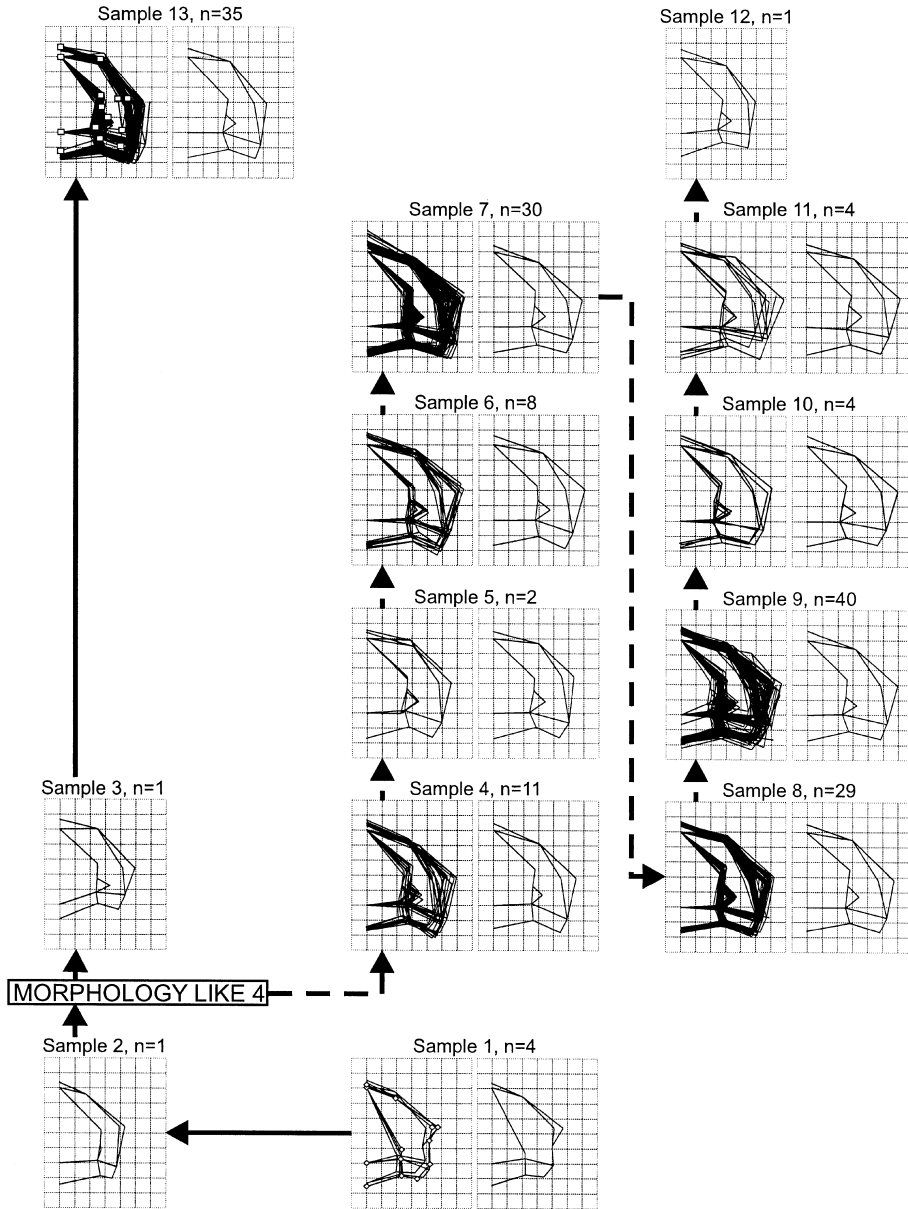
#### MORPHOMETRIC RESULTS

The morphometric results are shown in Text-figures 4–13. Text-figure 4 shows polygonal figures derived from measurements made on crania in dorsal view. Intra- and inter-sample variation in the calculated positions of x shape co-ordinates for landmarks 8, 13 and 15, and the y shape co-ordinate for landmark 7, are summarized in Text-figure 5. Landmarks 7 and 8 vary in relation to the length and width (respectively) of the baculae. Landmarks 13 and 15 vary in relation to the width of the cranium (Text-fig. 3B). In Text-figure 5, the total range of variation and two standard errors either side of the mean is shown. The population mean for normally distributed data lies within two standard errors of the sample mean with a confidence interval of approximately  $P = 0.05$  (Ebdon 1985).

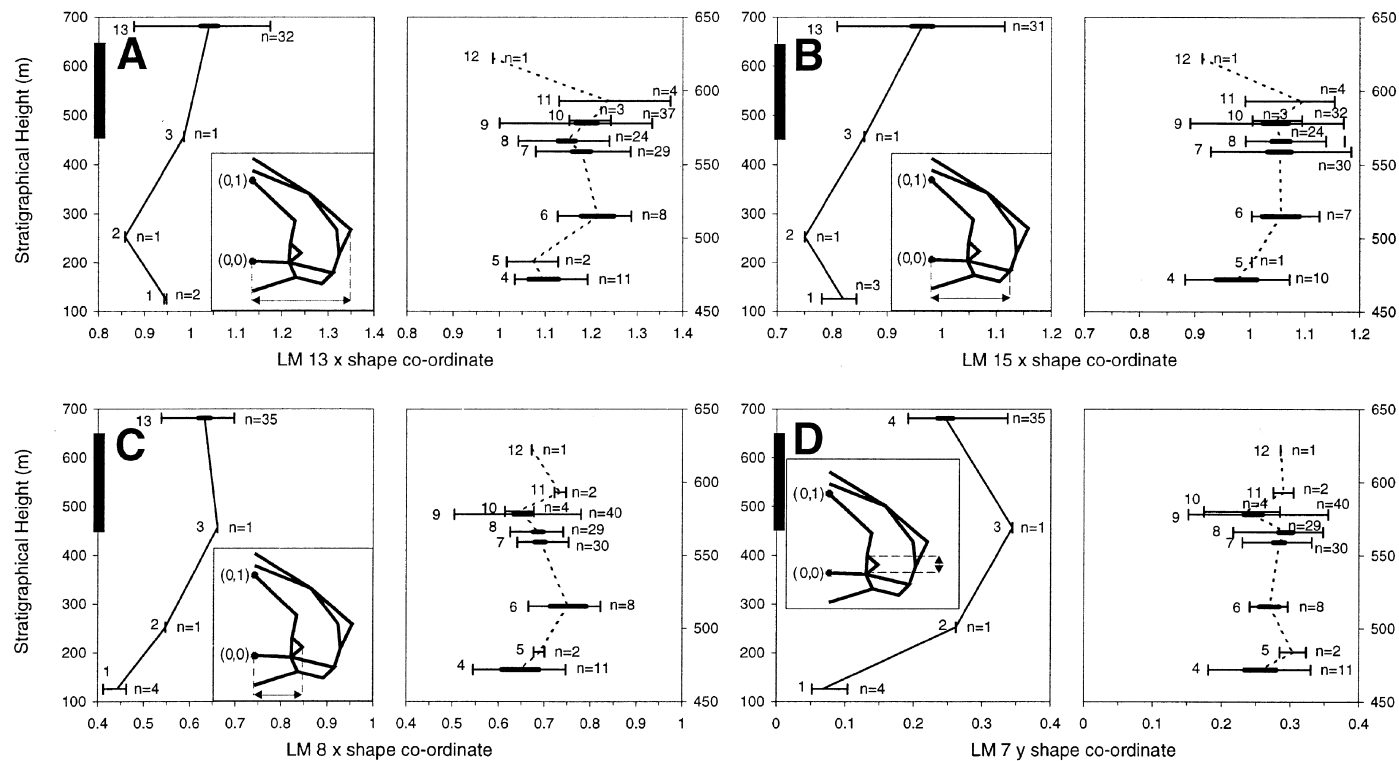
It is clear that Hintze's (1953) *Carolinites* sp. A (our sample 2) differs from *Goniophrys prima* (sample 1) in having palpebral lobes that extend posteriorly to the postero-lateral furrow and small baculae, with the widest point of the glabella a little way in front of the anteriormost extent of the baculae (Text-fig. 4). The cranium is slightly narrower than in *G. prima*. In sample 4, which can be referred to *C. tasmaniensis*, the cranium is significantly wider than in sample 2, although the glabellar proportions are more or less unchanged. The anterior extreme of the palpebral lobe has migrated abaxially and a little backwards. The baculae have significantly greater lateral extent on the fixed cheek.

For reasons described above, we consider there to be two separate lineages derived from *C. tasmaniensis*. We will first consider the lineage comprising samples 4–12, which we will henceforth refer to as the '*tasmaniensis* – *ekphymosus* lineage'. Compared with sample 4, the cranial proportions in sample 5 are similar, although the palpebral lobes and the baculae extend a little further forward (but note that this sample consists of only two crania). Sample 6 has significantly wider fixed cheeks and baculae (Text-fig. 5A–C). The cranial proportions of samples 7 and 8, which exhibit typical *C. genacinaca* morphology (see above), are similar to those of sample 6, but the base of the glabella is a little more 'pinched in' and the baculae do not extend so far abaxially (Text-fig. 5C). Samples 9 and 10 have baculae which are slightly reduced in abaxial and exsagittal extent in comparison with samples 7 and 8 (Text-fig. 5C–D), but are otherwise very similar in cranial proportions. Crania from sample 11 have larger baculae, more like those of samples 7 and 8 (Text-fig. 5C–D) and a slightly wider glabella. The single cranium from sample 12 (*C. ekphymosus* of Fortey and Droser 1996) is narrower, measured across the widest point, than any other *Carolinites* in its lineage except *C. sp. A*. The sample 12 cranium also has narrow palpebral lobes. Its baculae are comparable in size with those of samples 9 and 10 (Text-fig. 5C–D).

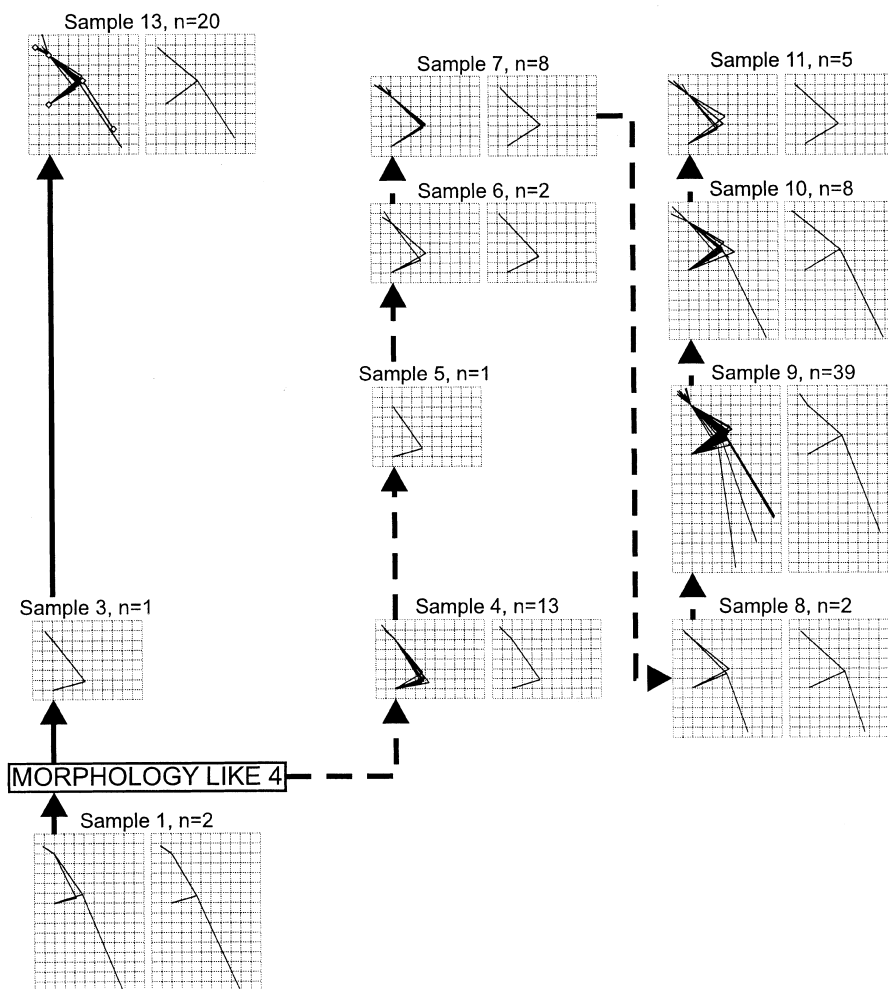
The alternative lineage comprises samples 3 and 13, and will henceforth be referred to as the '*killaryensis utahensis* lineage'. The single cranium available from sample 3 is wider than the one from sample 2, with more developed baculae. Crania from sample 13 have fixed cheeks similar in width to sample 3 when measured across landmark 13, but are wider measured across landmark 15 (Text-fig. 5). The baculae are slightly reduced exsagittally and transversely.



TEXT-FIG. 4. Intra- and inter-sample variation in crania of *Goniophrys* (sample 1) and *Carolinites* (samples 2–13) in dorsal view. The polygonal figures are based on shape co-ordinates calculated for the landmarks shown in Text-figure 3B, with unit-length baseline defined by landmarks 3 and 4. For each sample, the individual specimens are shown on the left, and the geometric mean shape co-ordinate configuration is shown on the right. Only specimens sufficiently mature to lack a preglabellar field are shown, with the exception of sample 1 for which all specimens are shown. Arrows indicate two separate lineages: solid arrows *killaryensis utahensis* lineage; broken arrows *tasmaniensis* – *ekphymosus* lineage. ‘Morphology like 4’ indicates that both lineages presumably derived from a morphology similar to sample 4. White diamonds on sample 1 show the landmark configuration for the specimen illustrated by Hintze (1953, pl. 20, fig. 1). White squares on sample 13 are for the holotype illustrated by Hintze (1953, pl. 20, fig. 10a).

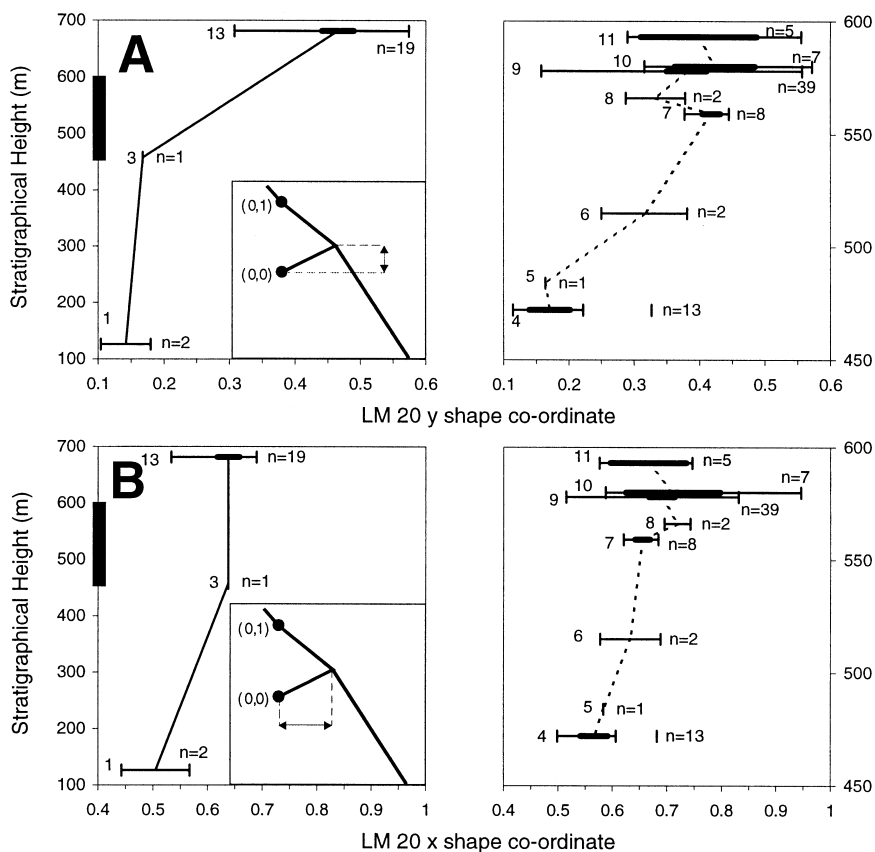


TEXT-FIG. 5. Intra- and inter-sample variation in selected shape co-ordinates on the cranium. A, variation in x shape co-ordinates calculated for landmark 13. Each sample is identified by its number. The plot on the right is an expanded view of the stratigraphical interval indicated by the vertical black bar in the plot on the left. The lines connecting mean values indicate two separate lineages: solid line *killaryensis utahensis* lineage; broken line *tasmaniensis* – *ekphymosus* lineage. B, same for landmark 15. C, same for landmark 8. D, variation in y shape co-ordinates calculated for landmark 7. The total range of variation and two standard errors either side of the mean (where  $n \geq 5$ ) are shown for each sample.



TEXT-FIG. 6. Intra- and inter-sample variation in free cheeks of *Goniophrys* (sample 1) and *Carolinites* (samples 3–13) in dorsal view. The polygonal figures are based on shape co-ordinates calculated for the landmarks shown in Text-figure 3c, with unit-length baseline defined by landmarks 18 and 19. Format of the figure as in Text-figure 4. White diamonds on sample 13 show the landmark configuration for the specimen illustrated by Hintze (1953, pl. 20, fig. 11). Free cheeks were not available for samples 2 and 12.

Text-figure 6 shows polygonal figures derived from measurements made on free cheeks in dorsal view. Text-figure 7 summarizes intra- and inter-sample variation in the x and y shape co-ordinates calculated for landmark 20, which is the point of attachment of the genal spine to the free cheek (Text-fig. 3c). Text-figure 8 is a bivariate plot showing how the location of landmark 20 varies during ontogeny in five of the samples; note that it is based on linear measurements made on specimens and not shape co-ordinates. In the *tasmaniensis* – *ekphymosus* lineage, the proportions of free cheeks from samples 1, 4 and 5 are similar, with the genal spine originating far back on the free cheek (Text-fig. 6). Samples 7–11 are also similar to each other, with the genal spine originating just behind the mid point of the free cheek. The genal spine shown for one of the specimens in sample 8 in Text-figure 6 is probably not complete. The marked change in the point of attachment of the genal spine between the stratigraphically earlier samples and the later ones



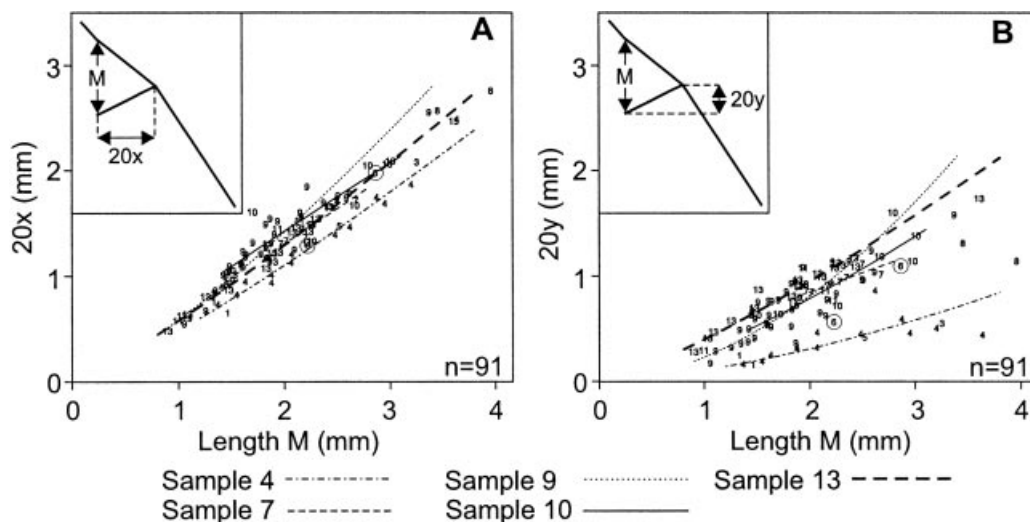
TEXT-FIG. 7. Intra- and inter-sample variation in the x and y shape co-ordinates calculated for landmark 20 on the free cheek. Format of the figure as in Text-figure 5.

is clear in Text-figure 7. Text-figure 8B shows that the anterior migration in the point of genal spine attachment between samples 4 and 7 is achieved by an increase in the slope of the growth trajectory. The simple allometry equation  $y = bx^a$  (Imbrie 1956) that best models sample 4 is  $y = 0.10x^{1.56}$ ,  $n = 13$ , while that for sample 7 is  $y = 0.46x^{0.88}$ ,  $n = 8$ , neither of which are significantly different from isometry ( $P = 0.5$ ). The point of genal spine attachment in sample 6 looks intermediate between the states in the preceding and succeeding samples (Text-figs 7–8) but only two free cheeks were available from that sample.

In the *killaryensis utahensis* lineage the free cheek from sample 3 is a little wider than the two specimens from sample 1, but the point of attachment of the genal spine is similar. In sample 13, the genal spine originates much further forwards, just behind the middle point of the free cheek, echoing the state shown by the stratigraphically higher samples in the *tasmaniensis* – *ekphymosus* lineage (Text-fig. 7).

Text-figure 9 shows polygonal figures derived for pygidia in dorsal view, and Text-figure 10 summarizes variation in the x shape co-ordinates of landmarks 34 and 35, which vary in relation to the width of the pygidium across the widest point on the pleural field and across the postero-lateral lobes. Pygidia belonging to sample 1 (*G. prima*) are somewhat semicircular in outline and have an axis that is relatively wide (measured across the inter-ring furrows; see Text-fig. 3D). Pygidia from sample 4 have relatively narrower pleural fields and are also narrower across the postero-lateral lobes. Pygidia from samples 5 and 6 show similar proportions. In samples 7 and 8, the axis is slightly narrower. Pygidia from sample 9 are as wide, or wider than, those from sample 8 both across the widest part of the pleural field and



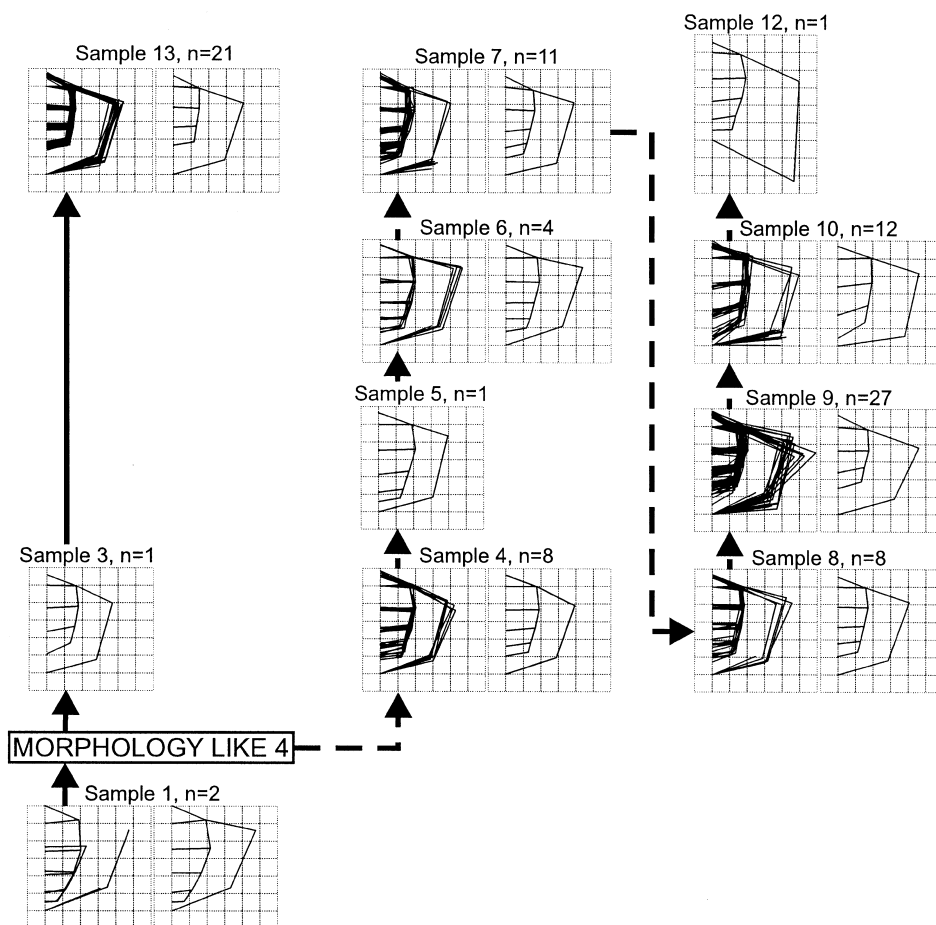


TEXT-FIG. 8. Growth trajectories for free cheeks. A, bivariate plot of x co-ordinates of landmark 20 vs. length M for each of 91 aligned free cheeks belonging to 11 numbered samples. B, y co-ordinates of landmark 20 vs. M. A broad size range of specimens was available for five of the samples, and the growth trajectories for these are modelled using the equation  $y = bx^a$ . Free cheeks were not available for samples 2 and 12. The two specimens belonging to sample 6 are highlighted on each plot. In B, stratigraphically older samples (1–5) have a less steeply sloping trajectory than younger ones (7–13). Sample 6 may be intermediate.

across the postero-lateral lobes. Posterior production of the first and second axial furrows (Text-fig. 2U–V) is of such a degree that the first inter-ring furrow is obscured in dorsal view. The three widest pygidia in sample 9 are the three smallest specimens measured in this study, all with  $Z_{1D} < 1.0$  mm (this measurement is defined in Text-fig. 3D). There is a clear ontogenetic shape change indicated at about  $Z_{1D} = 1.0$  mm in this sample, which may apply generally in *Carolinites*. Pygidia smaller than this size are relatively wide across the pleural field with reduced postero-lateral lobes, whilst larger pygidia are relatively narrower across the pleural field with more developed postero-lateral lobes. In sample 10, the inflation of the postero-lateral lobes is continued, the axis is slightly wider, and the posterior production of the first and second axial rings is increased, so that the inter-ring furrows are clearly directed posteriorly. In sample 12, the more ‘usual’ axis geometry is restored, in which all inter-ring furrows can be seen in dorsal view. The most striking feature of this single specimen is the greatly produced postero-lateral lobes which form blade-like extensions (Text-fig. 2x). This pygidium is also relatively wide, although this may be adversely affected by uncertainty in the location of landmark 28 on Fortey and Droser’s (1996) illustration, which would affect the calculated location of the shape co-ordinates.

In the *killaryensis utahensis* lineage the lone pygidium from sample three is narrower than sample 1 across the pleural field, and has a slightly narrower axis. Pygidia from sample 13 tend to be a little wider across the postero-lateral lobes (Text-fig. 10B) and have slightly narrower axes.

Text-figure 11 shows polygonal figures derived for pygidia in lateral view. Text-figure 12 summarizes variation in the x and y shape co-ordinates of landmark 44, which varies in relation to the degree of postero-dorsal production of the first axial ring. Text-figure 13 shows bivariate scatter plots showing how the location of this landmark varies during ontogeny in five samples. Like Text-figure 8, it is based on linear measurements, not shape co-ordinates. Sample 4 pygidia are of much greater convexity than those in sample 1, especially in the posterior part. The convexities of samples 5 and 6 are similar to sample 4. Pygidia from sample 7 are a little more convex, and slight posterior production of the first two axial rings is visible. This state is also discernible in sample 8. In sample 9 it is quite pronounced. It is even more pronounced in sample 10.

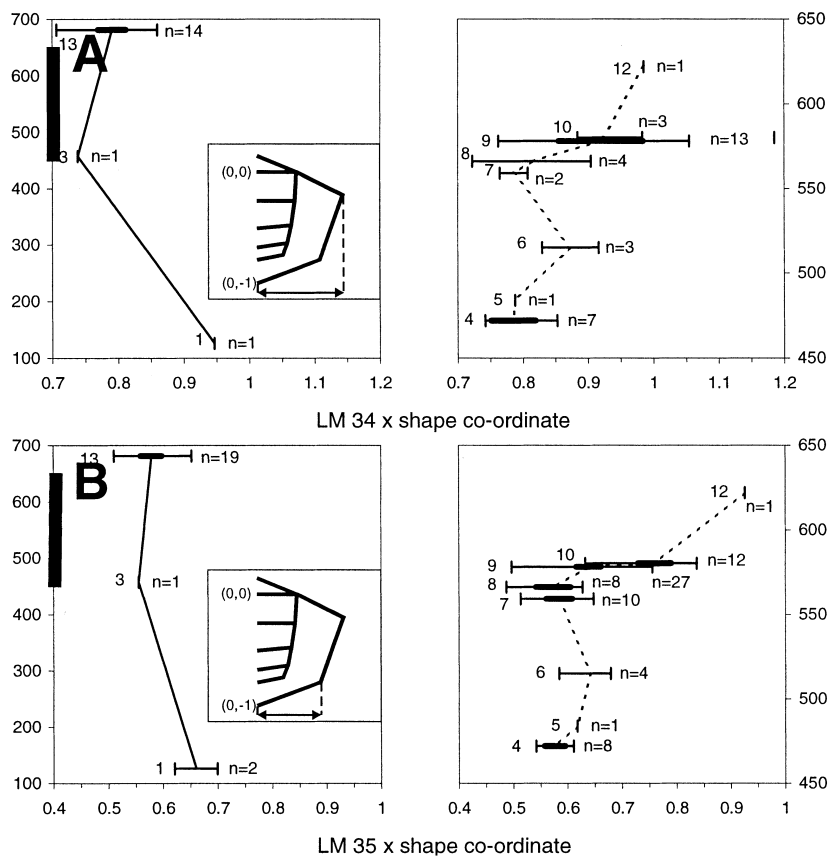


TEXT-FIG. 9. Intra- and inter-sample variation in pygidia of *Goniophrys* (sample 1) and *Carolinites* (samples 3–13) in dorsal view. The polygonal figures are based on shape co-ordinates calculated for the landmarks shown in Text-fig. 3D, with unit-length baseline defined by landmarks 23 and 28. Format of the figure as in Text-figure 4. Pygidia were not available for samples 2 and 11.

It is notable that the pygidia of sample 8 are consistently less convex than those of samples 4–7. Although these pygidia are of greater mean size than those in sample 7, the shape difference does not appear to be the result of different size ranges on one allometric growth curve (Text-fig. 13B, D). The growth trajectories shown for sample 8 are based on a broad size range of specimens, and the shapes of the curves do not appear to be unduly affected by the presence of two large pygidia. The specimens from sample 8 do not appear to be crushed, so this low convexity appears to be a genuine morphotype rather than a taphonomic artefact.

In the *killaryensis utahensis* lineage the single available pygidium from sample 3 is more convex than sample 1 and a terminal spine is developed. Note that the spine in this specimen is probably not complete. The proportions of pygidia from sample 13 are similar to sample 3 although the spine (where undamaged) seems more posteriorly directed.

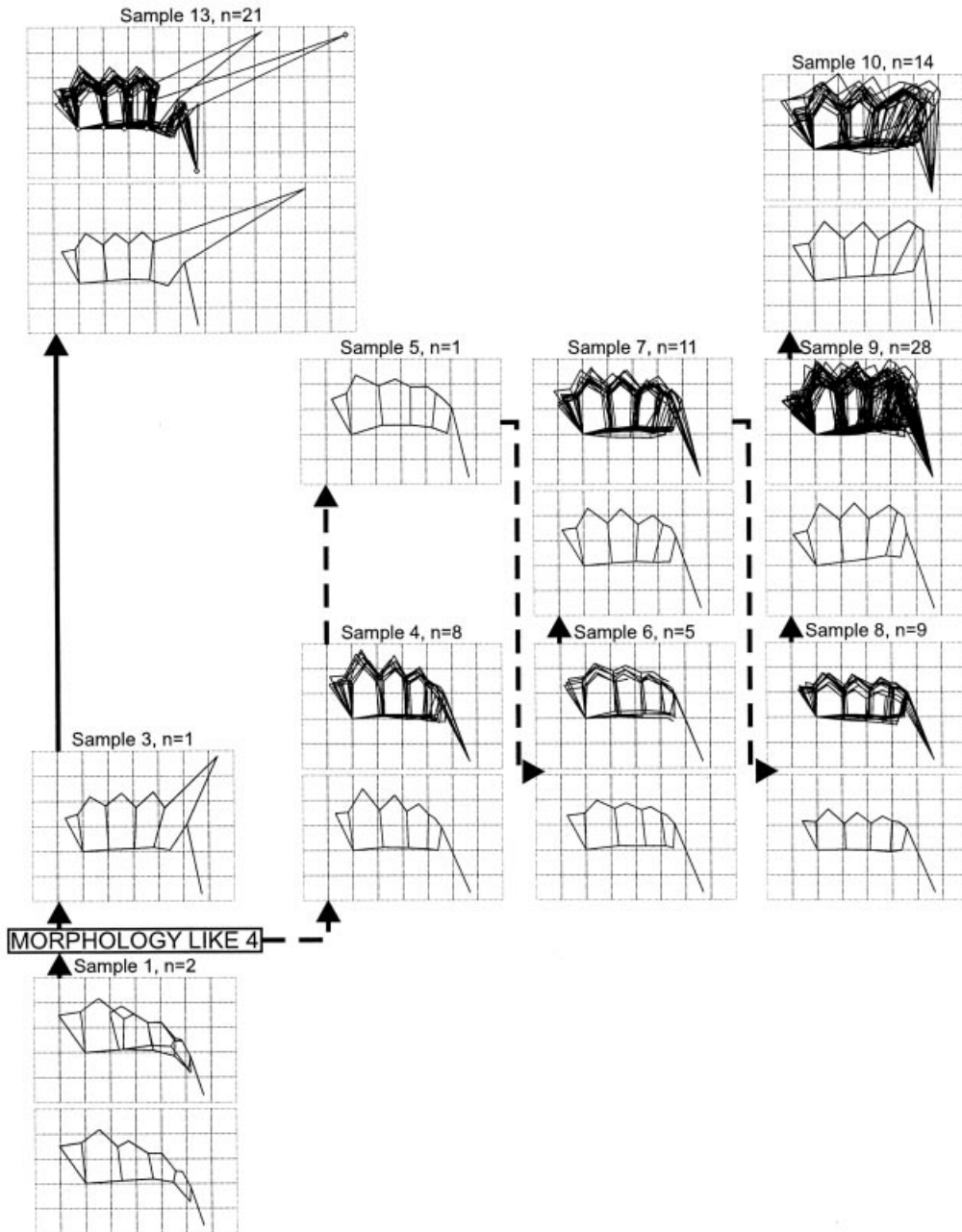
To summarize, there is a morphological discontinuity between samples 1 and 2, and between samples 2 and 4, exhibited in the form of the cranium and the pygidium, although free cheeks from sample 4 are not



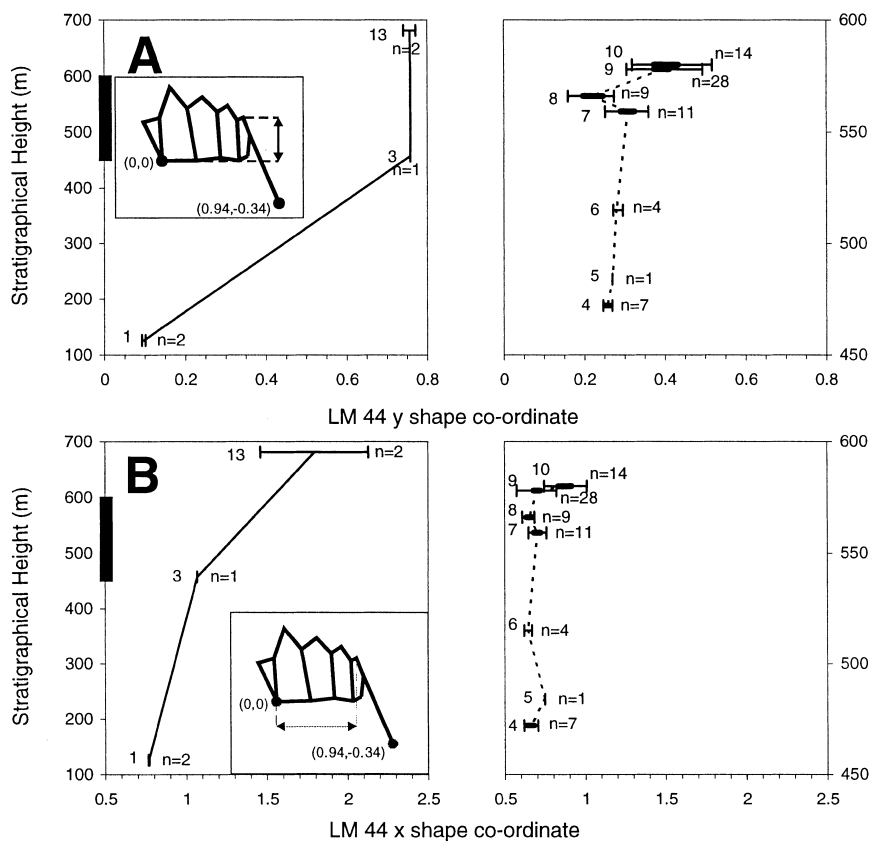
TEXT-FIG. 10. Intra- and inter-sample variation in the x shape co-ordinates calculated for landmarks 34 and 35. Format of the figure as in Text-figure 5.

unlike those from sample 1. The stratigraphical interval encompassing samples 4–7 (in the *tasmaniensis* – *ekphymosus* lineage) sees widening of the fixed cheeks, enlargement of the baculae, development of the anterior median sulcus on the glabella, anterior migration of the point of attachment of the genal spine on the fixed cheek, and transition from a tubular genal spine to a blade-like one (already accomplished by sample 6). This interval represents the transition from the *C. tasmaniensis* morphology to the *C. genacinaca* one. In the subsequent interval which includes samples 8–10, the baculae are slightly reduced but otherwise cranidia and free cheeks remain very similar to those in samples 7 and 8. What is noticeable is that the postero-dorsal production of the first and second pygidial axial rings, discernible in samples 7 and 8, becomes successively more pronounced in samples 9 and 10. There is then a punctuational change to sample 12 in both cranidial and pygidial morphology.

In the *killaryensis utahensis* lineage, there is a punctuational change between samples 2 and 3 in cranidial morphology (assuming the cranidium from sample 3 is not a misidentified *C. tasmaniensis*). The pygidium for *C. sp. A.* (sample 2) is not known, but there is certainly a major difference between the pygidia from samples 1 and 3, the latter possessing a terminal spine which the former lacks. There is remarkably little difference in cranidial and pygidial morphology between samples 3 and 13, in spite of the relatively large stratigraphical interval between (Text-fig. 2). The free cheeks on the other hand are very different. Free cheeks from sample 13 are less robust in appearance, with the genal spine joining the free cheek near the middle point, rather than close to the posterior as they do in sample 3. They also lack the pronounced subocular band.



TEXT-FIG. 11. Intra- and inter-sample variation in pygidia of *Goniophrys* (sample 1) and *Carolinites* (samples 3–13) in lateral view. The polygonal figures are based on shape co-ordinates calculated for the landmarks shown in Text-figure 3E, with unit-length baseline defined by landmarks 46 and 47. For each sample, the individual specimens are shown above, and the geometric mean shape co-ordinate configuration is shown below. White diamonds on sample 13 show the landmark configuration for the specimen illustrated by Hintze (1953, pl. 20, fig. 13b). Lateral views of pygidia were not available for samples 2, 11 and 12.

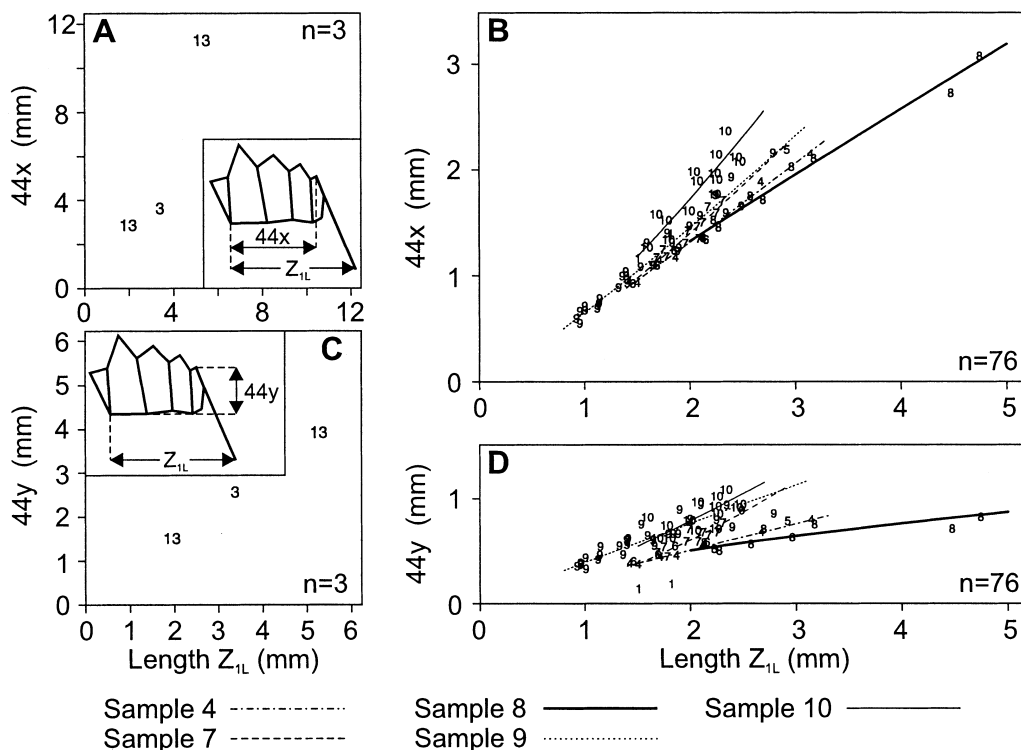


TEXT-FIG. 12. Intra- and inter-sample variation in the x and y shape co-ordinates calculated for landmark 44. Format of the figure as in Text-figure 5.

#### STATISTICAL TESTS FOR GRADUALISM AND PUNCTUATION IN CHARACTER EVOLUTION

Among the characters in the *Goniophrys prima* – *Carolinites tasmaniensis* – *C. ekphymosus* lineage focused on in Text-figures 5, 7, 10 and 12, shape co-ordinates 20x, 20y, 34x, 35x and 44y give the impression of directional change on the plots. They exhibit net change between the base and the top of the series, they have samples which are morphometrically intermediate between preceding and succeeding samples, and they have relatively few 'zigzags'. If sample 1 is taken as the base of the series and sample 12 (where present) as the top, the net change is statistically significant in all testable characters (significance cannot be tested for shape co-ordinates 34x and 35x because one or both end samples in the series have only one specimen). Whether this change is best characterised as punctuational or gradualistic is discussed below. The other characters shown in the figures seem undirected, showing little net change, especially if one ignores the *Goniophrys* sample at the base of each series and concentrates only on the *Carolinites* samples. These characters may be best classified as fluctuating. A special case might be shape co-ordinate 44x which seems very tightly constrained and is perhaps best characterised as exhibiting net stasis. But these are only visual impressions obtained by inspecting the diagrams. Placing some measure of objective confidence on these labels is another matter.

It seems likely that punctuational change and gradualistic change cannot be meaningfully separated unless there is consideration of stratigraphical resolution. An evolution event that appears punctuational at



TEXT-FIG. 13. Growth trajectories for pygidia. A–B, bivariate plots of x co-ordinates of landmark 44 vs. length  $Z_{IL}$  for each of 79 aligned pygidia belonging to ten numbered samples. Samples 3 ('*C. killaryensis utahensis*' of Young 1973) and 13 (*C. killaryensis utahensis*) are shown on the separate plot A for reasons of scaling and because they probably belong to a separate lineage (Text-fig. 1). C–D, y co-ordinates of landmark 44 vs.  $Z_{IL}$ . A broad size range of specimens was available for five of the samples, and the growth trajectories for these are modelled using the equation  $y = bx^a$ . Lateral views of pygidia were not available for samples 2, 11 and 12. A broad pattern of progressively steeper trajectory in successively stratigraphically younger samples is seen in B and D. Sample 8 is anomalous in both B and D.

coarse stratigraphical resolution may appear gradualistic at finer sampling resolution. These two alternatives can only be meaningfully discussed *at a given stratigraphical resolution*; i.e. we may attempt to classify evolution as either punctuational or gradualistic at the observed stratigraphical resolution, accepting that this classification may change if finer resolution data become available. Some of our characters appear consistent with gradualism at the observed resolution, at least over part of the total interval. Shape co-ordinates 20x, 20y, 34x, 44y all change monotonically through several successive samples in some part of their range. But it is well known that randomly fluctuating causal mechanisms can result in time series that exhibit all the characteristics of directed evolution, including trends and sudden jumps (Roopnarine *et al.* 1999). We are not helped by the fact that we can never know whether we really have more than one distinct biological species in a stratophenetic series because we do not know whether one form would be able to reproduce with another form elsewhere in the series. The best approach to objectively characterising a series as gradualistic, punctuational or static at a given stratigraphical resolution is probably to test it statistically for sustained unidirectional change.

Raup and Crick (1981), in studying evolution of single characters in the Jurassic ammonite *Kosmoceras*, devised a set of tests to do this. The tests work by determining whether observed morphology-time series exhibit behaviour that is statistically different from that generated by random processes. Their null hypothesis was that observed series showed the same characteristics as a symmetrical random walk. This is

a time series within each step of which there is an equal probability  $P = 0.5$  of an increase or a decrease in the magnitude of the variable under consideration. Raup and Crick noted a major difficulty in using the random walk as a null hypothesis. The variances in the predictions of the random walk model are large, so that many patterns that are in reality non-random may fall within its bounds. This is a major drawback to the approach, and was recently explored by Roopnarine *et al.* (1999).

It is important to note that tests against random walk predictions are not tests of whether or not evolution has taken place; we know evolution has taken place, we can see it in the plots (excepting the possibility of ecophenotypic change). The purpose of the tests is to classify the pattern of evolution. If an observed pattern turns out *not* to be consistent with the predictions of the symmetrical random walk null hypothesis, then we may infer that the character changed under the influence of some sustained selection pressure, and we are justified in searching for the source of that selection pressure. Alternatively, if the observed pattern turns out to be consistent with the random walk predictions, then we may infer that the character changed under the influence of a randomly fluctuating cause (or set of causes which interact in a way that is so complex that the sum of their actions appears random). Such causes include genetic drift or randomly changing selection pressures. Failure to reject the random walk null hypothesis is in no way a negative result.

Raup and Crick made four predictions for the symmetrical random walk null hypothesis. They are: (1) the number of runs up and down has a known probability distribution; (2) the mean value of a series of increments between data points does not depart significantly from zero; (3) the number of positive increments is not significantly different from the number of negative increments; (4) the frequency distribution of increment sizes is normal. These predictions are valid even when the random walk is sampled at irregular intervals, as is inevitably the case in geological situations. An observed stratophenetic series can be tested against each of these predictions, and the random walk null hypothesis rejected or not rejected accordingly. However, remembering the drawback noted above that non-random patterns may fall within the bounds of the random walk model, it is also more than possible to incorrectly accept the null hypothesis (Type II error). The best approach seems to be to compare a given series with all four predictions and use one's critical judgement in assessing the results.

Table 1 shows the results of testing each of the time-morphology series shown in Text-figures 5, 7, 10 and 12 (*Goniophrys prima* – *Carolinites tasmaniensis* – *C. ekphymosus* lineage) against the four symmetrical random walk predictions of Raup and Crick. Test 1 (of prediction 1) works by calculating the number of runs expected in a series under the random walk model,  $u_{exp}$ , given the number of positive and negative increments between samples,  $n_1$  and  $n_2$ .  $u_{exp}$  can be compared with the observed number of runs  $u_{obs}$ .  $u_{obs}$  and  $P(u_{obs})$ , the probability of getting the observed number of runs, are calculated using equations three and four of Raup and Crick (1981). Where  $u_{obs}$  is much less than  $u_{exp}$  for given values of  $n_1$  and  $n_2$  we can infer that the character has been subject to sustained directed selection. Where  $u_{obs}$  is much greater than  $u_{exp}$  we can infer that random processes have affected the character. Note that the test takes the values of  $n_1$  and  $n_2$  as given and has nothing to say about how likely it is to get these values in the first place. In Table 1,  $u_{obs}$  and  $u_{exp}$  are not significantly different in any series. This means that the observed number of runs is similar to what we would expect under the random walk in all characters *given the number of positive and negative increments*.

Test 2 of Raup and Crick works by comparing the mean increment magnitude in a series with the mean increment expected under the random walk, which is zero. The departure of the observed mean from zero can be assessed statistically using equations seven and eight of Raup and Crick, which are based on the  $t$ -distribution. The probability of getting a particular mean increment is given in Table 1 as  $P_{mean}$ . Again, none of the characters behaves in a way that is significantly different from the random walk prediction; none of the values of  $P_{mean}$  are significantly low. Test 3 is a simple comparison of the number of positive and negative increments,  $n_1$  and  $n_2$ . There is a large discrepancy of  $n_1$  over  $n_2$  in shape co-ordinates 20x, 34x and 44y. Test 4 is the comparison of the observed distribution of increment sizes with the random walk expectation, which is that they are normally distributed. The relatively small number of samples in each series (between ten and 13, depending on the character) makes statistical testing unfeasible in the present case. The frequency distributions of increment sizes for each character were inspected and all are approximately normal with the exception of shape co-ordinates 35x and 44x, both of which are bimodal

TABLE 1. Summary of the results of Raup and Crick's (1981) tests of stratophenetic series against the null hypothesis of unbiased random walk applied to selected shape co-ordinates in the *Goniophrys prima* – *Carolinites tasmaniensis* – *C. ekphymosus* lineage. *A priori* is the initial impression derived from inspection of Text-figures 5, 7, 10 and 12.  $n_1$  and  $n_2$  are the number of positive and negative increments in each series respectively.  $u_{exp}$  is the expected number of runs in a series given  $n_1$  and  $n_2$ ;  $u_{obs}$  is the observed number of runs and  $P(u_{obs})$  is the probability associated with this observation. The results of Raup and Crick's test 4 are not amenable to statistical analysis in the present case and are reported in the text.

Shape co-ordinate	<i>a priori</i>	Test 1			Test 2		Test 3	
		$u_{exp}$	$u_{obs}$	$P(u_{obs})$	Mean increment	$P_{mean}$	$n_1$	$n_2$
LM 20x	directed	4.45	4	0.36	0.0202	0.20	6	2
LM 20y	directed	5.00	6	0.21	0.0321	0.26	5	3
LM 34x	directed	4.45	4	0.36	0.0049	0.88	6	2
LM 35x	directed	5.00	4	0.29	0.0333	0.31	5	3
LM 44y	directed	2.86	3	0.86	0.0437	0.26	6	1
LM 44x	stasis	4.63	6	0.17	0.0150	0.72	4	3
LM 7y	fluctuating	6.00	8	0.13	0.0217	0.34	5	5
LM 8x	fluctuating	6.00	4	0.13	0.0229	0.30	5	5
LM 13x	fluctuating	6.00	7	0.19	0.0040	0.93	5	5
LM 15x	fluctuating	5.91	7	0.19	0.0094	0.78	6	4

with a negative and a positive peak. This indicates that these two characters fluctuate with greater increments than the random walk model predicts.

Table 1 does not give unequivocal support for sustained directed selection in any of the characters, but given the small number of samples and the problems associated with testing against the random walk hypothesis mentioned above, this is perhaps not surprising. Reading across all four tests, it seems that changes in shape co-ordinates 20x, 34x and 44y are the best candidates for a directional interpretation. This assessment is based largely on the results of test 3.

Bookstein (1988) developed another test which also compares stratophenetic series with the null hypothesis of symmetrical random walk, but which uses a different method. We know that a random walk has equal probability  $P=0.5$  at each time step of an increase or a decrease. We can choose a realistic frequency distribution for increment magnitude. Knowing these parameters, confidence limits can be placed to envelop the region within which 95 per cent (say) of all random walks with the same parameters lie after a given number of steps. There are two ways in which an observed time series may deviate from this confidence envelope: (1) series subject to sustained directional selection will deviate further from their starting point than any random walk, subject to the chosen confidence limit; (2) series subject to stabilising selection (i.e. stasis) will deviate less from their starting point than any random walk, subject to the chosen confidence limit. The relevant limits, against which the maximum excursion in the observed time series is compared, are calculated using equation two of Bookstein (1988).

Table 2 shows the results of applying the test to the selected shape co-ordinates in the *Goniophrys prima* – *Carolinites tasmaniensis* – *C. ekphymosus* lineage. With the exception of 44x, the maximum excursion of each series lies between the limits calculated for anagenesis (i.e. the limit beyond which directed selection may be inferred) and stasis (within which stabilising selection may be inferred). This means that none of these series behaves significantly differently from a random walk. Shape co-ordinate 44x has maximum excursion less than the stasis limit, suggesting that stasis is actively maintained in this character.

The results summarised in Tables 1 and 2 do not unequivocally indicate that any of the character transitions considered are the result of sustained directional selection. This result is discussed below.



TABLE 2. Summary of the results of Bookstein's (1988) test of stratophenetic series against the null hypothesis of unbiased random walk applied to selected shape co-ordinates in the *Goniophrys prima* – *Carolinites tasmaniensis* – *C. ekphymosus* lineage. *A priori* is the initial impression derived from inspection of Text-figures 5, 7, 10 and 12. \* indicates rejection of the null hypothesis in the direction of stasis.

Shape co-ordinate	<i>a priori</i>	Maximum excursion	Anagenesis limit	Stasis limit
LM 20x	directed	0.2147	0.2710	0.0747
LM 20y	directed	0.2812	0.4845	0.1335
LM 34x	directed	0.1614	0.5345	0.1473
LM 35x	directed	0.2660	0.5482	0.1511
LM 44y	directed	0.3061	0.5642	0.1555
LM 44x	stasis	0.1254*	0.5943	0.1638
LM 7y	fluctuating	0.2360	0.4865	0.1340
LM 8x	fluctuating	0.3091	0.4739	0.1306
LM 13x	fluctuating	0.2913	0.8856	0.2440
LM 15x	fluctuating	0.2746	0.6909	0.1904

## DISCUSSION

Geary (1995) pointed out that it is necessary to understand the geographical variation in a taxon before one can meaningfully interpret changes in a stratophenetic series. If the morphological variation on a single time plane is as great as the total variation in the time series, then it becomes likely that the vertical series reflects nothing more than successive waves of immigration. If, on the other hand, variation on a time plane is very low in comparison with the changes seen throughout the series, then it is more likely that the series reflects true evolution. McCormick and Fortey (1999) compared *C. genacinaca* from Ibex with specimens clearly belonging to the same species from approximately contemporaneous rocks in Alberta, Spitsbergen, southern France, north-eastern Siberia, Western Australia, Queensland, and eastern China. Some of these localities were extremely distant from Ibex during the Ordovician, but morphological variation over this vast palaeogeographical range was found by morphometrics to be very low indeed. Ibex-area *C. genacinaca* can thus stand as a proxy for its species worldwide. Similar observations have been made on a qualitative basis for other *Carolinites* species. *C. tasmaniensis* is known from Nevada, Alberta, Spitsbergen and Australia and all material is very similar to the Utah occurrence. *C. sibiricus*, while not represented in the Ibex succession, is present in Whiterockian collections from Siberia, Spitsbergen (Fortey 1975b) and the western United States (Ross 1967, figured as *C. angustagena*). Moreover, the same vertical succession of species can be recognised in Ibex, Spitsbergen and Alberta. It therefore seems reasonable to treat a stratophenetic series of *Carolinites* in a single area as representative of evolution in the genus worldwide. Geary's (1995, p. 79, fig. 3.7) case of Cretaceous cardiid bivalves in which the total variation in a vertical series representing approximately 6 My is not much greater than the geographical variation at two horizons is an example of the opposing situation.

The *C. tasmaniensis* – *genacinaca* transition at Ibex presumably correlates stratigraphically with the same transition in the Spitsbergen (Fortey 1975b) and Wilcox Pass (Dean 1989) successions. The transition can be traced through several stratigraphical samples at Ibex (4–7), affecting characters on the cranidium, free cheek and pygidium. Fortey's (1975b) view that there is a gradual transition rather than an abrupt punctuational change is thus borne out by the Ibex study. However, when the *tasmaniensis* – *genacinaca* transition is placed in the context of the whole stratophenetic series at Ibex, it becomes clear that most of the characters are in fact fluctuating (Text-figs 5, 7, 10, 12). If the transition between these two morphospecies was driven by directed selection pressures, those pressures did not continue to act subsequently in the lineage.

The subsequent development of the modified pygidial morphology at Ibex, in which the first and second

pygidial axial rings become developed postero-dorsally, has not previously been reported from any other locality. However, a similar pygidium has been discovered by us among bulk collections made by the second author high in the Olenidsletta Member of the Valhallfonna Formation, Spitsbergen (i.e. stratigraphically higher than occurrences of typical *C. genacinaca* morphology and lower than typical *C. ekphymosus*). It will be interesting to see whether a similar morphology is reported from very late Ibexian rocks elsewhere in the world.

There are two possible interpretations for the results of the comparisons with the random walk null hypothesis summarised in Tables 1 and 2. The first is that none of the character transitions considered is the result of sustained directional selection. Rather, they are all the result of purely random processes, or processes that appear random (with the exception of shape co-ordinate 44x which seems to be in stasis). Such processes include genetic drift, or rapidly changing selection pressures. This interpretation is perfectly reasonable for shape co-ordinates 7y, 8x, 13x and 15x, all of which appear to fluctuate. It is more surprising in the cases of shape co-ordinates 20x, 20y, 34x, 35x and 44y, which do appear to show directed change through the series. However, perhaps we should not be surprised. It is possible that many evolution case studies reported as representing gradualistic evolution are in fact consistent with the random walk model. The appearance of a sustained directed trend in a lineage could result simply from a combination of chance and stratigraphical resolution. Roopnarine *et al.* (1999) pointed out that this possibility has not been considered in most published case studies.

An alternative interpretation stems from the observation of Roopnarine *et al.* that many types of time series begin to resemble random walks statistically as sampling resolution decreases. In particular, application of tests using the random walk as null hypothesis without consideration of completeness (defined as the ratio of sample number to estimated number of generations elapsed) increases the probability of Type II error (incorrect failure to reject the null hypothesis). This means the tests may become inapplicable as sampling resolution is reduced. The series under consideration here have only between ten and 13 samples. This is many fewer, and they are more widely separated, than is common in Cainozoic microfossil and mammal studies, and the ratio of samples to generations elapsed will be extremely low (although still better than most other Palaeozoic macrofossil studies because of the quality of the Ibex succession). It is possible that the resolution of Palaeozoic stratophenetic series can never be good enough to statistically test the observed pattern against random walk.

If the tests are valid, then we can conclude that the observed changes in these fossils are more likely to be the result of random or fluctuating causes than directed selection. Of course this does not alter the fact that change does occur in *Carolinites* up-succession, and that these changes can be used for taxonomy and biostratigraphy. Moreover the fact that the *C. tasmaniensis* – *C. genacinaca* transition, and potentially the subsequent transition to a new pygidial morphotype, are recognisable in other widely separated localities shows the usefulness of *Carolinites* in intercontinental stratigraphical correlation.

#### CONCLUSIONS

1. We follow Levinton (1983, p. 115) and infer that gradualistic evolution is occurring when 'change up a geological section is monotonic and when periods of character stasis do not preclude phyletic divergence of two morphs sufficiently different to be recognised as distinct 'species'.'
2. It has been previously argued that the Lower Ordovician trilobite *Carolinites* exhibits gradualistic evolution. We set out to test this assertion.
3. An ideal microevolution case study should offer the following characteristics: (1) thick rock sequence without stratigraphical breaks; (2) confacial rock sequence; (3) abundant fossils; (4) correlation with other sequences by some means independent of the study organism.
4. We performed a morphometric study on *Goniophrys* and *Carolinites* sampled from the Lower–Middle Ordovician type Ibex succession of western Utah. This sequence is probably as close to the ideal case as is likely to be found in Palaeozoic rocks.

5. Two evolving lineages were recognised. Within the better-sampled lineage we discovered examples of each of the following types of measurable characters: (1) characters which fluctuate but showed little or no net change between the base and the top of the sequence; (2) characters which change between the base and top of the sequence via an abrupt 'step' change; (3) characters which change between the base and top of the sequence via a series of intermediates. Examples belonging to (2) and (3) exhibited reversals.
6. Fortey's (1975*b*) claim of a transitional relationship between *Carolinites tasmaniensis* and *C. genacinaca* was confirmed in the Ibez succession.
7. Testing of the characters against the null hypothesis of symmetrical random walk, using the methods of Raup and Crick (1981) and of Bookstein (1988), indicated that none of the characters was changing under sustained directional selection, even those which pass through a series of intermediate states. Two interpretations are possible. The first interpretation is that all characters, including those that appear gradualistic, are in fact responding to random causes (these include genetic drift and rapidly fluctuating selection pressures) or to causes that interact in so complex a way that they appear random. This observation may be applicable to many claimed cases of gradualistic evolution in the literature. An alternative interpretation is that the evolving lineages are just sampled at too poor a resolution to allow meaningful testing against the random walk. If this is the case, then this situation is likely to apply in most evolutionary case studies involving Palaeozoic macrofossils.

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