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ABSTRACT. Morphospace studies are rich in pattern and process. Techniques for adequate description and mapping of morphologies have been increasingly refined and applied, the same being true of metrics for relevant parameters (like disparity). However, the testing of process hypotheses for specific patterns of morphospace occupation in time and space is less refined and demands more intensive scrutiny. The polarization of ecological and developmental explanations entails a need to properly tease apart their respective contributions. There are different ways to go about this problem. Here I describe one approach: the isolation of development as a target for testing via the construction of developmental morphospaces.

Comparison of differently constructed morphospaces (one reflecting development directly, the other indirectly) provides a way of consistently studying the impact of development in constraining or facilitating changes in diversity. Congruence in range and/or location of "developmental" and "non-developmental" morphospaces, when properly interpreted to account for possible stochastic effects, is powerful evidence for a controlling influence of ontogeny. Appropriate choices involve three kinds of contrasts (with qualifications): theoretical (generative) vs. empirical (descriptive), abnormal (teratological) vs. normal, and juvenile vs. adult morphospaces. Theoretical morphospaces encapsulate logically simple principles of form generation, mimicking the potential simplicity of epigenetic processes. Teratological morphospaces are based on unsuccessful experiments in evolution, but any regularities encountered must reflect internal constraints and opportunities. Juvenile morphospaces are likely to depict a range of pronounced allometries that can serve as raw material for evolution. I provide an extended example of juvenile vs. adult morphospace comparisons with a case study on the evolutionary history of the echinoid order Spatangoida.

The broad pathways of morphospace occupation for adults in the order are contrasted with the distribution of juveniles in a developmental morphospace constructed from geometric morphometrics of post-metamorphic specimens. To ensure comparability,

the same homologous landmarks are used for adults and juveniles. Disparity between pooled adults and pooled juveniles is compared, and also interpreted in a phylogenetic framework. The distributions of resampled total juvenile and adult disparities are indistinguishable, but there is much dissociation of growth trajectories in morphospace, with many instances of taxonomically heterogeneous juvenile/adult clusters. There are cases of demonstrable association of derived juveniles and primitive adults, pointing to peramorphosis, and of primitive juveniles and derived adults, pointing to paedomorphosis. Instances of clustering of juveniles from different taxa also occur, thus partially supporting Von Baer's second law. Different composite variables, however, suggest no consistent support for VBSL, with cases of similar disparity in juveniles and adults (contra VBSL), of higher disparity in adults (pro VBSL), and of higher disparity in juveniles (contra VBSL). When developmental disparity is mapped on a phylogeny, lack of support for VBSL is again implied: juvenile/adult disparity contrasts based on clade ranks indicate that within subclades juveniles tend to be more variable than adults. There is thus no single vector of change in disparity through ontogeny. Still, all such developmental action potentially driving evolution occurs within a constrained morphospace which is similarly partitioned in ontogenetic and evolutionary time. These results are in disagreement with what can be inferred from vertebrate model systems; their generality should be further explored with analyses of developmental disparity in other invertebrate groups.

I - Introduction

As the field of morphospace studies expands and the approach becomes more and more familiar to biologists and paleobiologists in general, it is apparent that there is no one way of studying morphospaces. There is variation in kind (theoretical, empirical), in method (mathematical modelling, qualitative description, uni- and multivariate analysis of discrete and morphometric data), in level of analysis (from population to kingdom), in temporal scope (single interval to several or many intervals), and in language (with focus on isolated morphological parameters or on composite variables like disparity).

As statements about pattern, morphospace analyses are usually accompanied by inferences about possible processes involved, either through the comparison of morphological distributions and associated descriptors with ancillary data of taxonomic, environmental, or functional nature (Foote 1993; Roy 1994; Lauder 1995, 1996), or through the recasting of the morphospace description itself in terms of such ancillary data (e.g., Moore and Ellers 1993; Hickman 1993). It is noticeable, however, that developmental data are much less frequently considered in morphospace studies (but see Alberch 1989; Ellers 1993; David and Laurin 1996; Zelditch and Fink 1996). To the extent that morphological evolution expresses the interplay of underlying intrinsic (developmental) and extrinsic (ecological) factors, it is of interest to evaluate the relative importance of such factors in explaining patterns of morphospace occupation. While functional interpretations of morphospaces have a long tradition in ecomorphological and performance studies, functional studies are not always feasible when taxonomic breadth is wide (certain taxa may not be available to experimental work) or temporal coverage is extended (with inclusion of fossils). In addition, given the dominance of adaptational thinking in evolutionary biology, exclusive focus on function often masks a plethora of evolutionarily relevant questions such as heterochrony, heterotopy, asymmetry of amount of variation in developmental time, and links between phylogenetic and ontogenetic trends. If ontogenetic data are available, developmentally meaningful morphospaces can be constructed instead, thus

complementing deficiencies (or for some groups, absence) of functional studies and suggesting novel interpretations of morphological patterns. Logically, developmental morphology has the same status and the same potential utility in understanding evolution as functional morphology. The idea, meaning, and application of developmental morphospaces in evolutionary biology forms the subject of this paper.

II - Developmental and non-developmental morphospaces

There are multiple ways to study the role of development in evolution (see Eble 1998a). Although a phylogenetic framework is always beneficial and mapping of developmental information onto cladograms can be invaluable in ascertaining developmental trends, a morphospace approach to development and evolution can be advantageous for several reasons: (1) The precept that the order recovered through phylogeny is a mirror of ontogenetic order (Nelson 1978; Patterson 1983), while true in many cases, has been disputed on theoretical and empirical (Alberch 1985; Ho 1990, 1992) grounds -- a morphospace, in turn, allows unambiguous representation of both ontogenetic and temporal order and "disorder", whether it is recoverable by phylogenetic algorithms or not; (2) because of homoplasy, there will often be multiple equally or near-equally parsimonious trees, generating uncertainty in the choice of a reference phylogeny (Foote 1997; this is compounded by controversies over combinability of different kinds of data) -- a morphospace, however dependent on choice of analytical technique, is a unique representation of the statistical structure of both homologous and homoplastic characters across taxa; (3) phylogenies are statements about sameness and the hierarchical distribution of homology, and when homoplasies are considered phylogenies can at most take into account total differences -- morphospaces allow both sameness and difference to be economically considered together, and thus can capture the net differences (including plesiomorphies) that underlie the developmental hierarchy of levels of distinctness, or disparity (Eble 1998a). Clearly, a morphospace approach to the study of the relationship

between development and evolution has intrinsic value and is not subordinate to knowledge of phylogenetic relationships. Phylogenetic and morphospace approaches are best viewed as complementary (see also Foote 1996a).

Developmental morphospaces are here defined as morphospaces built in a manner that reflects development directly by reason of either the variables or the entities depicted in such morphospace carrying meaningful developmental information. Although non-developmental morphospaces need not be devoid of developmental meaning, their information content is often removed from the axis of ontogenetic action as a result of representation of adult forms only. As will be seen below, the distinction between developmental and non-developmental morphospaces is not absolute; they can and will often overlap, but the former will tend to encapsulate implications of process (much in the same way as with functional or design spaces), while the latter will be imbued with a more pattern-oriented quality. Much of the field of morphospace studies is concerned with temporal, spatial or taxonomic partitioning of non-developmental morphospaces. As inferences move from pattern to process, intrinsic ontogenetic biases stand as one possible explanation for observed regularities.

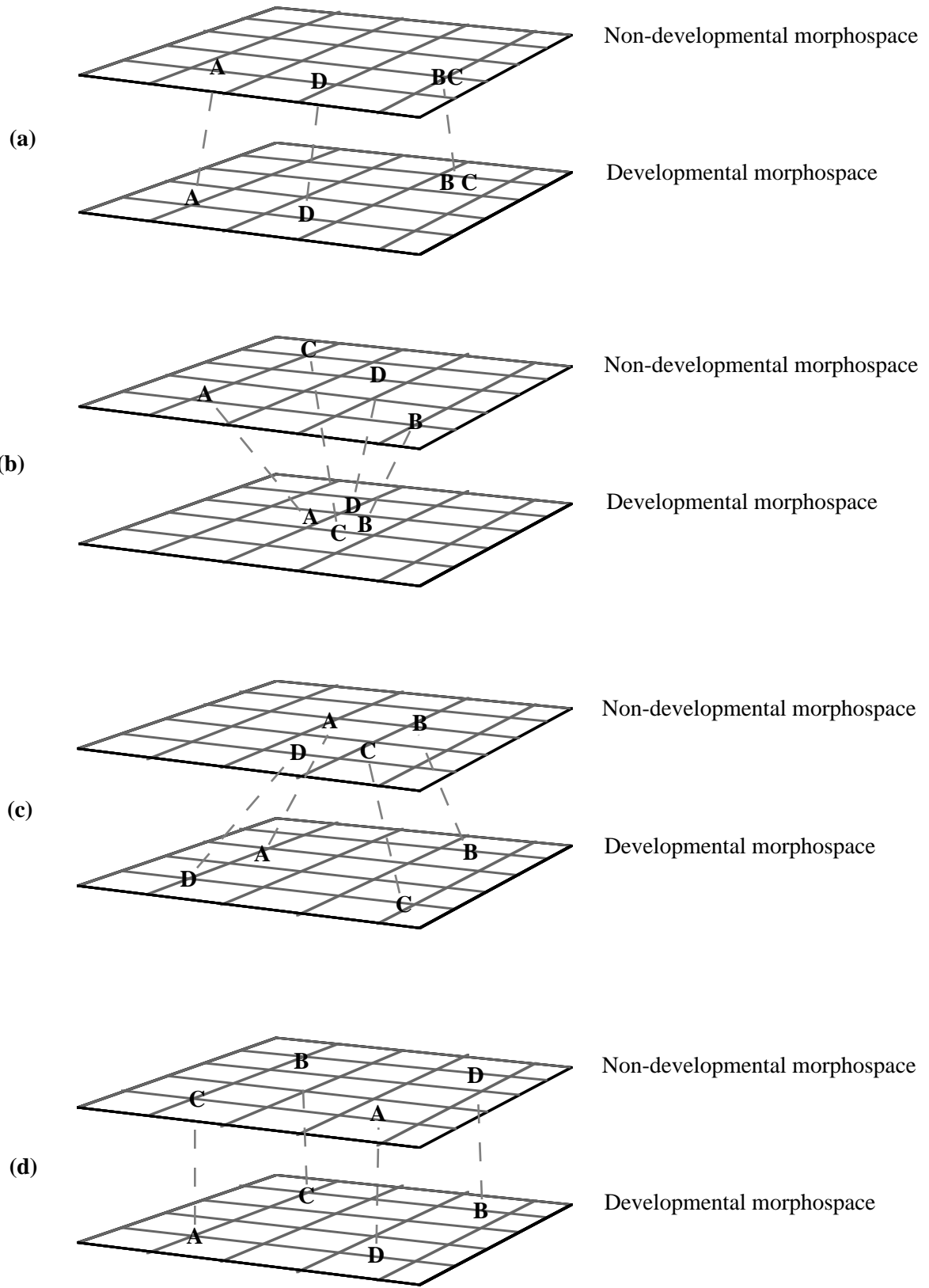
The idea of developmental morphospaces is by no means new, for it can be seen as a logical morphological extension of Waddington's metaphor of the "epigenetic landscape" (Waddington 1957), Goodwin's notion of "epigenetic space" (Goodwin 1963) and Alberch's rendition of "parameter space" (Alberch 1989). While such developmental spaces are suitable for understanding of the genotype-phenotype map (Wagner and Altenberg 1996), developmental morphospaces are more useful for the inference (though by no means ultimate explanation) of more focally phenotypic phenomena like heterochrony, heterotopy, and developmental constraints. In addition, they allow coverage of patterns of developmental variation in the fossil record.

Although developmental morphospaces can be studied indirectly through clade/clade or clade/subclade comparisons, our best hopes of understanding how

developmental variation structures the evolution of adult form should be tied to the comparison of developmental and non-developmental morphospaces. This is equivalent to the time-honored principle in statistical data analysis of using ancillary data to better understand a given pattern. If the spaces are commensurate, much insight can be gained by analyzing the statistical concordance in range and/or location of forms across spaces. Similar analyses can also be performed with comparisons of non-commensurate spaces (e.g., a comparison of larval and post-metamorphic morphospaces), but in this case the range of inferences is restricted to statements about the relative distance of forms in each space, and the issue of differential filling of morphospace through ontogeny becomes difficult to address. Thus, although the commensurability requirement is not absolute, it immediately suggests the use of homologous features whenever possible.

To illustrate developmental and non-developmental morphospace comparisons diagrammatically, an iconography recently used by Lauder (1995, 1996) in the context of functional analysis is adapted for the present purposes, and shown in Fig. 1. Both concordances and discordances can reveal a potential role of developmental factors in structuring (adult) morphological distributions in non-developmental morphospace. The interpretation of distributions, however, is dependent on the specific kinds of developmental/non-developmental comparisons, a function of which data and which theoretical outlook is used. Three kinds of contrasts are immediately relevant: theoretical/empirical, abnormal/normal, and juvenile/adult morphospaces (see also Eble

Fig.1 (next page). A typology of developmental versus non-developmental morphospace comparisons. (a) Clustering, location and range is strictly predicted by developmental morphospace (this is an expectation in comparisons of theoretical and empirical distributions equally parameterized); for abnormal/normal and juvenile/adult comparisons this is consistent with a developmental control of adult distribution or with some other variable acting in both situations. (b) Location and range is not predicted by developmental morphospace because of deviation of forms across spaces. (c) Location and range is not predicted by developmental morphospace because of convergence of forms across spaces. (d) Extensive dissociation in ontogeny is suggested by lack of congruence in clustering and location of equivalent objects across both spaces. The clustering of forms from non-developmental and developmental morphospaces belonging to different species suggests much potential for heterochrony. The similar variance and range implies developmental bounds to adult variation.



1998a). Each of these is discussed in detail below, both in terms of a reappraisal and reconceptualization of past work and of suggestions for future research. The discussion on juvenile/adult morphospaces is accompanied by an empirical example using echinoids.

III - Theoretical vs. empirical morphospace comparisons

Phenomenologically, the distinction between theoretical and empirical descriptions has occupied a central position in morphospace studies. The distinction is sometimes made not so much in terms of means of production of representation spaces (by simulation as opposed to by measurement) but in terms of scope: theoretical spaces are able to represent what is possible, or occupiable, and empirical spaces are renditions of what has actually been occupied (McGhee 1991; Arthur 1997). Theoretical morphospaces are "developmental" due to their generative nature (explanans), to their ability to specify predictions of possible natural occurrence. Empirical morphospaces are, in this context (but not in others -- see discussion on juvenile morphospaces), non-developmental because they are built in terms of the theoretical generative parameters; they are the object of explanation (explanandum), and thus subordinate in this particular framework of deductive-nomological explanation (see Hempel 1966).

The comparison of theoretical and empirical morphospaces allows, to different degrees as the case may be, the interpretation of empirical distributions in terms of boundary conditions specified by a relatively small number of parameters. The success of any theoretical model in portraying realistic possibilities, some or all of which are empirically realized, is already evidence not only for the potential simplicity of controls on morphological distributions (the machinery of variation), but also for the existence of a phenotypic logic of morphological transformations which is partly independent of direct gene control, implying a hierarchical organization of development and a non-linear genotype-phenotype map (see Alberch 1982; Wagner and Altenberg 1996; Webster and Goodwin 1996). Congruence of the kind portrayed in Fig. 1a should accrue.

Differential filling and density of actual occupation of different regions in theoretical morphospace, in turn, are separate issues, reflecting historical contingency, historical constraint, the distribution of biomechanical optima, and developmental constraints based on unconsidered generative parameters (Raup 1987). In effect, these issues suggest the desirability of complementing morphospace studies with approaches such as stochastic simulations and sensitivity analysis of morphospace colonization (e.g., Foote 1991), mapping of phylogenies onto morphospaces (e.g., Bookstein et al. 1985; David and Laurin 1996), assessment of functionality of different forms (e.g., Raup 1967; McGhee 1980, 1995; Hickman 1993; Thomas and Reif 1993; Lauder 1995), and modelling based on more refined developmental parameters, capable of codifying inequiplausible renditions of form (Goodwin and Trainor 1983; Shubin and Alberch 1986; Alberch 1989; Webster and Goodwin 1996; Rice 1998).

Three points of contention are particularly relevant in theoretical/empirical morphospace comparisons, and affect how much information about developmental controls on evolution can be extracted from theoretical morphospace constructs: (1) the extent to which anisometry is taken into account; (2) the biological meaning of different underlying models (geometric, physical, morphogenetic); and (3) the meaning of modelling in general and what it can tell us about the workings of development and its potential role in evolution.

(1) Often, occupied empirical morphospaces have been contrasted with occupiable theoretical counterparts based on sampling of adults alone (e.g., Raup 1966, 1967; Ward 1980; McGhee 1995; but see Raup 1967, 1968; McGhee 1980). But if inferences about constraints are to be sought in comparisons of the occupied and the occupiable, more attention should be paid to ontogenetic variation -- regions inaccessible to adult morphologies may well be occupied at different stages in ontogeny. For example, adult cassiduloid echinoids do not have lanterns, but juveniles do. Atelostomate echinoids, having an oval or heart-shaped outline, actually start out after metamorphosis very round-

shaped. Whenever allometric growth is present, the relationship between occupied and occupiable is liable to change through ontogeny. By the same token, explanations for differential filling, like those relying on biomechanical considerations and optimality criteria, must whenever possible incorporate the precept that different stages in life-history may be subject to different living requirements. In short, different morphological distributions may hold at different stages in ontogeny, such that the realized morphospace may often be broader than an adult-oriented representation may grant, with consequences for causal interpretation.

(2) It has been argued that a desideratum of theoretical morphospace models should be their possession of biological meaning, often equated with the presence of morphogenetic parameters (Savazzi 1995; Rice 1998). Certainly, in a literal sense, a purely geometric morphospace model says nothing about underlying developmental controls. But meaning is what an effective translation preserves, literally or not (Audi 1995), and it thus can be argued that the "translation" of form generation in terms of geometric (as opposed to morphogenetic) parameters still effectively permits exploration of the developmentally relevant issues of the relationship between possible and actual, the unevenness of filling of morphospace, and the suggestion that unoccupied regions may reflect developmental prohibitions. "Non-morphogenetic" theoretical morphospaces are thus not devoid of developmental meaning, at least for the majority of questions raised by theoretical/empirical morphospace comparisons.

In addition, it can be argued that the use of actual biological parameters is not the only way to study morphogenetically meaningful morphospaces. Physical models of form have been shown to be very suggestive of actual principles involved: some echinoid plate arrangements, including angles between units, resemble soap bubble arrangements and seem to obey purely physical rules of packing (Raup 1968); limpet-like, bivalve-like and brachiopod-like morphologies can be simulated by wax accretion at the interface of air and water, with temperature appearing to be an important variable (Seilacher 1994); and spatial

aggregating patterns of slime mold amoebas mimic with remarkable fidelity self-organizing spatial patterns of chemical waves produced by the Belousov-Zhabotinsky reaction (Goodwin 1994). Many other examples are given in the work on D'Arcy Thompson (1942). To the extent that such physical principles are involved in development, they become part and parcel of the developmental matrix that is potentially involved in structuring evolution in morphospace. Theoretical morphospaces, however produced, are always bound to reflect principles of development, because they are invariably generative in producing expectations of natural behaviour based on intrinsic principles of organization. Precise biological meaning is a goal, but this does not detract from the heuristic power that different degrees of approximation to the logic of development can afford.

(3) What is the ultimate purpose of a theoretical model? Realism or simplicity? Realism is the ultimate judge of the worthiness of any model, but simplicity is the *sine qua non*. Mathematical models are not explanations (Murray 1989), and thus the requirement of realism has to be a relative one. Overly complex models have the potential to be intractable, insoluble and unintelligible (Levins 1966), thus deceiving the very purpose of modelling. Biologically meaningful insights can arise under varying approximations of reality. In terms of development, computer models that succeed in simulating morphology imply that the "actual biological system (...) need not be more complicated than that used in the computer simulation" (Raup 1968). Thus, even very simple models can be useful, by suggesting potentially simple underlying morphogenetic controls. While the goal of theoretical modelling is to achieve a realistic representation of an underlying generative logic, aspects of this logic may well be quite simple. This should encourage a more complete appreciation for the complementarity of models with different degrees of elaboration (Rice 1998).

A final comment pertains to the problem of commensurability of empirical and theoretical morphospaces. Form is ultimately n-dimensional, and many empirical studies

have quantified morphospace so as to take into account a broad range of features (see Foote 1997), regardless of whether a generative logic can be found for them through theoretical modelling. Indeed, for many discrete characters, theoretical morphospace construction is a rather intractable problem, although attempts in such direction have been made (e.g., Thomas and Reif 1993). A possibility not yet explored, but which bridges the gulf of incommensurability, is the partitioning of n-dimensional empirical spaces into m- and p-dimensional components, with p representing parameters derived from a given theoretical model of form generation, and m corresponding to all additional variables. With appropriate scaling, both p- and m-dimensional spaces can be compared in terms of relative spread and spacing of forms, behaviour of extremes, differential filling, etc. The extent to which patterns suggested solely by generative theoretical parameters (p) are concordant with those derived from additional descriptive parameters (m) can thus be assessed, in effect achieving an evaluation of how predictive of patterns of morphological disparity (e.g., Foote 1996b, 1997; Roy 1994; Wagner 1995; Eble 1998b) biological versatility (sensu Vermeij 1973) can be.

IV - Abnormal vs. normal morphospace comparisons

Alberch's work (e.g., 1980, 1983, 1989) resurrected the elegance and the goal of the work of 19th century teratologists like Isidore Geoffroy Saint-Hilaire. By studying the "logic of monsters" (Alberch 1989), the goal was to learn about the logic of morphological transformations in normal systems. Abnormalities become natural experiments in developmental transformation, and stand as manifestations of the underlying structure of developmental space. The importance of teratology to evolution is tied to the working hypothesis that the nature of normal forms in an evolutionary sense (and in a non-developmental space) is not different from the nature of abnormalities in a developmental sense (in a developmental space). In other words, discontinuous variation would be behind both phenomena, the respective phenotypic gaps would be isomorphic, and the

kinds of developmental (epigenetic) transitions that occur in the generation of abnormalities could actually take place in evolution and contribute raw material to evolutionary change.

If abnormalities can ever be defined in a more or less objective way (see below), and if sizeable samples are available (not a trivial problem), interesting lines of investigation arise. Fundamentally, they hinge on comparisons of normal and abnormal forms. Such comparisons may involve:

(1) Abnormal intraspecific versus normal interspecific variation. If certain classes of clear abnormalities appear again and again within species despite the assumption of negative selection, hints on the constraints imposed by development and the rationality of developmental transformations can be gained (Alberch 1989). If they happen to mimic interspecific variation, a strong claim can be made to the effect that evolutionary transformation itself may ultimately hinge on radical developmental change. Most comparisons of intra- and interspecific variation to date have been qualitative (see Oster et al. 1988; Alberch 1989). A more rigorous approach would involve phenetic (or even phylogenetic) analyses of normal and abnormal forms.

(2) Clade-wide interspecific comparisons of morphospace occupation between normal and abnormal forms. If morphological evolution proceeds by selection acting on small variations, pushing morphologies toward adaptive optima, then we should expect that the pattern of morphospace occupation for normal forms would be considerably different from that of abnormal forms. On the other hand, if development can play a role in evolution by providing not only constraints on variation but also raw material and creativity in terms of discontinuous variants, then one should expect a coincidence in the pattern of total morphospace occupation of normal and abnormal forms. The coincidence is not expected by default, and would be highly improbable by chance alone, given sufficiently large sample sizes. If coincidence of occupation holds, the claim that macroevolution is at least partially controlled by intrinsic developmental potentials is supported, and vice-versa. An illustration of this is given by the work of Dafni (1986, 1988; see also Seilacher 1991).

The approaches outlined above rely on the assumption that abnormalities can be identified unequivocally. But how to define an abnormality? Clear teratologies are obvious abnormalities, and an extensive descriptive literature exists for a number of model systems. The definition of a teratology is always somewhat subjective, however, and is often restricted to discrete variation, which allows all-or-none categorizations. It is more productive, thus, to focus on the notion of abnormality per se. An abnormality is, almost by definition, anything that extends beyond normality. At a minimum, this implies variants subject to strong negative selection, but not necessarily lethal; at the limit, abnormalities may be so sweeping as to allow the epithet "teratological".

If the abnormal is to be identified objectively, rigorous comparison with the normal is necessary. This is a statistically tractable problem. For any measurable character, means and standard deviations can be characterized for ensembles of specimens. Standard models of stabilizing selection naturally lead to the expectation that the higher the deviation from the mean, the lower the selective value. Since standard quantitative genetic models can be viewed at face value as a representation of the present null hypothesis (i.e., evolutionary change as a result of selection acting on small variants), one can look at population and quantitative genetics for estimates of pronounced lack of fitness. Given uni- and multivariate normality, cutoffs usually involve 2 or 3 standard deviations. This approach is indefensible because it stems from the null hypothesis and it is used in the testing of the alternative hypothesis. It also has the advantage of allowing consideration of both meristic and metric variation in a rigorous framework.

A quantitative framework encompassing approaches (1) and (2) is summarized for an arbitrary character in Fig. 2. It relies on a modification of the subclade test for the identification of trends (McShea 1994). If the subpool of abnormalities displays a distribution that matches that of the normal pool, despite the absence of selection on the generation of abnormalities, a case for developmental constraint on the generation of normal forms can be made (Fig. 2a). However, if the abnormal subpool and the normal

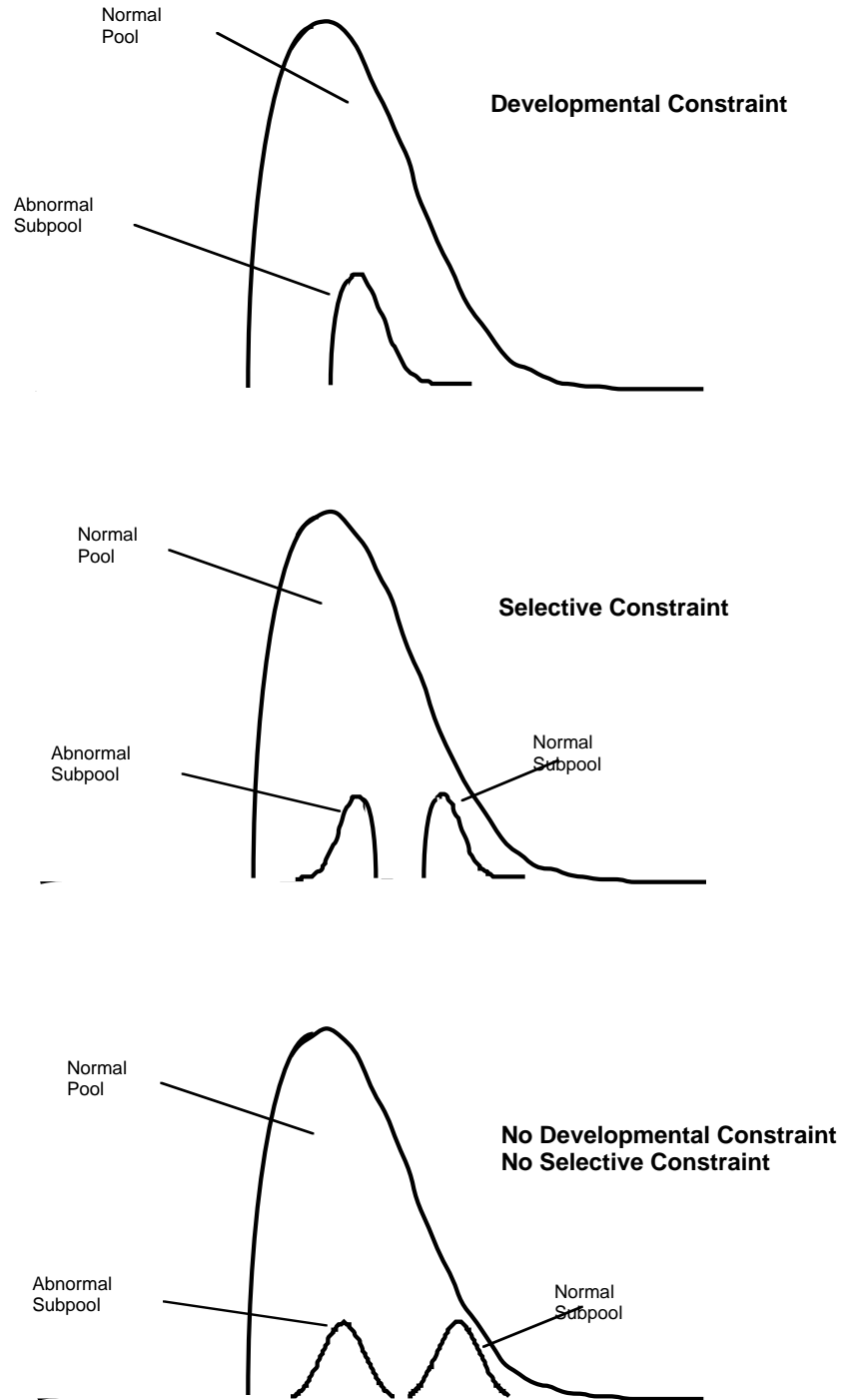


Fig.2. Distinguishing developmental from selective constraint with comparisons of normal and abnormal forms. In (a), congruence of abnormal subpool and normal pool distributions is evidence in support of developmental constraint. In (b) lack of congruence supports selective constraint instead. In (c), normal and abnormal subpools bear no concordance with the normal pool, suggesting the absence of constraint.

pool differ (comparisons with normal subpools can also be incorporated), a case for selective constraint on the distribution of normal forms is tenable instead (Fig.2b). Finally, if abnormal and normal subpools match but at the same time differ from the normal pool, unconstrained evolution is taking place (Fig.2c). This framework for the quantitative comparative study of normal and abnormal forms has never been implemented. Given an operational definition of abnormality as outlined above, studies of this kind should be tractable.

V - Juvenile vs. adult morphospace comparisons

An extensive allometric and heterochrony literature exists with detailed descriptions of and comparisons between ontogenetic trajectories of related species (e.g., McKinney 1988; McKinney and McNamara 1990). This taxon by taxon approach has yielded a wealth of information and delineated current theories about the relationship between development and evolution (e.g., Alberch et al. 1979; McKinney and McNamara 1990). From the perspective of morphospace studies, however, an ensemble approach focused on clade-wide comparisons can allow a more synthetic account of general issues like clade shape in ontogenetic time, trends in changes of rate and timing, testing of developmental "laws", and parallels between phylogenetic and ontogenetic trends. Few studies have explored the approach to date (e.g., David 1989, 1990; David and Laurin 1996; Eble 1996, 1997).

Perhaps more so than in the case of theoretical morphospaces and abnormality morphospaces, the inferences from which must rely on consistency arguments, juvenile morphospaces are closer to the actual dynamics of evolutionary change in development. The intergradation of developmental and non-developmental morphospaces is more clear here as well, since at least in commensurate spaces (e.g., after metamorphosis) the total set of features under investigation can be easily modelled with allometric functions (in the case of abnormalities, outliers make such an exercise potentially more difficult). In this vein, juvenile morphospaces can be said to be an intermediate level within the genotype-

phenotype map (Wagner and Altenberg 1996). Purely phenotypic juvenile-adult comparisons can be very useful in understanding the large-scale structure of such mapping: because development is hierarchical and genes behave more as parameter values in epigenetic feedback loops than as a central directing agency (Webster and Goodwin 1981), phenotypic variation is as useful a target of study in understanding the relationship between development and evolution (and of genotype and phenotype) as genetic variation. Even in the absence of innovation (see Rice 1998), the range of juvenile allometries can at least potentially suggest many pathways of change in adult form (e.g., David 1989, 1990; David and Laurin 1991, 1996; Zelditch et al. 1992). An empirical study of juvenile vs. adult morphospace and disparity comparisons is presented next, using echinoids of the order Spatangoida as a model system.

Spatangoids. Spatangoids constitute a monophyletic group of heart urchins that appears in the early Cretaceous (145 m.y. ago) and ranges to the Recent, experiencing substantial losses at both the end-Cretaceous and late Eocene extinction events. As heart urchins, they display bilateral asymmetry superimposed over radial symmetry, an anteriorly displaced mouth and a posteriorly displaced anus. In addition, ambulacral areas often have enlarged pores, producing a petaloid appearance; a frontal furrow of variable depth is often present; very enlarged plates form a plastron in the oral side; and diverse profiles of the test with different implications for burrowing (Kanazawa 1992) have evolved. Spatangoids are the most diverse group of sea urchins -- 12 families, circa 200 genera and hundreds of species together display a number of themes of echinoid evolution (see Kier 1974).

Developmentally, however, little is known about this group. Interestingly, in at least some species it is known that the very youngest stages after metamorphosis display virtually no bilateral symmetry, resembling instead the more primitive regular echinoids in general outline (Gordon 1926; David and Laurin 1991). This suggests that Von Baerian recapitulation (Nelson 1978; Loevtrup 1989) might be expected for other features as well.

Data. Although spatangoids have a rich fossil record, and variation in size of the order of 4 can be commonly sampled, it is difficult to ascribe precise ages to different specimens beyond the categorization of sexual maturity in terms of the opening or not of the genital pores in the apical system. Growth is for the most part indeterminate, and although the accretionary nature of plate growth register growth bands, these are very difficult to reveal even in Recent specimens. In addition, it has been suggested that allometric nonlinearities (implying raw material for extensive developmental variation) in heart urchins are particularly prominent in very small specimens (David 1989, 1990; David and Laurin 1991, 1996). Thus, although juvenile-adult comparisons of fossil forms are amenable to study, I chose to focus on sampling of Recent species in long-ranging genera, and on representation of all the main families of spatangoids, so as to guarantee representation of the broad features of phenetic and phylogenetic differentiation in the group. A survey of dedicated collections at museums in Paris, London, Copenhagen, Washington, San Francisco and Berkeley, as well as of illustrations in the literature dating back to the work of Agassiz (1881) and Mortensen (1907), allowed sampling of the smallest post-metamorphic specimens reliably identified in the past. The data used in this study comprise 14 juvenile-adult sequences in 14 species, 14 genera and 8 families of spatangoids.

Methods. The primary data for the present morphospace and disparity analyses consists of (mostly) three-dimensional cartesian coordinates for 18 landmarks that comprehensively capture test architecture (see Eble 1998b, submitted). The morphometric scheme is illustrated in Fig 3. This scheme, with 18 repeatable and relevant landmarks (sensu Roth 1993), nonredundantly codifies several standard morphometric parameters (height, length, width, etc.) and accounts for important test features such as general profile, relative positions and relative size of aboral ambulacral regions and their modifications (petals), extent of frontal furrow, geometry and relative size of plastron plates, and relative positions of the apical system, peristome and periproct. Because plastron landmarks vary

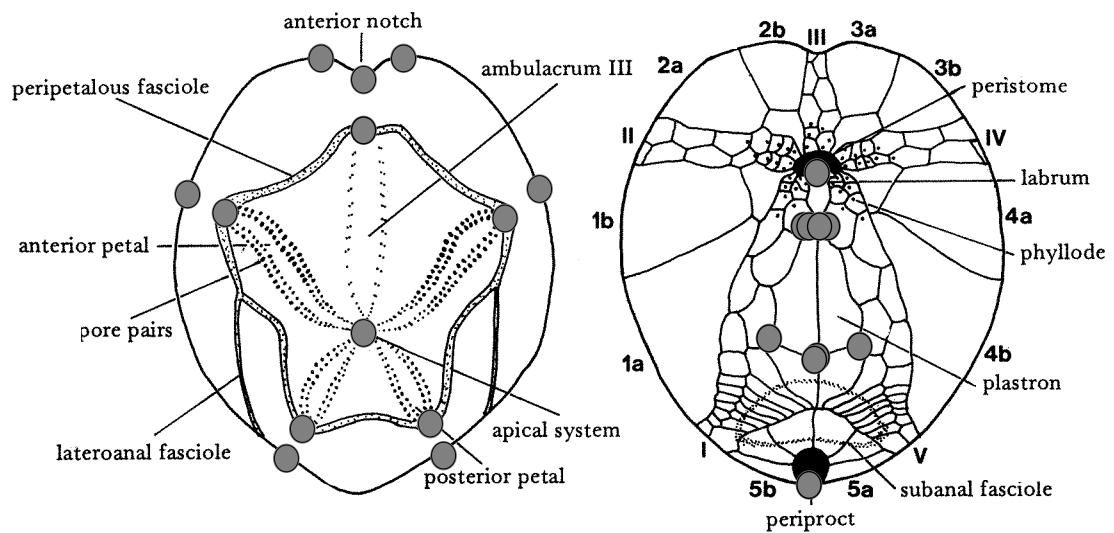


Fig.3. Morphometric scheme used in the study. Points represent landmarks from which x,y,z coordinates were collected for all of the specimens considered in this study.

little in the z-direction, and because such variation might be confounded by measurement and orientation error, they were constrained to lie in a single plane. Also, redundant landmark information was averaged and non-informative (invariant) or unreliable (due to difficulties in measurement for very small specimens) coordinates were removed. From 18 landmarks, the final number of variables was then 36. Landmark data collection consisted of image acquisition, digitalization, and analysis using a video camera and BioScan OPTIMAS[®] image analysis software.

Landmark coordinates for all specimens were scaled to a common size using a reference baseline (the y-coordinate for the tip of the periproct, with the origin of the coordinate system centered between the frontal genital pores of the apical disc), and row normalization was performed for each specimen, rendering the sum of squares of variates for each object equal to one. Row normalization retains the proportionality of variables within objects, and destroys differences in magnitude between objects (Reyment and Jöreskog 1993). Further, standardization was carried out to guarantee equal weighting of

the variables; although they are all on the same scale, the range of plastron coordinates tended to be an order of magnitude smaller than that of other coordinates, thus making standardization necessary. The final data matrix used in the analyses consisted of standardized variates.

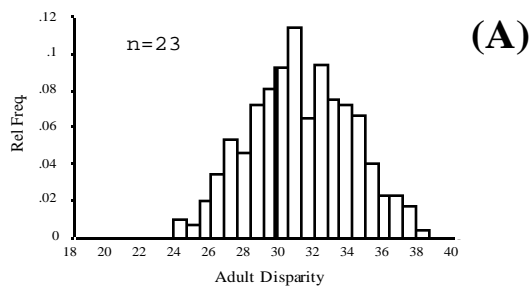
To produce an ordination space, the resulting correlation matrix was used as input in a principal components analysis. The first six ordered PC's were retained for further analysis, encompassing 83% of the total variance. Based on natural breaks in the decay of eigenvalues, the first 4 PC's were chosen for graphic portrayal of dispersion and location of forms in morphospace. Morphological disparity per se at each stratigraphic interval was measured as the total variance in the original, size-normalized and standardized morphospace. The total variance is the sum of the univariate variances and is equivalent to the mean squared Euclidean distance between each point and the centroid; it is also equal to the sum of the eigenvalues (Van Valen 1974, 1978). Unless otherwise noted, throughout the text the term "disparity" will be used in the sense of variance.

Results and discussion. Fig. 4 presents a comparison of total disparity between pooled adults and pooled juveniles. Three different criteria of partitioning of juveniles from adults were used to assess the sensitivity of the results. In Fig. 4a, a strict maturational partitioning was used, i.e., specimens were considered juveniles if they were not sexually mature (genital pores were not open). In Fig. 4b, a looser criterion was used, based on size differences: juveniles in a given species were defined as such if they were smaller than the largest specimens by at least an order of 2. Finally, in Fig. 4c, an extreme size-based

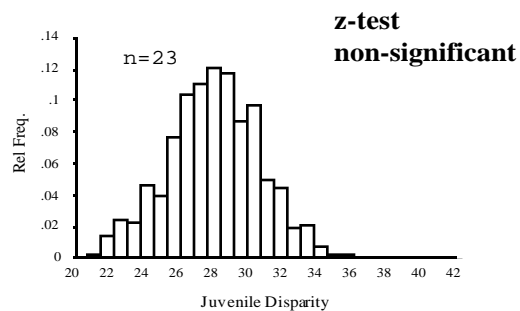
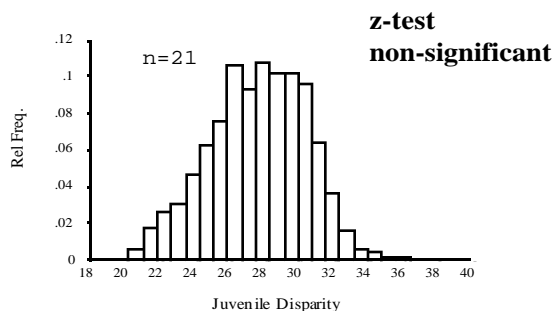
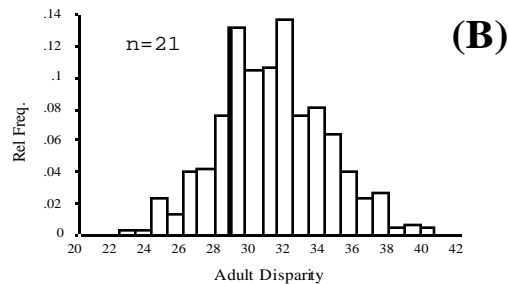
Fig.4 (next page). Comparison of bootstrapped total disparity between pooled adults and pooled juveniles across 14 genera of spatangoids, under three different criteria for partitioning juveniles. (a) Maturational partitioning, based on sexual maturity. (b) Allometric partitioning, based on size differences of the order of at least 2. (c) Extremal partitioning, with consideration of the smallest juvenile and the largest adult sampled only. In all three cases, no statistically significant difference in levels of disparity is detectable.

Juvenile-Adult Disparity Compared (500 bootstrap replicates)

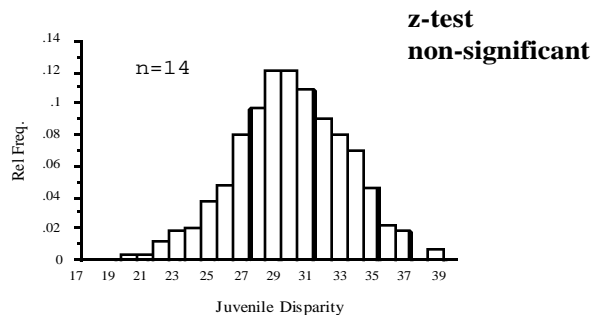
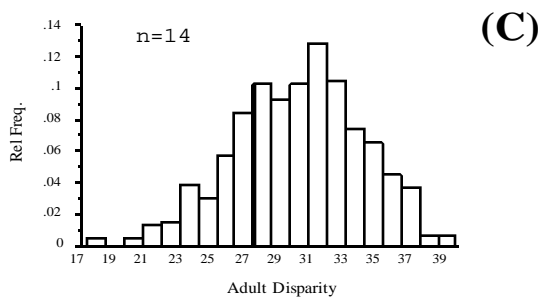
Maturation Partitioning
(juveniles defined by reproductive maturity)



Allometric partitioning
(juveniles defined by size relative to a corresponding adult)



Extremal Partitioning
(smallest juvenile and largest adult sampled for each species)



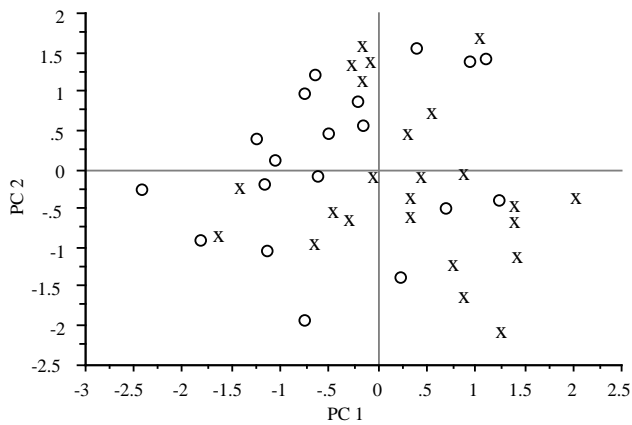
criterion was used, with only the smallest juvenile and the largest adult in each ontogenetic series being considered.

As is clear from Fig. 4, in all cases the distribution of bootstrapped disparities for adults is indistinguishable from that of juveniles. This is remarkable, given the common assumption that, especially after the phylotypic stage (in this case, the urchin rudiment upon metamorphosis), Von Baerian deviation should be the rule. Interspecific adult variation would seem to occur within a developmentally constrained morphospace which is not statistically exceeded.

This of course is a general description of the large-scale structure of morphospace, in terms of the mean distance among forms. One might expect different variables to show different ontogenetic topologies of variation. Fig.5 presents principal component plots for several composite variables (maturational partitioning was used here). The juvenile (developmental) morphospace is superimposed over the adult (non-developmental) morphospace (since the spaces are commensurate, one is in effect considering a single "developmental morphospace"). There is a lot of overlap, suggesting much fluidity in variation, but the variance behaves differently in different dimensions. The variance of adults and juveniles along each composite dimension is indicated alongside each plot. PC I and PC II (accounting for roughly 50% of the total variance) display no difference (a bootstrap test was used) between the disparity of juveniles and that of adults, which supports the general inference of pervasive developmental constraint. PC III, however, has juveniles displaying significantly less disparity than adults, in conformity with Von Baer's second law. In contrast, PC IV has adults showing significantly less disparity than juveniles, thus contra Von Baer's second law.

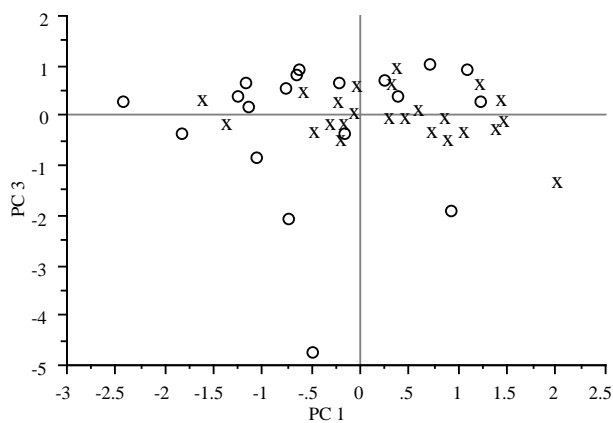
Fig.5 (next page). Juvenile and adult morphospaces superimposed into a single "developmental morphospace". PC I is plotted against PC II, PC III and PC IV, respectively. No difference in variance between juveniles and adults is apparent for PC I and PC II (a bootstrap test was used); the variance of juveniles is significantly smaller than the variance of adults along PC III, in agreement with Von Baer's second law; and the variance of juveniles is actually significantly larger than the variance of adults along PC IV, contra Von Baer's second law.

Juvenile-Adult Contrast in a "Developmental Morphospace"



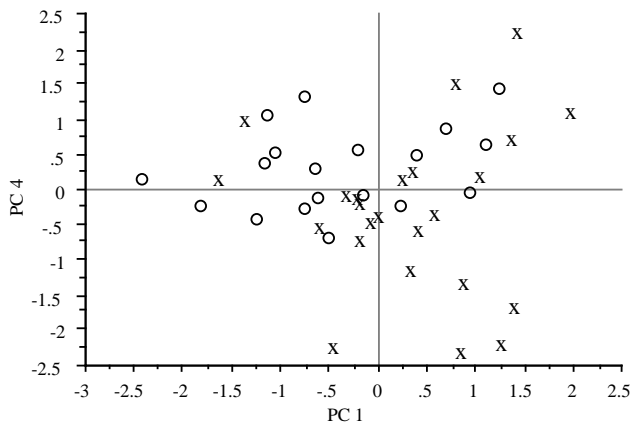
Variance

	PCI	PCII
ADULTS	134	42
JUVENILES	108	39



Variance

	PCI	PCIII
ADULTS	134	28
JUVENILES	108	3*



Variance

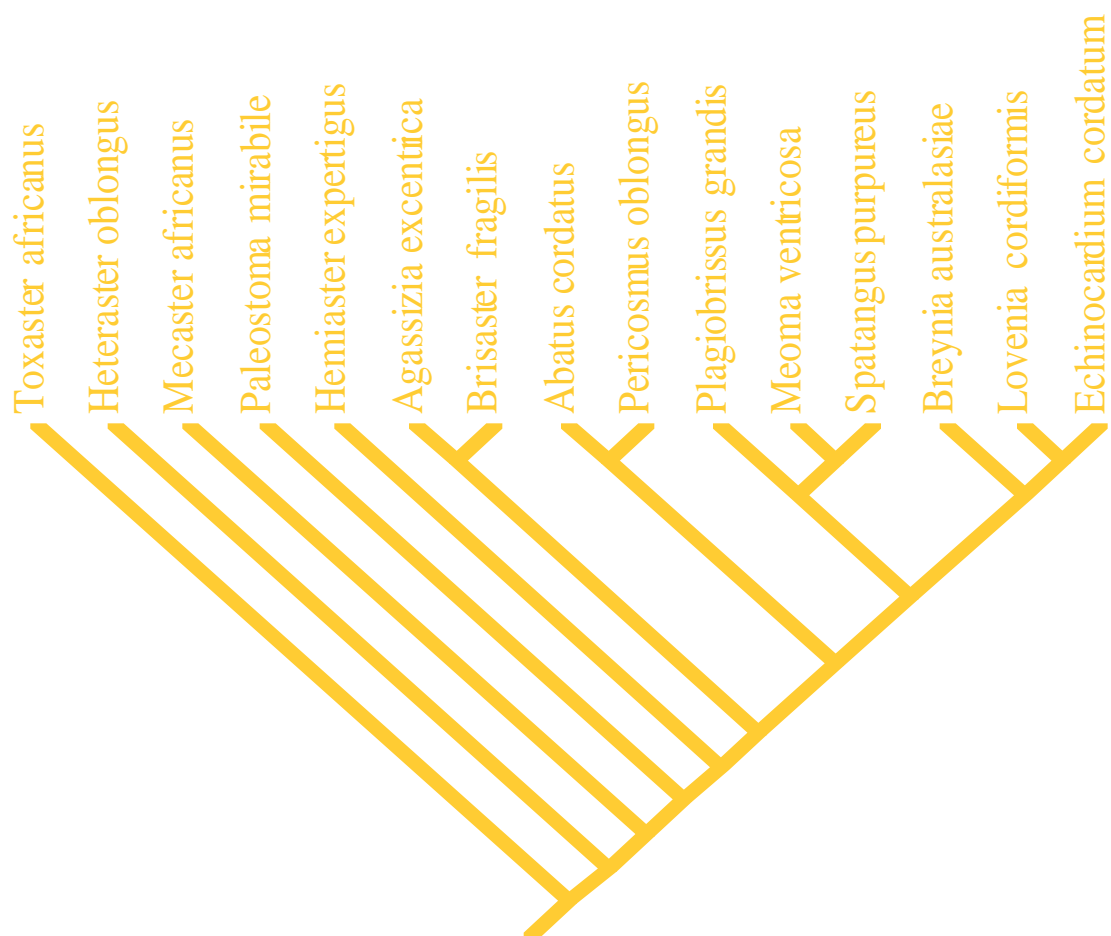
	PCI	PCIV
ADULTS	134	6*
JUVENILES	108	18

Therefore, of the four main composite variables in the system, only one supports a major prediction of developmental evolutionary biology. It is possible to further examine this result by focusing on nearest neighbor distance analyses (cluster analyses) in light of a phylogeny. A phylogeny for all the taxa involved (the first spatangoid species, appearing 145 million years ago, was used as an outgroup) is presented in Fig.6 (Eble, submitted). The tree depicted is the single most parsimonious tree, produced by a posteriori weighting by the consistency index. Except for the node that follows Hemiaster and the Abatus-Pericosmus node (51% bootstrap support), all other nodes had a bootstrap support of 100%.

The spatangoid phylogeny of Fig. 6 was used to assess the relative primitiveness or derivedness of species in the nearest neighbor distance analyses. Samples of the overall cluster analysis are presented in Fig. 7. It is clear that the overlap in juvenile and adult distributions in morphospace results from taxonomically heterogeneous adult-juvenile clusters. Much dissociation of ontogenetic sequences in morphospace is apparent, and this by itself suggests that changes in rate and timing of development are taking place. In Fig. 7a there is association of a derived juvenile with more primitive adults, thus suggesting overall peramorphosis leading to derived adults. Fig. 7b shows an association of primitive juvenile with a derived adult, suggesting overall paedomorphosis leading to derived adults. In Fig. 7c, overall peramorphosis is again suggested, with derived juveniles clustering with a more primitive adult. Finally, in Fig. 7d, one finds evidence in support of Von Baer's second law, with association of juveniles from different taxa (this is also apparent from Fig. 7c). Although here we find some evidence for Von Baer's second law, it is by no means pervasive.

Von Baer's second law would also predict that over phylogenetic/stratigraphic time, adults from different species would be more and more divergent in comparison with juveniles. This prediction is tested in Figs. 8 and 9. In Fig. 8, the disparity implied by adults and by juveniles in each subclade is shown. In Fig. 9, the respective clade ranks are

SPATANGOID PHYLOGENY



15 Taxa

20 Characters

Tree Length: 69

CI=0.52

Fig.6. A phylogeny of spatangoids. All taxa included in the juvenile-adult study were incorporated. The tree is the single most parsimonious topology generated by successive reweighting by the consistency index, with the first spatangoid in the fossil record used as the outgroup. High bootstrap support is found for the majority of nodes. Data matrix available from the author.

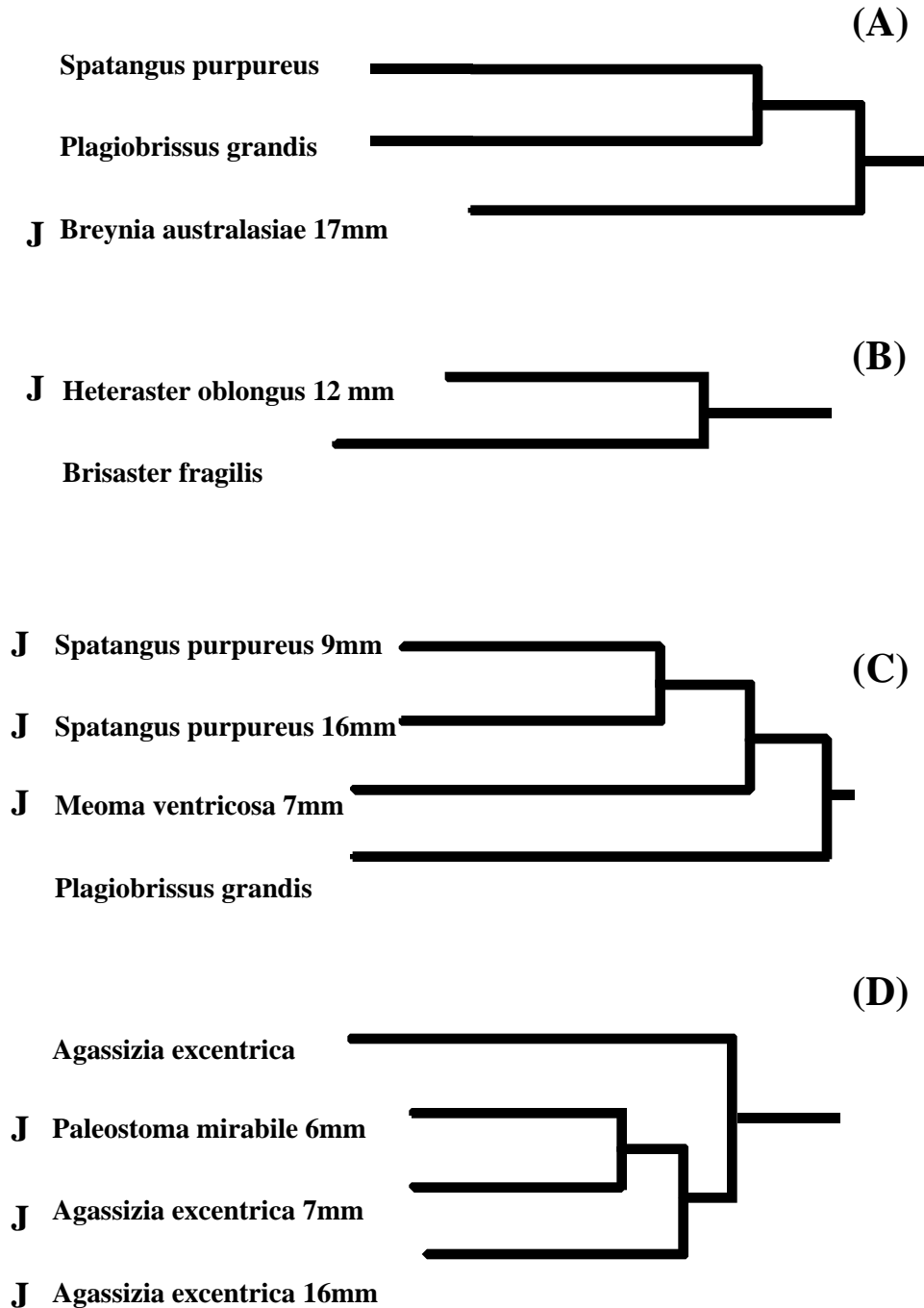
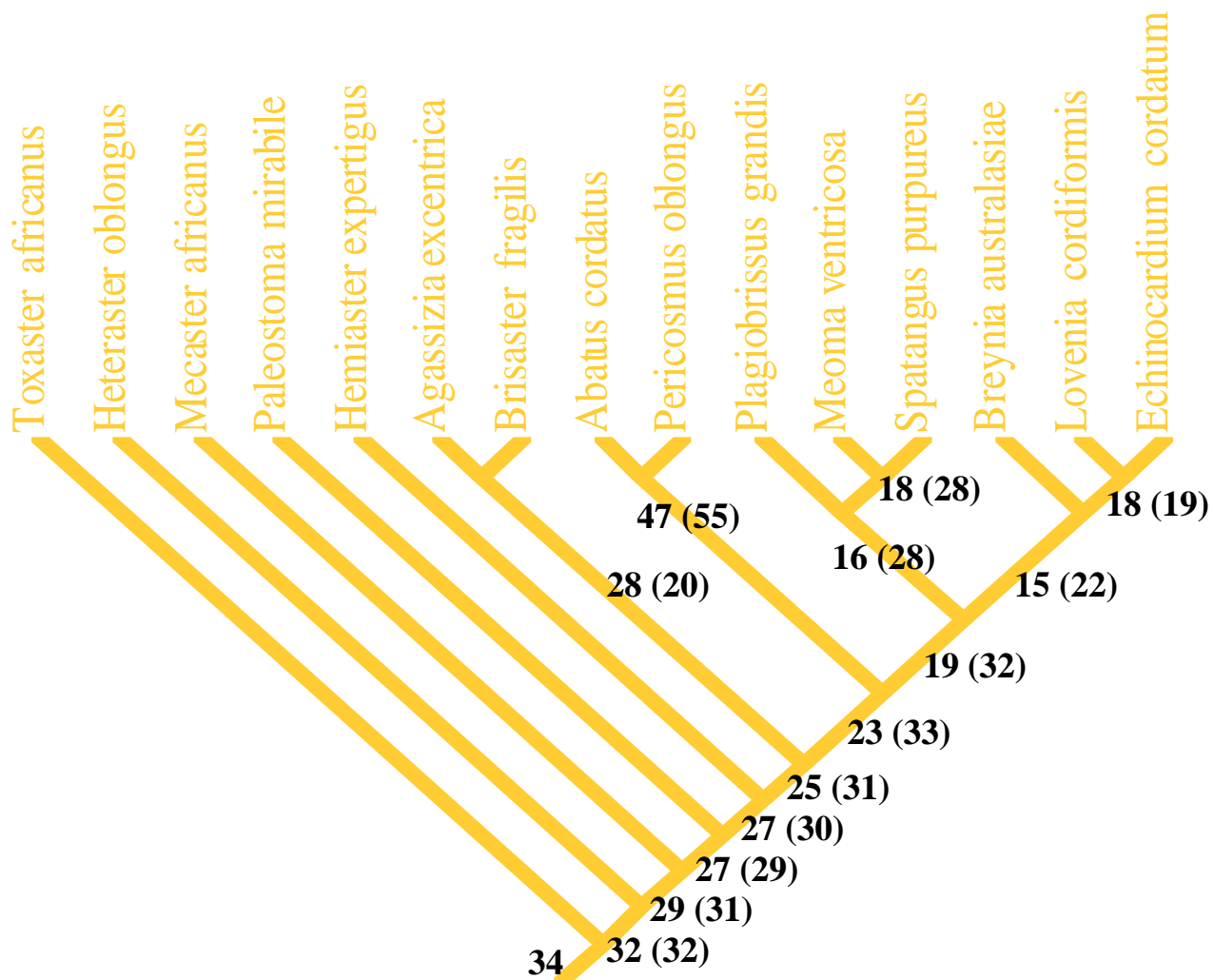


Fig.7. Samples of overall cluster analysis (using nearest neighbor distances) of all spatangoid juveniles and adults considered in this study, so as to illustrate the multiplicity of phenomena encountered. Note the taxonomic heterogeneity of juvenile-adult clusters. In (a), a derived juvenile clusters with more primitive adults, suggesting overall peramorphosis. In (b), a primitive juvenile clusters with a derived adult, suggesting overall paedomorphosis. The same is suggested in (c). In (c) and (d), clustering of juveniles from different taxa supports Von Baer's second law.

Disparity of adults and juveniles at different levels of phylogenetic inclusiveness



() - JUVENILE DISPARITY

Fig.8. Mapping of the disparity implied by adults and juveniles in various subclades against the phylogeny illustrated in Fig. 6. Values in parentheses correspond to the disparity of juveniles. See text for discussion.

Clade Rank vs Disparity for Juveniles and Adults

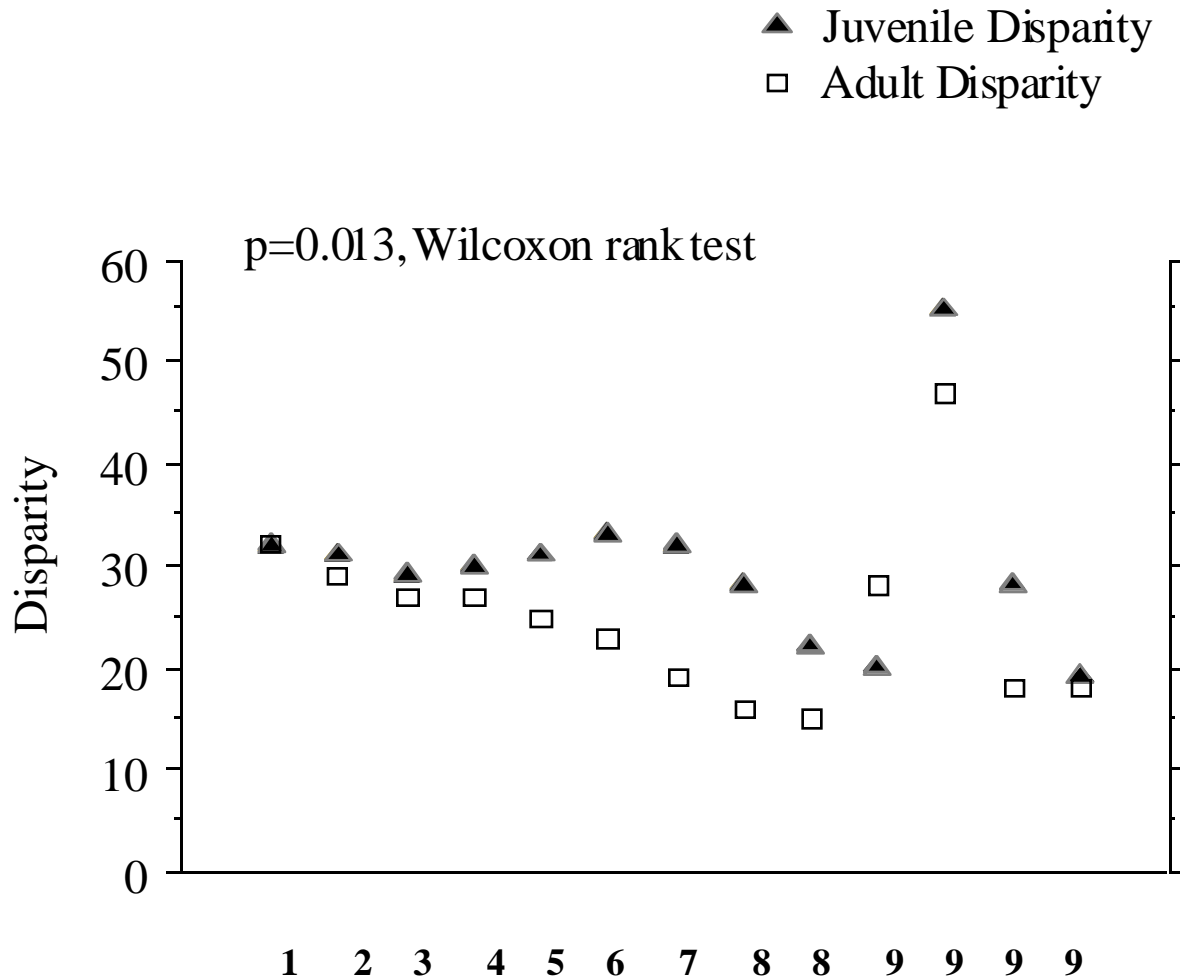


Fig.9. Plot of clade ranks versus the disparity of juveniles and adults for each subclade. A Wilcoxon rank test indicates significantly higher disparity of juveniles within subclades. This disagrees with Von Baer's second law.

plotted against the levels of disparity of adults and juveniles. A Wilcoxon rank test indicates that within subclades, juveniles tend to be more variable than adults, which runs against the prediction of Von Baer's second law.

As we see, although total juvenile disparity falls within the range of bootstrapped adult disparities (in effect suggesting that overall variation is similarly constrained throughout ontogeny), a multiplicity of patterns is encountered when different composite

variables are analysed in isolation. In a few cases the patterns are in agreement with Von Baer's second law, but at least in spatangoids the evidence is overwhelmingly against it. This is in conflict with what is generally predicted from vertebrate model systems. The multiplicity of results pinpoints the complexity of the relationship between development and evolution. There is a lot of potential for developmental evolution to happen, which is realized, and no single vector of change in disparity through ontogeny. Still, all such developmental action potentially driving evolution occurs within a constrained morphospace which is fully (and somewhat haphazardly) occupied but never truly statistically exceeded. While the generality of the present results should be explored in other groups (especially invertebrates), the approaches outlined do underscore the general utility of the comparative analysis of clade-wide juvenile and adult morphospaces.

VI - Conclusions

Morphospace and disparity studies have over the years suggested a number of large-scale inhomogeneities in morphological evolution, from discontinuities inherent in the construction of organisms to general asymmetries in disparity profiles through time. When interpretations of process are attempted, it is important to balance the usual focus on functional and ecological explanations with consideration of the potential structuring role of development itself. Intrinsic ontogenetic biases stand as one major framework of explanation in evolution, and to the extent that morphospaces can be partitioned into developmental and non-developmental components, the notions of developmental disparity and developmental morphospaces become powerful tools in the determination of the relative importance of development in evolution. The morphospace contrasts outlined in this paper (theoretical vs. empirical, abnormal vs. normal and juvenile vs. adult) are not meant to be exhaustive, and as implied the establishment of the developmental/non-developmental dichotomy is more heuristic than real, since development usually manifests itself along a continuum. It is hoped that further work can elaborate and refine the

approaches here introduced. The construction of explicitly developmental morphospaces should become an important complement to other morphospace approaches to the study of macroevolution.

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