SOME ASPECTS OF SPECIES-LEVEL EVOLUTION IN PALEONTOLOGY

Though the history of invertebrate paleontology is one which emphasizes the stratigraphic utility of fossils, evolutionary biology is becomming ever more popular as a theoretical framework behind the study of fossil invertebrates.

Paleontologists of course cannot study the mechanisms of evoluton; all they can do is analyze the complicated, shifting patterns of phylogeny through time, which have implications on the general nature of evolutionary change. Most paleontologists would perhaps agree that the most important, uniquely paleontological aspect of evolution that they can study is the origin and development of the so-called higher categories, i.e. taxonomic categories usually no smaller than the family on up.

Increasingly common, however, are studies on a smaller scale, emphasizing the specific and subspecific categories. Such studies per se are of course not new to paleontology. In 1899 Rowe published a very modern-sounding study of species-level phylogeny of the sea-urchin Micraster through successive horizons of the English Chalk. Both gradual species-change through time -- termed "phyletic evolution" -- and divergence, which is speciation in the neontological sense, were observed by Rowe. Other species-level work has been done through the years -- Carruther's study in 1910 of the evolving lineage of the Lower Carboniferous rugose coral Zaphrentites delanouei, Trueman and others working on the oyster Gryphaea, and Newell on Upper Paleozoic clams are three outstanding examples that have become classics in the literature of paleontology.

What these and other similar studies have in common is a stress on a phyletic-model of species differentiation; paleontologists tend to view the origin of new species as gradual, progressive change through time. This is fine, as far as it goes, since a species

existing at any one point in time has three possible fates:

    1. Extinction

    2. Persistence as is

    3. Change into something a systematist recognizes as sufficiently distinct to warrant calling a new species. Of these, extinction is the commonest fate, and persistence without change the rarest, approaching zero if a large enough time span is considered.

But the enormous amount of literature amassed by neontologists in the last thirty years or so has focussed on a different model; if the paleontologist has emphasized the time component of a species' history, the neontologist has perforce emphasized the spatial distribution of species at a single time transect-- the present.

To summarize all this literature in a few words, neontologists feel that for a new species to originate and take its place beside its ancestor, a population of the parent species must spend some time in geographic isolation, enough time to allow some barrier called an isolating mechanism to develop which would prevent interbreeding with, hence resorption into, the parent species, should the geographic isolation break down. Apart from some recent suggestions that geographic isolation may not be as crucial in all cases as previously thought, this principle seems firmly established in evolutionary theory.

It is already clear from my brief characterization of the past work in evolutionary paleontology that this so-called allopatric model has not been extensively tested and applied to fossil organisms. But the development of an evolutionary theory stressing the role of populations of varying organisms coupled with the advent of electronic computers and a sophistication of statistical models have paved the way for paleontologists -- particularly those who study marine invertebrates -- to analyze the shifting patterns of

variation in populations of organisms in a spatial as well as temporal

sense. In other words, the techniques and interests of paleontologists

are now suited to a detailed examination of the fossil record to

test the general applicability of the allopatric model of speciation

and conceivably to expand this model by documenting what actually

does happen to different races, say, of a species through time.

PENNSYLVANIAN GASTROPODS

I will use some of my own work on middle and upper Pennsyl-

vanian gastropods from the mid-continent region as examples of

the types of phenomena that can be investigated at the population

level in paleontolgy.

The gastropods I will consider (Slide 1) are all members of

the super-family Pleurotomariacea, a primitive group of snails of

the order Archeogastropoda. These snails, represented today by

the highly-modified abalone Haliotis, some kinds of limpet-like creatures,

and some large, virtually unchanged species of the genus Mikadotrochus,

of the ocean deeps, have retained the bilateral symmetry of their

organ systems. In more advanced snails, the right-handed or-

gans, such as gills, kidneys, etc., degenerate, and the digestive

tract has been coiled back over the head, the anus emerging on

the right side of the head. Though this gut-coiling, or torsion,

is also present in pleurotomarians, the anus has a more central

position over the head. To avoid sanitation problems, pleurotomarians

early developed either a sinus, or a deepr, narrower slit some-

where along the periphery of the shell, back away from the head.

As the animal grows, this slit is usually filled in by a deposit

known as the selenizone. This selenizone is the outstanding hallmark

of pleurotomarians and is found only in two other small groups --

the bellerophontids and murchisoniids -- both of which are readily

distinguished from pleurotomarians on other criteria of shell shape.

Much of the allocation of fossil pleurotomarians into families has centered around the nature of the selenizone -- particularly its ornamental features and position on the shell. With few exceptions, each currently recognized family is characterized by a particuar type of selenizone which varies only within narrow limits. Put another way, the selenizone seems to be evolutionarily conservative, and most of the changes seen in a family during its geologic history involve shape and ornamentation of other parts of the shell.

The particular pleurotomarians we are interested in here belong to two different families. Worthenia tabulata is a middle and upper Pennsylvanian species exceedingly common in marine rocks across the United States. Its family, the Lophospiridae, first appears in the Ordovician; as a rule, the shell in this family is high-spired and the sinus or slit quite shallow.

The other three species shown here all belong to the genus Glabrocingulum; there are two subgenera represented here: Glabrocingulum sensu stricto, a low-spired, globose snail, and Ananias, a subgenus established for higher-spired species often found co-existing, but generally not intergrading with, the shorter species. Their family, the Eotomariidae, can be considered virtually the central stock of standard Paleozoic pleurotomarians; it, too, appeared in the Ordovician. The selenizone is always a slightly concave, simple band ornamented solely by so-called lunulae, representing growth lines of the selenizone, and always found on the outer edge of the whorl.

There are at least three advantages in studying these snails:

1. They are extremely abundant, with the exception of Ananias wannense.

2. They possess an anatomical feature -- the anal-slit-selenizone complex -- whose function is known and which effectively subdivides each whorl into three parts which are easily measured (Slide 2).

3. As in all snails, and molluscs in general, they carry their ontogeny around with them through life, making growth studies possible.

Returning to slide 1 again for a moment: My initial interest in these snails involved the seeming convergence between W. tabulata and G. (A.) welleri, which had not been detected until 1945, when J.B. Knight noticed that many museum collections of W. tabulata contained a more or less identical taxon with a radically different, typically eotomarian selenizone. As you can see on the slide, the three species of Glabrocingulum shown here are very similar in details of ornamentation and selenizone morphology, differing only in relative height of spire. Knight established the subgenus Ananias -- the biblical liar -- for G. wannense and G. welleri.

Rather than recount the details of the history of the convergence between G. (A.) welleri and W. tabulata, I would prefer to consider the phylogenetic relationship between the species of Glabrocingulum first, discussing the convergence only as it was affected by the evolutionary and geographic relations within the Glabrocingulum line.

At first sight, a simple, phyletic (straight line) phylogeny leading from G. (G.) greyvillense to G. (A.) wannense to G. (A.) welleri seems a safe inference. Each presumed ancestor in the sequence precedes its descendant stratigraphically (Slide 3). A simple trend, easily imaginable, for increase in whorl height, possibly by increasing the height of the lower whorl face, seems to have been in operation. Indeed, though I haven't studied G. (G.) greyvillense

there is excellent evidence that the two species of the subgenus
Ananias under consideration here were intimately related. But
though we may agree on the rough outlines of phylogeny, many com-
plicating factors are immediately evident. First of all, G. (G.)
greyvillense is extremely abundant and persistent throughout the
Pennsylvanian. It does not simply give rise to G. (A.) wannense
phyletically and then disappear. G. (A.) wannense is notable for its
rarity, though it too has been reported in isolated occurrences
across the United States. G. (A.) welleri, the highest spired species
which appears last, is far more abundant than G. (A.) wannense, but
is limited pretty much to the South-West, though it has been found
in one unit in Illinois. Moreover, G. (A.) wannense coexists with
G. (A.) welleri for a short time before finally disappearing.

So, there are are shifting patterns of geographic occurrence
through time, controlled to a degree by ecology --such as the
decreasing availibility of good marine limestones higher in the
Pennsylvanian in the east, by tectonics on a more direct level --
such as the several phases of orogeny in Oklahoma in the middle and
late Pennsylvanian, and also, most interestingly, controlled
by interactions between the populations themselves.

What I have to say about the relations between populations
within the Ananias lineage is a by-product of my interest in the con-
vergence. Consequently, I restricted my study to the area where
W. tabulata and A. welleri were presumably sympatric --i.e. living
at the same place and time -- in the southwestern United States.
Conclusions concerning the history of the Ananias lineage are
necessarily based on the data from the same area, and my geographic
distribution maps are therefore incomplete.

The notion of a phyletic change in the Glabrocingulum stock --
starting with a low-spired species like greyvillense and progressing

through _Ananias wannense_ and into _A. welleri_ was the initial working hypothesis I used when analyzing the convergence between _welleri_ and and _W. tabulata_. (Slide 1 if necessary). I felt it was likely that the spire height in the _Glabrocingulum_ line increased to the extent that it fell within the range of _Worthenia_, more-or-less preadapting _G. (A.) welleri_ for mimicking _W. tabulata_. It turned out, though, that _Worthenia_ probably converged on _Ananias welleri_. _Welleri_'s morphology at any given time and place depended on the occurrence of _G. (A.) wannense_, its presumed ancestor. The shifting distribution of populations of the two species in the south-west is shown in Slide 4. This slide is a series of 4 extremely crude maps prepared in some haste; I have paid no attention to the various orogenies in Oklahoma which affected the geography to a great degree, and I have divided the data into geologic series for the most part -- which nearly undermines my attempt to discuss relatively subtle changes in distribution. But the main story does emerge: In the lower and middle DesMoinesian we have only _G. (A.) wannense_ (the range should be extended south into Texas to cover a lone occurrence in the Dickerson formation). _G. (A.) welleri_ first appears in the upper Des Moinesian in the Wewoka formation of Oklahoma; it appears, so far as I am able to tell as yet, full-blown, and does not intergrade with _wannense_ which is also found in the Wewoka. Gradually, during the Missourian series, however, the pattern changes; _wannense_ disappears from Texas, and _welleri_ is most abundant in Texas. The cross on the map indicates 1 population of _wannense_ in Oklahoma where some specimens approach the _G. (A.) welleri_ shape. This just possibly may indicate a breakdown of reproductive barriers and hybridization. At any rate, neither is found in the tectonically active region of Oklahoma in the Virgilian, and all we have is _welleri_ in North Central Texas. So, one thing we can say is that _if_, as seems probable, these

two species are phylogenetically linked, it appears that 1 species, <u>welleri</u>, gradually replaced its ancestor, <u>wannense</u>.

I said earlier that the morphology of <u>welleri</u> was more closely dependent upon its geographic relations with <u>wannense</u>, its putative ancestor, than to <u>Worthenia tabulata</u>, its homeomorph. This is shown in the results generated by a statistic known as the distance function which calculates the relative distances between group centroids, or mean vectors. The investigator chooses which groups he wants studied on an <u>a priori</u> basis -- the natural ones in this study were the different species and different parts of the geologic column. (in futher work, groups further defined on a geographic basis would be desirable.)

It might be wise at this point to say something briefly about the strategy of the statistics commonly used in the analysis of population differences, before we pass on to the direct application. Traditionally, comparison between two or more groups is done by the analysis of variance, which contrary to its name, is basically a technique to determine whether or not two or more populations differ in their mean values of whatever measurement is made. This can be generalized into the multivariate case, where mean vectors or centroids of different populations are compared. The problem boils down to finding that plane or those planes which maximize the separation of the centroids in a statistically significant manner. These planes are generally called discriminant functions; once these are calculated, the multi-dimensional space is effectively reduced to a few dimensions -- the exact number coinciding with the number of significant discriminant functions. Within this reduced space, perhaps the most powerful type of statistic suited to paleontological needs can be calculated -- the aforementioned distance statistic.. The importance of summarizing relative morphological disparity and similarity between

populations in such a clear-cut manner cannot be overemphasized, as
it can be brought to bear on a whole range of evolutionary and
biostratigraphical problems in paleontology.

At any rate, the next slide shows the result of a distance f
function run (Slide 5.) We see that G. (A.) welleri and G. (A.)
wannense are farthest apart during the upper DesMoinesian and
lower Missourian, which was the time when both were in existence,
and their geographic ranges at least partially overlapped. Follow-
ing the disappearance of wannense in the middle Missourian, welleri
relaxed, so to speak, and did not remain as rigidly different (in
terms of spire height) from the wannense shape. The simplest ex-
planation for this comes from studies of recent animals: when a
newly evolved species whose ecological requirements have changed
only slightly from those of the parent species, comes back into
contact with the original parent species, three things can happen:

1. Either partial or total hybridization may occur,
destroying the newly developed species.

2. or, the two species may remain distinct, but com-
petition between them drives one of them out of the area,

3. or, finally, at the place of contact, the behavior
and morphology may change to opposite ends of the variation
spectrum in both species, in effect subdividing the territory
ecologically. Thi

This last phenomenon, called character displacement, was
first shown to occur by David Lack, who worked with the Geospizine
finches on the Galapagos. In an area of overlap of two closely related
species, one had a blunt, thicker beak for consuming larger seeds,
while the other tended to develop a narrower, more pointed beak,
useful in consuming smaller seeds. In areas of non-overlap, both
species regularly consumed a broader range of seed size, and each con-
centrated on seeds of the median size range.

Though any possible adaptive reason for the observed pattern
in the two _Ananias_ species other than maintenance of genetical iso-
lation is difficult to conceive of and impossible to prove, neverthe-
less the pattern itself is strongly reminiscent of the character dis-
placement phenomenon recognized by neontologists. Furthermore,
we are able to follow, on a gross level at least, the history of
this pattern; the zoologist must go laterally, in a geographic
sense, in an effort to infer the probable patterns that will emerge
through time. At best he can only make probabilistic statements
based on his analysis of the phenomenon on one time transect. The
paleontologist can follow the actual pattern as it developed, docu-
menting what actually happened, and possibly identifying the major,
general features of such phenomena.

The shifting patterns of occurrence and biological interaction
between populations of these two species of _Ananias_ emerged, as I
have said, incidentally, in a study of convergence between one of those
species (_welleri_) and _Worthenia tabulata_. Consequently, the results
I have given you are rather incomplete and tentative; the problem
deserves much closer attention, though I do think the general picture
of the relationships between these two species have been clarified
already.

The convergence itself, though cutting across family lines,
is also really best understood on a population basis, though here the
interest lies in sympatric interactions between phylogenetically
unrelated species rather than geographic relations of closely related
species. The convergence is close, and remains so from the upper
DesMoinesian through the Virgilian, and we are justified in hypothesi-
zing an instance of some form of mimicry, i.e. that one species is
purposefully (in a non-teleological sense) apeing the other. The
question is, which species is apeing which? We have already seen that

the shape of G. (A.) welleri evidently depended to a large degree
on the spatial and temporal distribution of its close relative
wannense, and this alone is enough to make us suspect that W. tabu-
lata might be mimicking A. welleri -- the opposite of our first hypo-
thesis. A second source of inference to support this idea also comes
from the distance matrix.

(Slide). In most instances, when both species from two
consecutive horizons are compared, the stratigraphically younger
W. tabulata is closer to the older welleri than vice versa, but the
distance between coeval populations of the two species generally
does not change much at all. Generalizing, we have a sort of
parallelogram affair, if we force these relations into two dimensions.
(((Sketch on blackboard and explain more fully))).W. tabulata seems
to be lagging behind G. (A.) welleri, always coming closer to what
welleri had been. Welleri for its part seemed to be strongly affected
by the presence of wannense. The pattern is exceedingly complex,
and certainly incomplete as I have stated it here, but it should serve
as an indication of the potential depths of complex evolutionary
phenomena paleontologists are now becomming able to plumb.

Paleontologists are rapidly approaching the point where the
dynamic interactions of populations can be reconstructed. The two
brief examples drawen from the three Pennsylvanian gastropods species
show documentation of shifts in allopatric and sympatric relationships
between two closely related species, and interactions between two un-
related species. With the addition of the time dimension unique
to paleontology, the two phenomena are seen, in a sense, to be themselves
interrealted, something which could not be shown by analysis of these
organisms during any one short time span.

Integration of the allopatric model with the phyletic model is
one of the more important changes going on in paleontology in the
last few years. It is but one aspect of the larger process of reorgan-

izing our thinking along population lines, which automatically virtu-
ally demands statistical treatment. Statistical analysis of popu-
lations is also crucial to more subtle analyses of such time-honored
pursuits as documentation of phylogenetic trends: for instance,
and unsuspected parallel trend for increase in whorl height was
found in the two convergent species, and variations and deviations in
the trend were easily seen. Another area of growing importance is
the solution of many problems in functional anatomy and adaptation
which have plagued paleontologists for many years. Patterns of integra-
tion of different anatomical characters as revealed by clustering tech-
niques, a process hit on by Olson and Miller of Chicago in the early
50's, can show up important biological relations of a functional and
developmental nature. Recently, Raup has been drawing various molluscs
with an analogue computer, using only 4 basic parameters to define the
geometry of coiling; his basic conclusion so far seems to be that each
class is limited to a certain small percentage of the total number
of possible shapes open to it mathematically. We still don't know
why this is so; but merely recognizing this is a step forward and
eventually some of the answers are sure to emerge.

The future progress of paleontology, as in so many sciences,
seems inextricably bound up with the computer. I have tried to give
a few examples of the types of phenomena currently actively under investi-
gation. Paleoecological and biostratigraphical paleontology are
equally active and equally open to the applications of new techniques.
Rather than a moribund science properly relagated to the 1830's, pale-
ontology has kept pace with modern ideas and modern tools of investi-
gation, and will remain in the fore-front in the study of the his-
tory of the earth's crust.