June 21, 1971

Dear Tom:

Here is the final version of the ms., plus the review copy you sent back to me. Sorry for the slight delay, but I had to confer with Steve on the alterations, and naturally this took a little time.

You will find that, though we have made some changes in phraseology in response to the criticisms you sent us, on the whole there are no radical changes in content or organization of the paper. I propose to discuss first the issues you raised in your letter of May 24, then the three reviews, and finally the comments and suggestions you made on the ms. itself.

The only general criticism that bothered me at all was the assertion that we either state or imply that "we have discovered something new." We haven't, of course, nor do we claim so. We are merely pointing out the (largely unconscious, perhaps) sway that "phylectic gradualism" holds over our thinking -- despite the fact that most of us have a coherent version of the allopatric model in our minds. The point is that on the whole we don't use it when confronted with "species-level" phenomena in the fossil record. Intellectual appreciation of modern neontological theory is one thing -- but its application is quite another, and I believe that our paper pinpoints why this is so.

I have made a thorough search of the ms. for hints that we feel that we "have discovered something new," or that we are the only paleontologists who have read Ernst Mayr. You will note the disclaimer of the latter thought on page 12. I have indeed found 1 word which might be objectionable in this regard: on page 13, line 5, ("We wish to pose an alternate..."), I have changed the word "pose" to "consider," not because I feel the latter is a better word (it actually isn't as good), but because it seems as if some readers were getting the feeling of "propose" from "pose." Beyond this, we don't feel any changes in the ms. are called for as far as our "discovering" anything is concerned. Incidentally, thanks for the interesting Bernard extract; neither of us had seen it before. But again, since there really isn't any issue of "discovery," it needn't bear on our paper.
You attack the use of the term "biospecies." We are of the opinion that it aids clarity, since, as we discuss in the text, "paleo-" and "chrono-" species, etc. are still around, and there is still a lingering belief that, however interesting the evolutionary biologist's concept of a species might be, it is of no "use" in paleontology because (1) we deal with continua, and (2) it causes "insoluble" problems in taxonomy. For clarity, we must insist on using biospecies as we do, in the initial phases of the discussion; the prefix "bio-" is dropped later on, after our meaning of "species" has been established.

You raise two other main objections -- both dealing with theoretical positions adopted in the paper. The first involves the discussion on page 14 concerning our claim that morphological differences between two sister species are present close after, if not actually prior to, the onset of genetic isolation. We are aware of the existence of sibling species, which are distinguishable, if at all, on the basis of minute behavioral, biochemical, morphological, etc. differences. The question is, if two such sister species are morphologically distinct (by definition the case when grappling with two fossil taxa), at what point(s) in both their mutual and separate histories does the allopatric model predict them to attain a significant degree of morphological uniqueness? We are on firm ground here, Tom, because adjustment (of any biologic feature of an organism) to local edaphic conditions (1) frequently occurs before total isolation, and (2) is easier to effect in a small peripheral isolate. This is as true of cross shell morphology as of anything else. To reiterate -- we do not claim that conspicuous morphological change must accompany genetic isolation, but that when there is significant morphologic change it is most likely to occur (1) before, on, and right after genetic isolation of the peripheral isolate, and (2) when and if the two sister species become sympatric. Nowhere do we claim that "isolating mechanisms are instantly expressed in the external phenotypic

As to pp. 31-32 (homeostasis), upon rereading we maintain that an explanation of stability is a most fitting adjunct to the paper's conclusion, though we are, of course, disappointed that your students had a difficult time with it. But we feel our position is eminently defensible. The quotes from Lerner are not to mask confusion but to lend clarity. Of course both kinds of Lerner's homeostasis relate to heterosis, since they are the 2 major reasons why heterozygotes are selected. Homeostasis definitely does apply to a species ranging over widely different environments without extensive gene flow, since selection favors (1) those individuals capable of a broad norm-of-reaction in morphogenesis, and (2) organisms which are relatively "eurytypic" (within, not among species, now. Thus we are saying that the argument holds whether or not a given species is considered relatively eurytypic or stenotypic when compared with other elements of its own and neighboring communities). Homeostasis, in this light, is a much more effective means of perfecting adaptations to local edaphic conditions while maintaining genetic stability.

One last issue from your May 24 letter: my feeling is that Pete Palmer's biomere is not a model of evolution, though it may be for bio- and time-stratigraphic units. The "kind" of speciation he is dealing with may be relevant here, but it is, after all, only a particular, special case of the general model. We prefer to leave it out of the discussion. Stitt (Jan. '71, J. Pal.) tried to make a four-fold evolutionary model out of Palmer's and his own data, but it was so vague as to be rendered useless, at least insofar as our own deliberations are concerned.
Now, as for the three reviews:

Bergström's point about lack of foreign literature is correct, but we don't feel the necessity of providing an exhaustive catalogue of examples. Palaeontologie is correct for Zittel's original volume, incidentally, and while I think of it, Raup and Stanley is 1971, not 1970 as you claim, at least according to my copy. We accepted all but one of Ghiselin's suggestions, as you will see; all I can say about Bemson's review is that I guess I'll have to send him a copy of the full "rana" story when it's published -- and I don't blame him for his scepticism on the basis of the (necessarily) scanty documentation provided in the example.

Finally, before discussing the changes and non-changes page-by-page, there is your short note of May 28. Gould, 1971a and b, and Raup and Stanley (as above) are taken care of. Steve says that neither Hooke 1675 nor Newton, 1713, should be referenced. 1675 is the date Newton wrote the letter, and the statement itself is folklore, as is the motto; 1713 is cited simply to state when the motto was coined. It is in the 1713 edition of Principia; we don't know who published it or how many pages it has. Neither need be cited. Darwin 1861 has been taken care of by citing Medawar.

(I.e. A copy you marked which I return)

Now for a blow-by-blow run-down of the manuscript itself, especially taking into account your suggested changes. I will not note minor typos, etc.

Page 1. Please leave "Statement..." not "introduction..." since we are summarizing our argument, not gently leading into it.

4 lines from bottom: semi-colon instead of "and"

Page 7. We must leave "entire" -- this is our rendering of phyletic gradualism; anything short of "entire" will leave something behind, and you have speciation or some such -- not phyletic gradualism. Please leave it as is!

Page 8. "Feyerabend meant (p.)..." The blank page reference is an internal page reference to ms. page 3.

Page 10. Beerbower afforded us no juicy quotes. There are other textbooks which we also did not use.

Page 11 ff. We prefer to retain "biospecies" as discussed above.

Page 12. "As a plea..." We would prefer to leave... let the "plea" stand. Steve says: "I believe in appeal and gutsy science." I agree.

Pages 13-16. Subheadings: I would prefer not to chop this up, but if you insist, Tom, we could add them. I have changed "chapter" to "section" the 3 times I found it in the ms.

Page 13A. "parallel" is not necessary.

Page 14. I can't see taking the final 2 sentences of the top paragraph and making a new paragraph, unless you intend to run it into the next paragraph. If so, go ahead, but I have not marked the ms. The rest of your remarks are discussed above. We have accepted your remaining suggestions here.
Page 15. Internal reference to ms. Page 7. STET for the rest, please.

Page 16. We took the suggested change. (Lines 13-14). However, STET for line 4. PC metazoans (our topic) are rare enough!

Page 19. 1 suggestion taken, the other not, as you will note.

Page 20. Again, no suitable sub-heading suggests itself to us and we would prefer not to have one over Poecilozonites or Phacops. We accept the change from "eololianite" to "wind-blown sand"

Page 23. STET

Page 25. "exemplar" is actually used twice in the ms. To paraphrase Twain, an example is only an example, but a good example is an exemplar (Italics mine). Please leave exemplar.

Page 26. Line 1, STET. Rest of changes we accept.

Page 31. We accept the new paragraph as indicated.

Page 32. All definitions are tautologies; we feel this sentence is O.K. as is.

Pages 34-35. Some rearrangements in the bibliography have been made.

Well, that about does it. I hope you will react favorably to our stasis, as well as to our rapid accommodation, to the various points you and others have raised.

Have a productive summer with your moss animals — don't spend too much time fooling around indoors with a bunch of manuscripts.

I'll be around on and off during the summer to handle any howls of protest you might have for us.

Yours,

Niles Eldredge

CC: S.J. Gould