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SPECIES TOT SUNT DIVERSAE QUOT DIVERSAS FORMAS AB INITIO CREAVIT — A DIALOGUE ON SPECIES —

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“The free man always has time at his disposal to converse in peace at his leisure. He will pass, as we shall in our dialogue, from one argument to another; like us he will leave the old for a fresh one which takes his fancy more; and he does not care how long and how short the discussion may be. Time is an endless resource for him, if only it attains the truth. The professional, or the expert, on the other hand, is always talking against time, hurried on by the clock; there is no space to enlarge on any subject he chooses, but the adversary, or his editor stands over him ready to recite a schedule of the points to which he must confine himself. He is a slave disputing among fellow slaves...”

Based on Plato, *Theaetetus*, as interpreted by P. Feyerabend

(The scene is a working-class coffee shop located at a busy corner near a well-known museum in a remote location of the world. A shabby space with cheap furniture, sleepy waiters and reliable coffee. Through the large windows, one sees worn-out gray buildings, a few sickly trees and electricity poles maned with infinite cables in disarray. Busy pedestrians pass flickingly through the windows, in incessant flow of anonymous faces. Nearby traffic flows heavily in all directions, making the arrival at this little oasis a near-death experience for customers. At one table, two characters sit in front of each other, before their espressos, they are Crassus and Rusticus. They are friends at the museum and take their midafternoon break, an opportunity usually devoted to mutual provocation. Both are way past their youth, but not yet old enough to look wise effortlessly. An observant person could tell that their careless exterior reflected happily loosened mid-age convictions, rather than genuine disillusionment.)

(silence)

Crassus (out of the blue, after a sip of coffee): I believe species is the only real entity in systematics.

Rusticus: Is that so? Why?

Crassus: Because species is objective, and not based on opinion. A species either is or is not. Period.

Rusticus: Well, I already heard two slippery words in as many sentences: *real* and *objective*. What do you mean by those?

Crassus: Let's not split hairs about definitions here. I like to approach this subject as a biologist, not as a philosopher. Everybody knows what real and objective mean; well, at least in the real, objective world...

Rusticus: I am sure every single person has an idea of what those terms mean. The problem is that their meanings are not always the same.

Crassus: Let's say real is something which exists regardless of our ability to recognize it. And objective is anything that, given the same information and some honesty, everybody agrees on.

Rusticus: That is fine with me. Now tell me, when you say "everybody" you actually mean everybody?

Crassus: No, only people who are qualified to understand and interpret the information.

Rusticus: Ok, I can live with that for the time being. Now, on to your original statement. Why you think that species are real and objective, while other taxa are not?

Crassus: Because species are the only taxa that have an active, ongoing process that is responsible for their cohesiveness. They have stuff that glues them together, in real time.

Rusticus: And what is the stuff that glues species together?

Crassus: The flow of genetic material, of course. Bits of DNA-coded information which travel more or less freely among members of the same species, maintaining their relative uniformity, and which do not, or do not to the same degree, flow among those of different species. In having their genes shuffled together across generations, species maintain their uniformity. Therefore, they have a basis on a biological process which can be observed, measured and quantified. There is something happening that keeps the entities we call species as unified wholes. This does not happen with other taxa, even your dear monophyletic taxa.

Rusticus: I thought you believed in monophyletic groups as much as I do, having yourself proposed many of them.

Crassus: Of course I do think they are real, so much so that I even went through the trouble of messing up classifications just to conform to my hypotheses of monophyly.

Rusticus: Indeed. So they are real, but not as real as species then.

Crassus: Not exactly. They are both real, but species have an ongoing process responsible for their cohesion, while monophyletic groups have only past events as the reason for their

existence. There is no ongoing process that keeps monophyletic groups together, other than for shared history. An exclusive common ancestor is the reason why groups exist. And the novelties that this ancestral species developed before splitting are inherited by its descendants and constitute the reason why we are able to recognize groups in our distant future. I do not need to explain that to you. Do you not teach such things?

Rusticus: This is the orthodox view, of course. But who knows? There may be something we do not yet know about...

Crassus: You mean, something that holds monophyletic groups together, analogous to gene flow? That is completely impossible and you know that. No. Clades exist because of their past history and that is all. Hennig and everybody else got it right. Accept it. Unless you come up with some active process that nobody knows but you, it is useless to insist on that.

Rusticus: Feyerabend said that the only principle that does not inhibit progress is: anything goes.

Crassus: When you look into the literature on species, "anything goes" is certainly an endeared principle. As for progress...

Rusticus: Let's say you and the rest of the world are right: species are kept together by current processes, while clades are united by past processes. Still, the processes are the same: hypothetical ancestral species were united by the same kind of gene flow or whatever that unites current species. I would conclude then that you say current processes are better causes than past processes.

Crassus: Wrong again. They are not better. Past ancestral species, in their time, were maintained by processes as real as those acting in today's species. They simply are no longer active. We only see their results.

Rusticus: I guess then that you would say that monophyletic groups are neither individuals nor classes, but a third entic category called historical sets.

Crassus: I think the discussion of species as classes versus individuals is ridiculous in this time and age. This was an issue two millennia ago. Did you know that when physicists hear that we still seriously discuss classes *vs.* individuals in biology, they laugh at us? This is how old-fashioned that sounds.

- Rusticus:* Well, maybe it is still being discussed just because it has not yet been solved.
- Crassus:* And never will. This is one of those themes which simply become irrelevant with time. Many things in science are never resolved. They are simply forgotten, abandoned and science gets over them. Remember Newton discussing the shape of light corpuscles? If we waited for all questions to be resolved before following on to other issues, we would still be in the stone-age.
- Rusticus:* And the stone age did not end for lack of stone...
- Crassus:* It is high time systematics buries this class/individual business. It is an embarrassment to our field.
- Rusticus:* I must admit that the "radical solution" to the species problem never impressed me too much when I was a student.
- Crassus:* There you go. But then, sexual reproduction is the glue that keeps species together.
- Rusticus:* What about asexual species? How are they maintained?
- Crassus:* Do you really believe there are such things? Except for a few isolated cases of parthenogenetic species, short-lived and ephemeral, I really do not believe that asexual biological entities have any significance.
- Rusticus:* Well, there are bdelloid rotifers: hundreds of species and over 100 million years of age. And not a single one of them is sexual. Their very existence has been called an "evolutionary scandal". They seem pretty significant to me.
- Crassus:* But they are not asexual! It has been recently discovered that bdelloids are capable of massive horizontal gene transfer. This qualifies as sexual reproduction to me.
- Rusticus:* So, the evolutionary scandal is no longer scandalous. Morals change!
- Crassus:* Bdelloids enjoy great amounts of "sex". It just is not the regular kind of sex we usually see in metazoans and does not involve an "act" that can be easily observed. They make sex, so as to say, with their environment, rather than directly with each other. That is why it remained elusive for so long and was only discovered by modern molecular techniques. Therefore, they are a long-lived, diverse *and* sexual taxon. Just as we would expect.
- Rusticus:* So bdelloids make sex but are not into pornography. Do you predict that the same will hold true to all other diverse lineages reputedly asexual, such as cyanobacteria?
- Crassus:* I do think that all such cases eventually will be shown to display some sort of cryptic sex not yet observed. Remember that sex does not necessarily mean regular sex. Many organisms make sex, but only occasionally, like diatoms and bamboo. I believe sexual reproduction may be extremely spaced out in some groups, so fleeting that it has not yet been recorded.
- Rusticus:* That certainly will be tested, if we live long enough.
- Crassus:* I will be here to witness it, more likely than you. At least I do not smoke a pack of cigarettes before lunch.
- Rusticus:* On the other hand, I am not diabetic... Anyway, you say that species are more concrete than other taxa because there are ongoing processes that account for their cohesion as entities, exceptions discounted. But the same processes also acted when ancestral species were alive. Doesn't that make them just as good?
- Crassus:* No, because they are now gone, then only the results of such processes can be observed.
- Rusticus:* Does that then make ancestral species, and therefore monophyletic groups, inferior to species?
- Crassus:* Not "inferior" in an absolute sense. Their existence is due to processes which can no longer be observed directly.
- Rusticus:* Do you really believe that your gene flow is observed directly? How many cases have you tested? Or better still: how many cases have ever been tested by anyone? This is just a myth.
- Crassus:* Of course, reproductive isolation is inferred on the basis of observable traits, phenotypic or molecular. If you see complete segregation for at least one reliable characteristic, then isolation is inferred.
- Rusticus:* That is my point: the observation is not as direct as you claim.
- Crassus:* The data are directly observed.
- Rusticus:* But then monophyletic groups also are based on direct observations of characters, which makes them no less real than species.
- Crassus:* Ok, the evidentiary basis is ontologically equivalent. But there is a difference: in species we can potentially test reproductive

isolation, if we have the resources and the dedication. So, it stands as a hypothesis that can be tested, if one really wants. You cannot do the same with hypothetical ancestors.

Rusticus: But in that case there would be no point. The equivalent hypothesis for monophyletic groups, or their ancestral species if you want, has already passed the test: in retrospective, they were definitely reproductively isolated from each other. No uncertainty there.

Crassus: Except that the individual organisms which composed such hypothetical ancestors are not observed. The ancestral species themselves are a hypothesis. The observed data come from their descendants only.

Rusticus: You are right if you want to consider hypothetical ancestors as actual ancestors in the full-color biological splendor of the term. However, one may simply say that they are hypotheses, or nodes in maximally-informative scheme of relationships, reflecting a dimension of biological organization without complete correspondance to what is usually called species.

Crassus: This sounds like the pattern cladist view of things. Decades have gone by and that mysterious dimension has never surfaced.

Rusticus: True, but you cannot deny the historical fact that groups, or taxa, were recognized long before there was any thought about evolution, or descent with modification.

Crassus: The ancients realized the pattern, but had no explanation for it. Now we have one. And a very good one at that.

Rusticus: They had an explanation too. It was just not the explanation we consider correct today. But I want to return to the question of the few, isolated and, according to you, irrelevant truly asexual species. There are unquestionably some of those, no matter how despicable you think they may be in the grand scheme of life. They exist in the real world, in a manner concrete enough for them to be recognized, readily diagnosed and given proper names.

Crassus: Yes indeed.

Rusticus: What keeps them together, then? How they maintain their uniformity and cohesion?

Crassus: They are just leftovers of evolution, lingering on with their pathetic little existences

in very special circumstances. Their uniformity is simply a result of a similar genetic package to start with, developmental constraints and selection. The latter eliminates deviants from their very strict tracks, keeping the survivors similar and “conspicuous-like”.

Rusticus: And you think that is enough to maintain such aspect of uniformity?

Crassus: Sure it does. Look at the lineages of garden plants which have been propagated by budding alone for centuries and still look exactly the same. It does take a lot of time to change such things.

Rusticus: We should therefore conclude that asexual species are not actual species, since they lack the most important element that keeps species together.

Crassus: I agree, we should not consider them as real species in the sense of sexual ones. Some call them agamospecies, precisely for that reason.

Rusticus: But then, there were forces which kept them together in the past, before they became asexual. So their basis is the same as that of normal species.

Crassus: Again, they are not currently maintained by forces which normally keep species together, like monophyletic groups.

Rusticus: But agamospecies can be as relevant biologically as any other. After all, they are composed of individuals who are active players in the drama of life. An invasive agamospecies may drive a good native species extinct by predation or competition.

Crassus: Their ecological role is irrelevant. Abiotic factors have relevant ecological roles too, and they are not even living entities.

Rusticus: What about prokaryotes? What you suggest we do with them?

Crassus: Applications of concepts of species to prokaryotes is weird, based on a rather arbitrary cutoff of overall genotypic similarity. Two isolates are placed in the same bacterial species when they display a value equal or greater than 70% in standard DNA-DNA hybridization. Alternatively, they are not considered conspecific if their small subunit (SSU or 16S) rRNA sequence falls below 97% identity. These values are consensual.

Rusticus: Where these numbers came from?

- Crassus*: Apparently, they were found to be the values which resulted in boundaries conforming to species traditionally recognized on the basis of other criteria, such as old tests of physiology, biochemistry or microscopy.
- Rusticus*: So, they were calibrated to conform to traditional species limits. Rather circular. This seems to fit that old adage: “a species is what a good taxonomist says it is”.
- Crassus*: Do you know who first said that?
- Rusticus*: I think some ichthyologist called Regan, in the 1920’s.
- Crassus*: Ichthyologists have always been weird. But anyway, that makes one think whether the estimates of microbial biodiversity have any meaning.
- Rusticus*: As I remember, among vertebrates, DNA-DNA hybridization values below 70% often results from species belonging to different orders.
- Crassus*: I think many microbiologists are skeptical of a meaningful concept of species for most prokaryotes. No wonder they came up with so-called “fuzzy species concept”.
- Rusticus*: But still, there is some real discontinuity to be found there. And I do not think it necessarily derives from usual concepts of interrupted gene flow. To me, species as a special entity remain restricted to rather narrow situations.
- Crassus*: I will put it another way: species evolve, while other taxa do not.
- Rusticus*: But other taxa are composed of species, which themselves evolve, thus, in a way, they evolve too.
- Crassus*: You know what I mean: species speciate, genera do not “generate”, families do not “familiate” etc. Species can generate other species, higher taxa do not generate other higher taxa.
- Rusticus*: This is nonsense.
- Crassus*: (sighs, looking half bored, half condescending)
- Rusticus*: Let me make an analogy. Consider a chain of volcanic islands, only the last of which still has an active volcano vomiting magma. All the others are also obviously volcanic, with craters and all, but are now inactive. Does that make them less real? No. They are as real as the single active island. The latter may help us understand the details of the formation of the archipelago, but it is no more real than the rest.
- Crassus*: This example is simplistic. Volcanic islands do not replicate and evolve in the way biological systems do.
- Rusticus*: Seems like a nice analogy to me. Ok, then: consider an imaginary world where all species were extinct, known by fossils only. You came there with the task of being their taxonomist. You split them into species and higher groups, as a perfect scheme of relationships and corresponding classification. Would you doubt their reality?
- Crassus*: No I would not, but I would have a tough time understanding their biological properties and ultimately, the processes which formed that diversity.
- Rusticus*: That is my point then. What you call species are simply circumstantial situations where some processes are still operating, but they are no more real than entities which were formed by the same processes in the past. Active species – in analogy with the volcano – can be wonderfully pedagogical about how certain things operate, but are no more real or concrete than equivalent entities where such processes no longer operate. Paleontologists recognize species as well as any neontologist.
- Crassus*: Paleontologists have no alternative. You know what they joke about paleontologists? If they find a specimen which is slightly different from the holotype, it is described as a new genus. If it is exactly identical to the holotype, then it is only a new species...
- Rusticus*: You do not offend me, I am not a paleontologist. I only published one paper on fossils. But in view of your dismissal, let us stick with Recent species then. Consider the recently extinct Chinese paddlefish. There are specimens in museums only. No reproduction, no gene flow. Still, nobody questions their existence as a good species. They are as real as their North American sister group, which still enjoys all the delights of active life.
- Crassus*: The entities which I think are special are equivalent to your “active species.”
- Rusticus*: But that means you restrict your category to living species. One big restriction.
- Crassus*: But you agree that the processes seen in “active species” are instructive about the forces which shaped all species and ultimately all taxa?

Rusticus: Yes I do, but I think that is pretty obvious.

Crassus: Obvious? Ok then. Based on our knowledge about active species, do you believe that isolation is the reason why species split?

Rusticus: If isolation is broadly defined, yes.

Crassus: So, isolation is the ultimate cause of cladogenesis?

Rusticus: No problems there.

Crassus: What about two populations obviously isolated from each other, but with yet no sign of divergence. Say, there were isolated yesterday. Are they different species?

Rusticus: Well, they are potentially different species.

Crassus: "Potential" is not actual. I conclude that you consider that they are not separate species, and thus that having them isolated as separate individuals is not enough.

Rusticus: It is enough. They are already separate entities, subsequent divergence is just a consequence. The stuff that glues them together is no longer gluing them.

Crassus: Thus, would you describe and give names to them? Remember, they cannot be conspecific with their ancestor. So, you will need two new names.

Rusticus: I would not do that, because there is no point in creating official names that carry no useful information. We must name species when they represent an addition to our knowledge of diversity. It would be silly to describe species that are identical to each other. What would be the point?

Crassus: The point would be to underscore the fact that we have now two entities evolving independently. Let us say you justify that as part of an experiment on biological prediction. You plan to describe the species as new and follow them as time goes by. A nice long-term project.

Rusticus: You mean, something like a preemptive species description? Describe it before someone else does! We might have some problems with a proper diagnosis...

Crassus: We diagnose them on the basis of their geographical location.

Rusticus: It won't work. The International Code of Zoological Nomenclature explicitly states that the mention of a locality in itself does not constitute a valid description.

Crassus: We can make a description alright. It is just the diagnosis that will have to wait a bit. We will add them as the years go by

and our species dutifully diverge. A simple case of revised diagnosis.

Rusticus: Then let's hope there will be systematists millions of years from now.

Crassus: No need for that long, we could be talking about bacteria or viruses. A few years may suffice. The *E. coli* artificial evolution experiment has produced a dramatic metabolic novelty in 50.000 generations. There are also more natural examples, such as the London underground mosquito.

Rusticus: What is that?

Crassus: It is a variety of *Culex* which got adapted to the environment of the underground tunnels of the subway system in London. It is markedly different from the species above the ground in physiology, behavior and morphology and has evolved pronounced, perhaps total, reproductive isolation. That subway is 150 years old and thus that is inferred as the age of the new mosquito species. Interesting story. Google it.

Rusticus: I don't know how you remember such things.

Crassus: Neither do I. Would you name the new species and the other surface species as new?

Rusticus: I would only name the underground one as new. The ancestor can retain its old name.

Crassus: But that goes against the phylogenetic logic of the stem species going extinct by definition when there is a speciation event!

Rusticus: I admit that the application of phylogenetic classificatory system gets impractical when applied to biological systems evolving in real time, human time. We simply cannot rename everything all the time.

Crassus: I hope you realize you are fltering with theoretical inconsistency. No, worse still. I say you are in bed with inconsistency.

Rusticus: We all have to make concessions in dealing with the dirty real world (takes a large gulp of coffee, accidentally soling his chin and shirt in the process). But don't you think that such inconsistency is restricted to fast-evolving cases, or real time as you put it. There are documented cases of coastal islands being independently and successively colonized by a single widespread species on the continent. Then each island differentiates into its own species. That makes the continental species paraphyletic, because

parts of it may be more closely related to one of the island species than to members of its own continental “species” (quotes implied by movements of index and middle fingers). That is why some people prefer to call such cases metaspecies.

Crassus: Then you conclude that species must be monophyletic groups, after all?

Rusticus: No, I do not. Metaspecies should be reserved for reproductive communities that are demonstrably non-monophyletic. If they are not monophyletic but cannot be shown to be para- or polyphyletic either, then they can be a species.

Crassus: Giving a pretty name to an ugly fact will not make it less ugly.

Rusticus: You know what I find amusing in philosophical discussions on species?

Crassus: hummm...

Rusticus: They encourage people who have no idea how to describe a species to speak with confidence about the ontological reality of species.

Crassus: Are you being sarcastic?

Rusticus: Yes, but very unfairly. You are entitled to a low blow.

Crassus: Here it goes then: did you know there are proposals to use Bayesian statistics to determine species boundaries?

Rusticus: Oh no!

Crassus: Indeed.

Rusticus: More Bayesian stuff to constipate us again. I need another profession. Statistics bores me to tears. And how in hell they do that?

Crassus: By estimating posterior probabilities of species-delimitation models.

Rusticus: On the basis of...?

Crassus: Reversible-jump Markov chain Monte Carlo simulations, in association with a user-specified guide tree.

Rusticus: Did anyone actually apply that?

Crassus: Yes, they inflicted it on some poor African lizards, genus *Hemidactylus* if I remember well.

Rusticus: They are not lizards, those are geckos.

Crassus: Geckos are not lizards? Ok then. In any event, the authors apparently got inebriated by their Bayesian booze and forgot to comply with ICZN rules when describing their new species. So, they were all declared *nomina nuda* shortly thereafter.

Rusticus: Tough luck. How were their descriptions done?

Crassus: Some number expressing some degree of support for some cluster under some model.

Rusticus: Next time they should compute insanity as a prior.

Crassus: They sure should...

Rusticus: That reminds me of that case of some polychaete species described according to the “rules” of Phylogenetic Taxonomy, but unavailable according to ICZN. Some guy who knows nothing about the group came and, just for the fun of it, republished the information. Only this time he included a proper binomial and made the species available under his own authorship.

Crassus: Tough luck...

Rusticus: What is amusing is that still today there are many papers every year, and even entire volumes, dedicated to concepts of species. People are addicted to it. There is so much published on the subject that an exhaustive review of the literature would demand an entire career.

Crassus: Let's not exaggerate. Much of that literature is just junk. It can be safely thrown in the trash.

Rusticus: Indeed, but in order to say that, one needs to read them first! The thought of that alone is enough to throw the healthiest of us in perpetual depression.

Crassus: Some years back, someone made a survey and came up with 22 different species concepts proposed in modern times. Since then, the number has grown even more.

Rusticus: Another study has shown that all the discussion on species concepts is completely ignored by botanists who actually deal with species-level diversity: authors of taxonomic monographs. Most authors do not as much as mention which species concept they are using. A few cite their concept, but do not bother to follow them anyway. So, the entire discussion seems pretty vacuous to the people who do the actual work of delimiting species-level taxa.

Crassus: On the other hand, just a couple of years ago there was a paper nearly doubling the number of species of Bovidae, a rather important group in the history of our civilization. The increase was caused mainly by a different species concept employed. So, the concepts may have some consequence after all.

Rusticus: I remember an edited volume where there was a series of papers, followed by attacks on them and respective replies, all in succession, as a debate. It was an interesting way to treat the mess.

Crassus: Is that the thin book with black cover and a radiographed nautilus shell?

Rusticus: Yes. You have it too?

Crassus: You stole it from me.

Rusticus: Oh. It wasn't theft, I just borrowed it for all eternity.

Crassus: Your eternity is over.

Rusticus: Tough luck. Should have kept my mouth shut.

Crassus: Indeed.

Rusticus: Anyway, this eternal discussion and lack of resolution means something. And this something smells bad. All the theoretical and philosophical mumbo-jumbo around the concept of species seems like a smoke screen. It just covers up a central void. This is like the invisible man, who covered himself all over, gloves, sun glasses and all, so people did not see that he was invisible. I think species are just like that. There is nothing to see. It is a chimeric concept imposed upon the world by our categorization-freak brains. You know what Haldane said about species concepts? He said that the concept of a species is a concession to our linguistic habits and neurological mechanisms. We argue over it like medieval monks discussing how many angels could dance on the head of a pin. Nobody cares about angels anymore.

Crassus: Well, there may be millions of bacteria dancing on the head of a pin... People care about bacteria. The monks were right: there are crowds of tiny creatures living there. And we still cannot name them to species!

Rusticus: *Species tot sunt diversae...*

Crassus: Don't try to recite all that. I will not be impressed because I know you do not really know Latin.

Rusticus: But did you know that even Linnaeus did not hold a completely fixist view of species?

Crassus: I read that he dropped that famous sentence from late editions of the *Systema Naturae*.

Rusticus: And he did it for a reason. He came to the conclusion that new species could

originate after all. Not all of them had been created. Late in life, he went as far as concluding that only three species of plants were originally created. All others originated by hybridization.

Crassus: So, even Linnaeus was an evolutionist!

Rusticus: Yes, of sorts, if we take his "hybridization" to mean mechanisms of genetics and inheritance that he couldn't possibly have known in the 18th century. Regardless, he realized there was something going on with species in nature.

Crassus: The old fellow was smart.

Rusticus: Smarter than most people realize.

Crassus: (looking at his watch) Enough of that. It's late. Hurry up. I need to finish the description of that new species from Yucky Muck I told you about. Really odd critter. You have to come see it one day. Maybe it is even a new genus.

Rusticus: How many specimens you have?

Crassus: Just one. Rare beast.

Rusticus: No gene flow with any other species?

Crassus: Who cares? It is definitely new. Let's go.

Rusticus: Don't forget the check.

Crassus: It is your turn today.

Rusticus: No, I paid yesterday.

Crassus: Really, we never agree on anything.

Rusticus: No, sometimes we do!

Crassus: You talk too much.

Rusticus: I promise one day I will shut up forever, you will see.

Crassus: You bet.

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