Pan-Biota J. Wagner 2004 (as *Panbiota*) [J. Wiemann, K. de Queiroz, T. B. Rowe, N. J. Planavsky, R. P. Anderson, J. P. Gogarten, P. E. Turner, and J. A. Gauthier], converted clade name

Registration Number: 299

Definition: The total clade of the crown clade *Biota*. This a crown-based total-clade definition. Abbreviated definition: total ∇ of *Biota*.

Etymology: Derived from the Greek *pan-* ("all" in reference to a total clade) and *Biota,* the name of a crown clade (see *Biota* entry in this volume for etymology).

Reference Phylogeny: Figure 1 in Hug et al. (2016), in which *Homo sapiens* is part of the clade *Opisthokonta*. *Biota* (this volume) includes all taxa depicted on that tree, and *Pan-Biota* includes not only all members of that crown clade but also all yet-to-be-discovered stem bioentities that share common ancestry with them (see, e.g., Cornish-Bowden and Cardenas, 2017: Fig. 4). There are no phylogenies for early divergences within *Pan-Biota* because no unambiguous stem biotans are known, which is unsurprising given that their potential fossil remains would be very unlikely to preserve substantial morphology or genetic information enabling inferences about their phylogenetic placement. Evolutionary scenarios discussing chemical steps leading to the first ancestral replicator and its organismal assembly giving rise to *Biota* can be found in Comments.

Composition: No unambiguous stem biotans are currently known. Nevertheless, if life on Earth is monophyletic (Theobald, 2010), then *Pan-Biota* necessarily includes all biologically replicating entities (bioentities) that have ever existed on this planet (or spread from it in the past, present, or future), including all extant and extinct bioentities, whether known or not. It thus includes the crown clade *Biota* (this volume) plus all non-biotan cellular and molecular (acellular) entities descended from the first replicator ancestral to that crown clade (= ur-replicator or ur-ancestor), even if that replicator had a deeper extraterrestrial ancestry (viz., Panspermia and derivative hypotheses). Prebiotic molecules do not qualify as pan-biotans unless they are either actively or passively replicated biologically (see Diagnostic Apomorphies and Comments) and that property is homologous with replication in the biotan crown. Well-known replicators considered here as ancestral pan-biotans include DNA single- and double-strands (DNA world), RNA single- and double-strands (RNA world), (hypothetical) nucleic acid-protein complexes (see Comments) and their replicating ancestors (Gilbert, 1986; see critical comments by Orgel, 2003). Additional, protein-only world scenarios predict prion-like protein templating as the ancestral mode of "exchange of biological information" (Pruisner, 1998; Rode et al., 1999; Lupi et al., 2006); however, such protein-protein templating would not fulfill the requirement of biological reproduction. A hypothetical ancestral prion-like protein would be unrelated to extant prions, which are parts of biotans, and emerged multiple times independently in different protein families. Therefore, a hypothetical ancestral prion-like protein would not be part of *Pan-Biota* but would be considered prebiotic chemistry. Other candidate compounds of either hypothetical or in vitro-synthesized nature include (double- and single-stranded) pyranosyl RNA (Eschenmoser, 1999), as well

as (single- or double-stranded) peptide nucleic acids (Nielsen and Egholm, 1999). These potential replicators may derive from the biotan stem, or may have formed independently, or may represent only hypothetical replicators. If such artificially synthesized compounds formed naturally, and originated in the biotan stem, they would be considered part of *Pan-Biota*; otherwise, they would be regarded as products of prebiotic chemistry. Ribozymes (a functional term referring to RNA with biocatalytic—including autocatalytic—potential) are bioentities composed of single-stranded RNAs considered central to the currently prevailing RNA-world hypothesis (Gilbert, 1986). Ribozymes are present in all cells (and some viruses), and facilitate, for example, protein biosynthesis. They are therefore parts of *Biota* and *Pan-Biota* as parts of cells, but it is not clear if these extant ribozymes are descendants of an ancestral replicator, and evidence against ribozyme-like pan-biotan replicators is accumulating (Orgel, 2003; see Comments for details). Because most replicator candidates listed here cannot reproduce on their own (except for the aforementioned ribozymes), they require close association with replication catalyzers that can be of inorganic, bioinorganic, or biomolecular origin. While the most popular 'pan-biotan origins' scenarios are compound-exclusive (e.g., RNA world; see Comments), evidence is accumulating for a concurrent emergence of building blocks comprising the ancestral pan-biotan (Patel et al., 2015). The potential coexistence of different molecular building blocks suggests that multiple biological replicators (i.e., RNA and DNA) may have formed simultaneously, while only one of them gave rise to *Biota*. Only this single replicator and all of its descendants would be members of *Pan-Biota*. If other replicators, or their parts, were later to become incorporated into biotans and thereafter descended along with them, then they would also be parts of *Pan-Biota*.

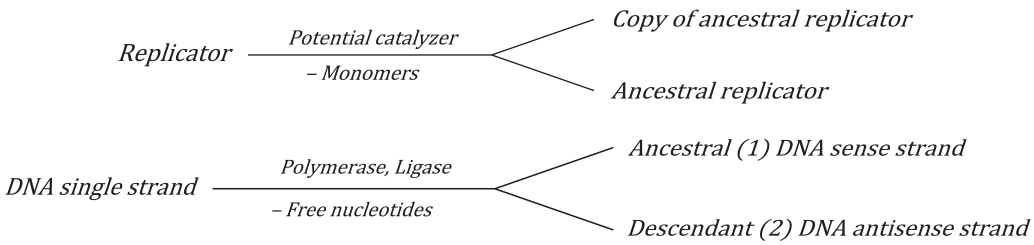
Diagnostic Apomorphies: The total-clade definition adopted for the name *Pan-Biota* embodies the idea that this name applies to the very largest clade on Earth (containing *Homo sapiens*). To form clades, common ancestry and thus genealogical connectivity via biological replication (an ancestral bioentity giving rise to descendant bioentities) is the only necessary property. That property would then be the fundamental diagnostic apomorphy of *Pan-Biota*. Whether replication occurs through molecular templating, external catalysis, internal catalysis, or autocatalysis does not matter. While we are referring to "biological ancestor-descendant" replication, rather than a chemical educt–product relationship, it should be emphasized that a simpler form of replication likely preceded the complex processes involved in either cellular fission or sexual reproduction. This concept of "biological replication" versus "chemical reactivity" is illustrated below. Given the templating potential of various biomolecules common to *Biota* (this volume), such as DNA, RNA, and even proteins, *Pan-Biota* is expected to contain multiple types of such replicators through sequential integration into an organism derived from the one ancestral replicator (bioentity).

Chemical Reactivity (insufficient for inclusion in *Pan-Biota*)

$$\begin{aligned} &Compound\ A + Compound\ B \\ &\quad \rightarrow Compound\ C + Compound\ D \\ &\qquad + Compound\ F \end{aligned}$$

$$\begin{aligned} RNA\ strand + H_2O \xrightarrow{Base} &Part\ 1\ of\ RNA\ strand \\ &+ Part\ 2\ of\ RNA\ strand \end{aligned}$$

Biological Replication (creates genealogical relationships required for inclusion in *Pan-Biota*)



Synonyms: Most of the names listed as synonyms of *Biota* (this volume), as well as *Biota* of Trifonov and Kejnovsky (2015) and others, can also be considered approximate synonyms of *Pan-Biota* in that previous authors seldom distinguished clearly between crown and total clades (some are also partial synonyms). Partial synonyms that refer to paraphyletic taxa that were more clearly considered to have originated in earlier ancestors than the most recent common ancestor of the crown clade include: *Aphanobionta* Novák 1930; *Protobiota* Hu 1965; *Acytota* Jeffrey 1971.

Comments: As in the case of the crown clade (*Biota*), the literature records few instances in which the corresponding total clade has been given a formal taxon name. We take this opportunity to name it using an explicit phylogenetic definition following the general approach of Wagner (2004), which is based on the idea that there is no clade more inclusive than the one being named, although the wording of our definition differs. In the interest of developing an integrated system of clade names (see de Queiroz, 2007), we have chosen *Pan-Biota* as the name for the total clade of *Biota* (this volume). We have attributed the name *Pan-Biota* to Wagner (2004) and treated it as a converted clade name. Although Wagner (2004) used the orthographic variant *Panbiota*, that variant employs the same letters, base name, and prefix as *Pan-Biota*; it differs only in the absence of a hyphen separating the base name and prefix and in the absence of capitalization of the first letter of the base name. Both of those orthographic conventions were adopted in the *PhyloCode* subsequent to Wagner's proposal. Moreover, Article 17.1 implies that the hyphen is not part of the spelling of the name, given that deletion of a hyphen from a preexisting name does not prevent it from being treated as a converted name. Similarly, we do not consider the difference in capitalization of the letter "b" to constitute a difference in spelling (see Art. 17.5).

There are several hypotheses for the nature of the ancestral replicator that gave rise to the clade *Pan-Biota*; we will discuss the more widely accepted alternatives here. Each potential ancestral pan-biotan will be introduced and critically evaluated in light of the defining apomorphy for this clade: biological replication (see Comments in *Biota*, this volume).

The Ancestral Replicator: One of the key problems in diagnosing the clade *Pan-Biota* is that the exact nature of the ancestral replicator remains elusive and the subject of considerable speculation (i.e., Orgel, 2003). In the absence of an informative fossil record, and given the drastic difference between this ur-ancestor and the complex cellular ancestor last shared by all bacteria, archaeans, and eukaryotes (BAEs), theoretical and experimental works have inspired innumerable hypotheses about the

features of the ur-ancestral replicator, and how it was initially assembled. The most popular scenarios include the RNA-world (Gilbert, 1986), the DNA-world (Forterre, 2001, 2002), the Protein-only world (Pruisner, 1998; Rode et al., 1999), and further elaborations of these hypotheses that include both terrestrial emergence and extraterrestrial delivery to Earth.

Summarizing the most plausible and established scenarios on the emergence of pan-biotans, it seems reasonable to assume that the ancestral replicator entity was likely composed of (single or double-stranded) RNA and/or DNA (Forterre, 2002; Orgel, 2003). That inference is based on the fact that the "genetic" material found universally among Recent organisms and viruses (or viral derivatives) is composed of either DNA or RNA.

It is often assumed that the ancestral replicator must have been a single compound. This assumption finds expression in the well-established and widely accepted hypothesis that an autocatalytically reproducing ribozyme was the ancestral replicator (RNA-world sensu Gilbert, 1986). Ribozymes are single-stranded RNA with catalytic properties, functionally comparable to enzymes. They are characterized by having both a genotype and phenotype that determines their catalytic activity. Ribozymes perform various functions, including autocatalytic amplification (Doherty and Doudna, 2001). In vitro, ribozymes have been demonstrated to drastically increase in reaction selectivity and yields when functionally selected (Tsang and Joyce, 1996). Within a few dozens of generations—with generation times that can vary from minutes to decades depending on substrate availability—ribozymes can improve from minimal to maximal reactivity (i.e., Tsang and Joyce, 1996). This renders them suitable candidates for an ancestral replicator, but it also raises a crucial question: if the ancestral replicator was a ribozyme in an RNA-world, efficiently catalyzing its own amplification, why is the genetic material in all biotans (and candidate bioentities) stored in regular DNA or RNA that is replicated solely by proteins? The enhanced stability of DNA relative to RNA might explain selection for a different information-storage medium (i.e., if RNA was the initial storage medium), but this scenario has little empirical support. We will focus hereafter on the questions that must be answered to better understand the nature and origin of this largest clade on Earth.

The intertwined relationship of DNA, RNA, and proteins in biotans, also known as the central dogma of molecular biology (Crick, 1970), suggests strictly selected molecular coevolution of these compounds. Thus, rather than assuming that the ancestral pan-biotan replicator was formed by just one compound, it seems more plausible to regard it as having originated as a complex composed of a replication substrate and a replication catalyzer. A strand of DNA or RNA would serve as a reasonable substrate for replication that could be catalyzed by RNA (ribozyme) or a protein. In the following we review the key steps culminating in the ur-ancestral pan-biotan replicator and critically assess the requirements necessary and sufficient for the transition from chemistry to biology.

After the initial polymerization of pan-biotan building blocks, two different scenarios can be envisioned that set different stages for the emergence of biological replication: Scenario (1) is compound-exclusive and coincides with the RNA (or DNA)-world hypothesis, according to which only pure nucleic acids (DNA, RNA) formed the ancestral replicator. All other biopolymers (proteins, sugars, lipids) found in biotans are hypothesized to have emerged (spatially and temporally) independently. In this scenario, biological replication could have arisen in the form of a ribozyme

catalyzing self-replication, a ribozyme catalyzing the replication of a separate RNA strand, or, a ribozyme catalyzing the replication of a separate DNA strand. Scenario (2) is compound-inclusive; i.e., all single-stranded nucelic acids (DNA, RNA) emerged, as well as peptides with a polymerase function. There is growing evidence for a simultaneous origin of life's building blocks through one-pot chemistry (= all key ingredients react within the same compartment; Patel et al., 2015), which supports the concurrent presence and interaction of different types of short biopolymers during the emergence of biological replication.

All, a few, or only one of these hypothetical ancestral replicators and replicating bioentities may have evolved, but all indications are that only one of them is ancestral to humans (see *Biota*, this volume). Attempts to more accurately identify the ur-ancestral bioentity are plagued by the current lack of an acellular pan-biotan fossil record. Because the ancestral replicator can be thought of as a macromolecule, or macromolecular assembly, in aqueous solution, no morphological residue would be expected (see Briggs and Summons, 2014). DNA and RNA are generally associated with a low fossilization potential, while proteins have been shown to preserve in deep time through chemical transformation into N- and S-heterocyclic polymers (Wiemann et al., 2018). Ancient DNA has been retrieved from samples as old as 1.5 million years but suffers from substantial degradation and alteration (Willerslev et al., 2004). There is thus little reason to expect that there will ever be molecular fossils revealing the nature of the ancestral replicator.

Potential Members of Pan-Biota: The following discussion focuses on the validity of popular candidates as the ur-ancestral replicator.

Ribozymes: The appearance of self-replicating ribonucleic acid (RNA) is widely thought to have been the key innovation in this system and would fulfil the requirement of biological replication (Gilbert, 1986; Diener, 1989; Maynard Smith and Szathmary, 1995; Neveu et al., 2013; but see Bowman et al., 2015). As long as that RNA replicator directly preceded or contributed to the genetic makeup of biotans, it would be part of *Pan-Biota* (this volume). All extant ribozymes incorporated into biotan cellular systems are parts of *Biota,* even if they evolved independently of the ancestral pan-biotan replicator before biotan cells emerged and subsequently invaded them either as parasites or symbionts.

Viruses: As discussed in *Biota* (this volume), 'viruses' constitute a class of bioentities that parasitize cells (though they can also be viewed as symbionts); there are no data supporting their monophyly but there is considerable evidence indicating that 'viruses' comprise several clades. Two of the three hypotheses for the origins of viruses (Wessner, 2010) propose that they possess genealogical continuity with *Homo sapiens* (Forterre and Prangishvili, 2009). Regardless of whether viruses represent simplified cells, or even less-modified molecular replicators, their survival into the Recent renders them—if not independently evolved—members of crown *Biota* (see extensive discussion in *Biota*). In this case, viruses would also be pan-biotans. Moreover, viral replicators possess the apomorphy required for pan-biotans—the capacity for biological replication (as long as not independently evolved), regardless of the nature of the replication process (i.e., whether autocatalyzed or externally catalyzed).

It remains possible that some viral replicators could have emerged independently on Earth or elsewhere. Hypotheses for independent origins of viral replicators propose that they arose prior to (or in parallel with) the ancestral pan-biotan replicator, in an RNA- or nucleoprotein-world (e.g., Diener, 1989; Forterre, 2006). There, they

either coexisted with other nucleic acids (insertions) or used early nucleic acids as hosts, and later infected cellular (pan-)biotans. Under this hypothesis, "viruses" would have been derived from a replicator that evolved reproduction independently of the ancestors of *Biota*, and therefore would not be part of *Pan-Biota*. However, because biological reproduction is a complex process, and is often understood as the key to the success of life on Earth, independent evolution of this trait seems unlikely (see *Biota*, this volume).

DNA, RNA, Their Ancestors and Potential Derivatives: All currently known replicators, or rather replication substrates, present in biotans likely preceded self-sustaining cells or cellular assemblies (= typical organisms). All DNA and RNA bioentities, as well as their ancestors and derivatives, replicate through molecular templating, or under enzyme catalysis, and are therefore—if related to *Homo sapiens*—considered part of *Pan-Biota*.

Dating the Transition from Chemistry to Biology: Accurate dating of the emergence of the clade *Pan-Biota* may prove extremely difficult, given the absence of diagnostic traces, morphological or chemical, of acellular replicators in the fossil record. Recent evidence suggests that by 4.51 billion years ago (from the moon-forming Theia impact onward), the Earth was habitable by pan-biotans, contained liquid water and, contrary to speculation, was unlikely to have been sterilized by heavy bombardments occurring during the Hadean (e.g., Wilde et al., 2001; Abramov and Mojzsis, 2009). There is organic carbon with isotopic signatures consistent with carbon fixation in zircons older than the sedimentary rock record (Bell et al., 2015), and the Earth's oldest sedimentary rocks (ca. 3.8 billion years ago) contain numerous potential if debatable biosignatures (e.g., Schidlowski et al., 1979; Mojzsis et al., 1996; Rosing, 1999; van Zuilen et al., 2002). However, isotope signatures indicative of carbon fixation have been calibrated based on crown biotan metabolic activity. Simpler, pre-cellular pan-biotans may not have fractionated isotopes in exactly the same way as the compartmentalized anabolic and catabolic systems in cells. Furthermore, pronounced signatures resulting from cellular organisms may not differ among crown and stem members. For this reason, isotopic signatures indicative of carbon fixation cannot reliably distinguish between cellular stem-biotans vs. crown-biotans. There are several generally accepted indications of biological chemistry by 3.5 billion years ago including, most notably, isotopic evidence for carbon and sulfur cycling (e.g., Schopf et al., 2006; Roerdink et al., 2012; Bontognali et al., 2013). These metabolic capacities, however, seem unlikely to have been present in the earliest pre-cellular pan-biotans, as carbon and sulfur cycling requires compartmentalized reaction spaces that can only be generated in a "cellular" environment today.

Nevertheless, minimum age constraints for *Pan-Biota* can be inferred from the fossil record of *Biota*. The body- ("microbial") and trace- (stromatolite) fossil records of this age are difficult to interpret. The "microbial" record certainly reaches back 3.2 billion years with fossils of uncertain phylogenetic affinity (Javaux et al., 2010). However, some degree of cellular organization likely evolved in pan-biotans prior to the origin of *Biota*, and the cellular residues of these putative microbes do not allow an unambiguous assignment to *Biota*. Arguments for a variety of even older body fossils have been made, but their biogenicity is controversial (e.g., Schopf and Packer, 1987; Schopf, 1993; Brasier et al., 2002; Knoll et al., 2016).

In sum, the geologic record indicates the root of *Pan-Biota* may be more than 4 billion years old (but likely younger than 4.51 billion years), is certainly older than 2.3 billion

years (conservative estimate for *Biota*), and is probably older than 3.5 billion years ago. The definition of the name *Pan-Biota* may be clear, but as a practical matter, being able to conclusively apply it to potential examples in the rock record billions of years ago may forever lie beyond our grasp.

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