

A new species of *Tubella* (Porifera: Spongillidae) for the Brazilian Amazon: how misidentification can mask a potential species complex

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ABSTRACT

Sponges may be among the worst dispersers in the animal kingdom, however, some freshwater sponges produce resting bodies called gemmules, which have been used as the main explanation for the widespread distribution of some of those organisms. This is the case of *Tubella pennsylvanica* Potts 1882, which was originally described from Pennsylvania, USA, and is reported with a worldwide distribution but with scarce and confusing information to validate its taxonomy and dispersal mechanism. It has been registered in the Amazon and is the first species of *Tubella* reported outside the Amazon. In order to confirm the taxonomic status of the occurrences in Brazil, we collected specimens from three sites in the Amazon basin and compared their measurements and characteristics with the type material of *T. pennsylvanica*. Based on this specimen analysis, we consider all records in Brazil of *Tubella pennsylvanica* to be a different species, which is here described as *Tubella manauara* n. sp. In addition, we provide the first images of the spicules of the holotype of *Tubella pennsylvanica*. The new species differs from the type material of *Tubella pennsylvanica* by presenting larger spines in the megasclere acanthoxeas, and larger size of the spicules. The specimens of *Tubella manauara* n. sp show morphological variations according to the type of substrate on which the sponge has developed. This study reinforces the need to review South American freshwater sponge species with distributions that stretch to other continents.

KEYWORDS: *Tubella pennsylvanica*, *Tubella manauara* n. sp., gemmules, freshwater sponges

Uma nova espécie de *Tubella* (Porifera: Spongillidae) para a Amazônia brasileira: como erros de identificação podem mascarar um potencial complexo de espécies

RESUMO

As esponjas estão entre as piores dispersoras do reino animal, no entanto, algumas esponjas de água doce produzem corpos de resistência chamados gêmulas, que têm sido usados como a principal explicação para a ampla distribuição de alguns desses organismos. Esse é o caso de *Tubella pennsylvanica* Potts 1882, que foi descrita originalmente para Pennsylvania, EUA e foi relatada com uma ampla distribuição, mas com informações escassas e confusas que validem seus registros e seus mecanismos de dispersão. Ela foi registrada para a Amazônia e foi a primeira espécie de *Tubella* reportada fora da Amazônia. No intuito de confirmar o status taxonômico destas ocorrências no Brasil, coletamos espécimes de três locais na bacia amazônica e comparamos suas medidas e características com o material tipo de *T. pennsylvanica*. Com base na análise dos espécimes, consideramos todos os registros para o Brasil de *T. pennsylvanica* como sendo uma espécie diferente, a qual descrevemos como *Tubella manauara* n. sp. Além disso, fornecemos as primeiras imagens das espículas do holótipo de *T. pennsylvanica*. A nova espécie difere do material tipo de *T. pennsylvanica* por apresentar espinhos maiores nas megascleras acanthoxeas, e maior tamanho de suas espículas. Os espécimes de *Tubella manauara* n. sp apresentam variações morfológicas de acordo com o tipo de substrato no qual a esponja se desenvolveu. Este estudo reforça a necessidade de revisão de espécies de esponjas de águas continentais sul-americanas com distribuição em outros continentes.

PALAVRAS-CHAVE: *Tubella pennsylvanica*, *Tubella manauara* n. sp., gêmulas, esponjas de águas continentais

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INTRODUCTION

Sponges may be among the worst dispersers in the animal kingdom, as their ability to reach new habitats almost entirely depends on the lecithotrophic motility of their larvae (Maldonado 2006). The majority of sponge larvae can survive for 3–48 hours (Bergquist and Sinclair 1968) and, for that reason, it is almost impossible for the species to achieve widespread distribution based on this dispersion mode. However, some freshwater sponges produce resting bodies called gemmules, that can withstand adverse conditions for years (Manconi and Pronzato 2007). The presence of gemmules has been used as the main explanation for the widespread distribution of some freshwater sponges, but no additional evidence was produced (Manconi and Pronzato 1996).

Tubella pennsylvanica Potts 1882 is considered to have a widespread distribution, with records from North America, India, and Brazil, although the taxonomic information available on this species is scarce and confusing. The species was described by Potts (1882) from Pennsylvania (USA), without providing measurements of the spicular set. This was the first record of the genus beyond Amazonian boundaries. Annandale (1909) was the first to provide full spicule set dimensions of *T. pennsylvanica* from the material collected in Pennsylvania and identified by Potts. Additionally, Annandale also recorded the occurrence of the species from India. Volkmer-Ribeiro and Maciel (1983) recorded the species in the Amazon and Araguaia – Tocantins Basin and observed that these specimens had smaller megascleres and more conspicuous spine cover in the spicules than North American specimens. Volkmer-Ribeiro and Traveset (1987) proposed the type specimens of the species based on slides found in the Potts collections from the type locality. Potts (1887) reported that the first specimens found were minute incrusting with a poorly developed skeleton, and he probably used the entire original specimen to make the spicule slides. Finally, Ricciardi and Reiswig (1993) recorded the species from Canada with spicules up to twice the size of those analyzed by Penney and Racek (1968) and Annandale (1909) in the USA and Canada. In view of these inconsistencies, our objective in this study was to verify the taxonomic status of *T. pennsylvanica* in Brazil. We analyzed samples of *T. pennsylvanica* from the Brazilian Amazon and compared them with the type material of the species. The analysis led to the detection of a new species of *Tubella*, which is described in here. We also discuss the similarity of the type material with records of *T. pennsylvanica* in other parts of its attributed distribution range.

MATERIAL AND METHODS

Specimens were collected from three different sites in the Amazon basin in Brazil. Two sites are located by the Negro

River, one at Lake Tupé (3°02'44"S, 60°15'12"W) in the municipality of Manaus, in 2022, and the other at Iluminado's Beach (2°57'48"S, 60°37'32"W) in the municipality of Iranduba, in 2020. The third site was at Lake Amaná by the Japurá River (2°34'11"S, 64°35'35"W) in the municipality of Maraã, in 2019. All samples were stored and dried in Falcon tubes. Spicule slides and preparations of spicules for scanning electron microscopy (SEM) were made following Hajdu *et al.* (2011). Spicules were viewed on Tabletop SEM Hitachi TM4000PLUSII from the Zoology Department at Universidade Federal de Pernambuco (UFPE). Micrometric measurements were made of 30 spicules under a Leica microscope DM750 (400x) with an ocular micrometer and informed as minimum, average and maximum length and width. The general morphology, spicules, gemmules, and skeletal organization were compared among habitat and substrate of the collection sites. Our material was compared with images of the lectotype slides of *T. pennsylvanica* (ANSP-PO 4540), which were provided by Dr. Paul Callomon (collection manager of the Academy of Natural Sciences of Drexel University). It was not possible to obtain SEM images of the type specimens of *T. pennsylvanica* because all the type material was used to prepare slides of dissociated spicules. The type materials of the new species described in here were deposited in the Porifera Collection of the Federal University of Pernambuco, Brazil.

RESULTS

Tubella pennsylvanica Potts, 1882

Type specimens: Lectotype ANSP-PO 4540 (slide IV-4).

Type locality: U.S.A.: Lehigh Gap, Lehigh River (Pennsylvania State).

Diagnosis: Species of *Tubella* with acanthoxeas megascleres with blunt edges, small spines spread homogeneously throughout the spicule's surface, and possessing birotule gemmoscleres with uneven diameter rotules.

Description: Thin and incrusting morphology. Dry material has color varying from light yellow to light brown. **Megascleres** slightly curved acanthoxeas/acanthostrongyles with tips that vary from sharp to blunt. The spines are spread throughout the spicule's surface. **Microscleres** absent. **Gemmoscleres** an unequal birotule with the lower rotule five times larger than the upper rotule. The shaft has the same length as the lower rotule. **Gemmules** spheric and covered by gemmoscleres.

Distribution: Species widely distributed in Canada and the USA (Table 1).

Table 1. Micrometric data of specimens of *Tubella manauara* n. sp. and *Tubella pennsylvanica* from different sources.

Species	Region	Megascleres	Gemmoscleres	Source
<i>T. manauara</i> n. sp.	Amazon	68-168\5.2-13.1	2.7-22.6/1.3-9.3/	This study
<i>T. manauara</i> n. sp.	Amazon	54 - 150 \ 3 - 10	21-27	Volkmer-Ribeiro and Maciel (1983)
<i>T. pennsylvanica</i> (lectotype)	Pennsylvania/USA	167.64 \ 7.62	17.8 / 3.8 / 2.5/ 8.	Potts (1887)
<i>T. pennsylvanica</i>	Canada, US	140 - 210 \ 8 - 11	16 - 20 / 3.5 - 8.5 / 2 / 9 - 11	Penney and Racek (1968)
<i>T. pennsylvanica</i>	Canada	100 - 432 \ 6 - 25	13 - 41 / 3.5 - 23 / - / 11 - 41	Ricciardi and Reising (1993)
<i>T. pennsylvanica</i>	India	189 - 242 \ 8.4 - 15,5	18.9 / 8.4 / - / 12.6	Annandale (1909)
<i>T. pennsylvanica</i>	USA	160 - 210 \ 8.4	16.8 / 8.4 / - / 9.9	Annandale (1909)

Values are the minimum – maximum; length/width; gemmoscleres: bigger rotule / smaller rotule / axis/length. Data in μm .

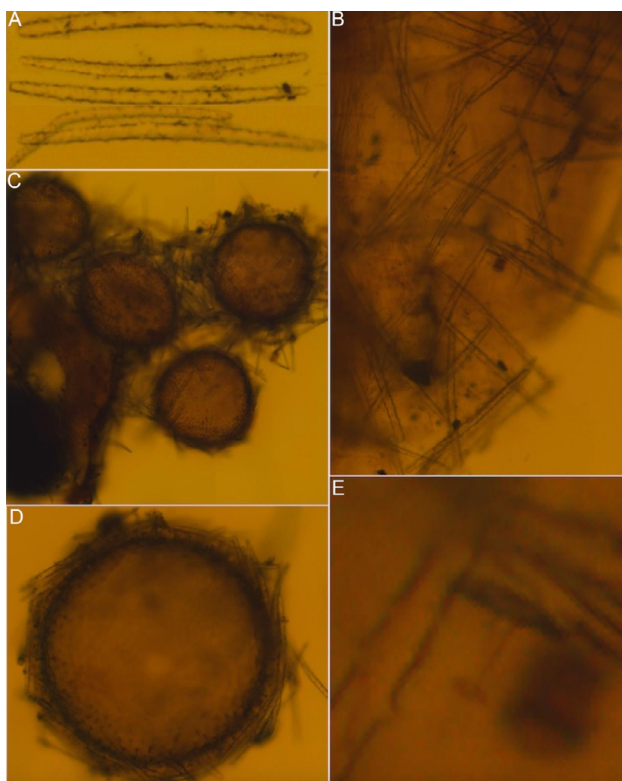


Figure 1. Microphotographs of lectotype slides of *Tubella pennsylvanica* (ANSP-PO 4540): A-B – Acanthostrongyle megascleres; C-D – Gemmules surrounded by megascleres; E – Tubelliform gemmosclere with different size rotules. Author: U. Pinheiro.

***Tubella manauara* n. sp.** Nunes, Custódio & Pinheiro

Zoobank registration: <http://zoobank.org/urn:lsid:zoobank.org:act:F33211C8-75DC-4FFB-B38F-0D70DC44256B>

Synonyms: *Tubella mello-leitãoi* Machado 1947: 134 (in part); Machado 1947b: 2 (in part).; *Trochospongilla pennsylvanica* Volkmer-Ribeiro and Maciel 1983: 257; Volkmer-Ribeiro and Tavares 1993: 187; Volkmer-Ribeiro and Almeida 2005: 126; Batista *et al.* 2007: 620.

Holotype: Amazon basin, Brazil, AM, Iranduba, right bank of Negro River, Iluminado's Beach, UFPEPOR 2947, col. G.S.S. Nunes 22/04/2020.

Material examined: BRAZIL. Amazon basin, AM, Manaus, right bank of Negro River, Lake Tupé, UFPEPOR 2948 (in part), UFPEPOR 2950 (in part), UFPEPOR 2951 (in part), UFPEPOR 2952 (in part), UFPEPOR 2953 (in part), UFPEPOR 2954 (in part), UFPEPOR 2955 (in part), UFPEPOR 2958 (in part), UFPEPOR 2959 (in part), UFPEPOR 2963 (in part), UFPEPOR 2964 (in part), UFPEPOR 2965 (in part), UFPEPOR 2967 (in part), UFPEPOR 2968 (in part), UFPEPOR 2972 (in part), UFPEPOR 2980 (in part), col. G.S.S. Nunes, 06/02/2022. Maraã (Boa Esperança community), Lake Amanã, Japurá River. UFPEPOR 2924, UFPEPOR 2925, UFPEPOR 2926, UFPEPOR 2927, col. G.S.S. Nunes 12/11/2019.

Diagnosis: Species of *Tubella* bearing acanthoxeas megascleres with spines uniformly distributed over the surface of the spicule and birotule gemmoscleres with rotules of uneven diameters.

Description: Incrusting morphology. On adventitious roots, the sponges formed small globules in the root surroundings (Figure 2). In epibiosis with *Drulia brownii* (Bowerbank 1863) and *Metania reticulata* (Bowerbank 1863), the sponge formed a thin crust. The gemmules are visible (Figure 2b). Dry material with color varying between white and clear yellow.

Megascleres are straight or slightly curved acanthoxeas with spines (2.5-5.0 μm) spread throughout the spicule surface (Figure 2c). Length 68-158 μm , width 5-13 μm . **Microscleres** absent. **Gemmoscleres** are birotules with uneven size rotules, the lower rotule (2-9 μm) much smaller than the upper rotule (9 -23 μm), which can be almost vestigial. **Gemmules** vary from circular to concave with coloration varying from light yellow to dark brown or black. Gemmules are arranged with the foramen upwards, diameter 240-400 μm (Table 2).

Etymology: The specific epithet *manauara* is meant to honor those born in Manaus.

Table 2. Micrometric data of examined specimens of *Tubella manauara* n. sp.

Specimen	Locality	Megascleres	Gemmoscleres
UFPEPOR 2947 - Holotype	Iluminado's beach, Negro River	89 - 157.5 / 7.87 - 10.5	12 - 20 / 2.7 - 5.3 / 1.3 - 2 / 6.65 - 13.3
UFPEPOR 2964 (in part)	Manaus, Lake Tupé	89 - 168 / 10.5 - 13.12	9.3 - 22.6 / 2.7 - 9.3 / 1.33 - 2 / 8 - 13.3
UFPEPOR 2980 (in part)	Manaus, Lake Tupé	94 - 152 / 5.2 - 10.5	13.3 - 22.6 / 2.7 - 6.7 / 1.33 - 2.66 / 6.65 - 13.3
UFPEPOR 2968 (in part)	Manaus, Lake Tupé	94 - 147 / 5.25 - 3.12	10.6 - 20 / 2.7 - 6.7 / 1.3 - 2 / 6.65 - 13.3
UFPEPOR 2972 (in part)	Manaus, Lake Tupé	99 - 142 / 5.25 - 10.5	13.3 - 19.95 / 2.66 - 5.32 / 1.33 - 1.99 / 6.65 - 11.97
UFPEPOR 2926 (in part)	Maraaã, Lake Amanã	115 - 157 / 7.87 - 10.5	- / - / - / -
UFPEPOR 2924 (in part)	Maraaã, Lake Amanã	105 - 152 \ 7.87 - 10.5	12 - 21.3 / 2.66 - 6.65 / 1.33 - 2.66 / 8 - 13.3
UFPEPOR 2965 (in part)	Manaus, Lake Tupé	79 - 137 \ 5.25 - 10.5	10.6 - 2 / 2.66 - 6.65 / 1.33 - 2.66 / 8 - 12
UFPEPOR 2927 (in part)	Maraaã, Lake Amanã	94 - 158 \ 5.25 - 10.5	13.3 - 19.95 / 2.66 - 9.3 / 1.33 - 4 / 8 - 13.3
UFPEPOR 2959 (in part)	Manaus, Lake Tupé	105 - 158 \ 7.9 - 10.5	13.3 - 19.95 / 2.66 - 5.32 / 1.33 - 2.66 / 6.65 - 14.63
UFPEPOR 2964 (in part)	Manaus, Lake Tupé	89 - 168 \ 10.5 - 13.1	9.31 - 22.6 / 2.66 - 9.31 / 1.33 - 2 / 8 - 13.3
UFPEPOR 2958 (in part)	Manaus, Lago Tupé	88 - 142 \ 5.25 - 10.5	10.64 - 19.95 / 2.66 - 5.32 / 1.33 - 2 / 9.31 - 13.3
UFPEPOR 2967 (in part)	Manaus, Lake Tupé	90 - 153 \ 6.25 - 10	15 - 20 / 2.5 - 5 / 1.25 - 3.75 / 9.31 - 13.3
UFPEPOR 2963 (in part)	Manaus, Lake Tupé	108 - 145 \ 7.5 - 10	10 - 20 / 2.5 - 5 / 2.5 / 7.98 - 13.3
UFPEPOR 2954 (in part)	Manaus, Lake Tupé	116 - 168 \ 10.5	13.3 - 18.63 / 2.66 - 3.99 / 1.33 - 2 / 9.31 - 12
UFPEPOR 2950 (in part)	Manaus, Lake Tupé	73 - 152 \ 7.87 - 10.5	14.63 - 19.95 / 2.66 - 6.65 / 1.33 - 2 / 9.31 - 12
UFPEPOR 2951 (in part)	Manaus, Lake Tupé	78.8 - 141.8 \ 7.87 - 10.5	14.63 - 18.62 / 2.66 - 4 / 1.33 - 2 / 10.64 - 13.3
UFPEPOR 2952 (in part)	Manaus, Lake Tupé	78.8 - 141.8 \ 7.87 - 13.12	15.96 - 19.95 / 2 - 5.32 / 1.33 / 10.64 - 13.3
UFPEPOR 2955 (in part)	Manaus, Lake Tupé	68.25 - 147 \ 7.87 - 10.5	13.3 - 19.95 / 2.66 - 6.65 / 1.33 - 1.99 / 9.31 - 13.3

Values are the minimum – maximum; length/width; gemmoscleres: bigger rotule / smaller rotule / axis / length. Data in μm .

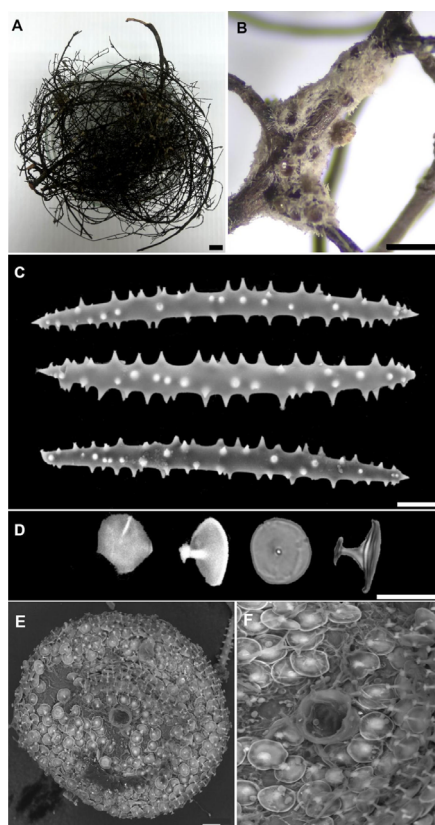


Figure 2. Holotype of *Tubella manauara* n. sp. (UFPEPOR2947). A – Specimen attached to a root network; B – Specimen's white skeleton and gemmules covering the root's surface; C – SEM image of megasclere acanthoxeas with spines distributed along the spicule surface; D – SEM image of gemmoscleres (notice the size variation of the lower rotule); E – SEM image of gemmule; F – SEM image micropyle of gemmoscleres. Scales: A-B = 1 cm; C-F = 20 μm . Credit: U. Pinheiro.

Ecology: *Tubella manauara* n. sp. specimens (UFPEPOR 2948, 2950, 2952-2955, 2958, 2959, 2963-2965, 2967, 2968 2972, 2980) were found in epibiosis with *D. brownii* or *M. reticulata* in the region of the Negro River. They were also found under the adventitious roots in muddy waters of the Japurá River and in black waters of the Negro River. By the Japurá River, they were associated with *Tubella paulula* (Bowerbank 1863) and *Oncosclera navicella* (Carter 1881) specimens.

Distribution: Brazil, Amazon Basin: **Amazonas State:** Locality not informed, Cuieiras River (Volkmer-Ribeiro & Maciel, 1983). Manaus, Negro River, Tupé Lake (Volkmer-Ribeiro & Almeida, 2005, present study). Iranduba, Iluminado's Beach (present study). Maraã, Japurá River, Lake Amanã, Boa Esperança community, **Rondônia State:** Porto Velho, Verde River (Volkmer-Ribeiro & Tavares, 1993); **Mato Grosso State:** Locality not informed, Sete de Setembro River (Machado, 1947; Volkmer-Ribeiro & Maciel, 1983); Araguaia-Tocantins: **Mato Grosso State:** Locality not informed, Tapirapés River (Machado, 1947); Cocalinho, Cristalino River (Batista *et al.*, 2007).

DISCUSSION

Tubella manauara n. sp. differs from the type material of *T. pennsylvanica* by having larger spines (2.5-5.0 μm) in megasclere acanthoxeas, and larger spicule size (Table 1). Our specimens share the same dimensions and characteristics described by Volkmer-Ribeiro and Maciel (1983) and Batista *et al.* (2007), therefore, we consider all records for Brazil of *T. pennsylvanica* as *T. manauara* n. sp. The specimens and gemmule morphology

of *T. manauara* n. sp. varied according to the substrate on which the sponge has developed. When in epibiosis with *D. brownii* and *M. reticulata*, the sponge exhibited a thin incrusting layer, with spherical and yellow gemmules. However, when the specimens colonized the adventitious roots of flooded trees (UFPEPOR 2947, UFPEPOR 2954), they exhibited small globose clusters with the gemmules being mostly concave brown or black, and rarely spherical and yellow. Despite these external morphological variations, we have not found any difference concerning spicule composition and dimensions.

This is the first time that images from slides of the type specimens of *T. pennsylvanica* have been published. When analyzing the images of the type material it was possible to observe a minute distinction in megasclere morphology among North American populations of *T. pennsylvanica*. While megascleres have invariably sharp extremities in images by Reiswig *et al.* (2010) and Miller (2023), they have conical extremities in the type material (see Figure 1a). Regardless of these differences, the spination pattern remains consistent throughout the North American material. The specimens of Ricciardi and Reiswig (1993) from Canada should be revised as they present double the size of the type material. Additionally, their gemmoscleres present variations with equal (rare) and unequal rotules. The records of *T. pennsylvanica* from India by Annandale (1909) were ignored in the revision by Penney and Racek (1968) and other authors until Jakhalekar and Ghate (2014) highlighted the necessity of revision of this material since no optical or SEM images of Indian spicular sets are available. In this sense, we prefer to restrict the distribution of *T. pennsylvanica* to North America, until specimens from India are analyzed.

The co-specificity of widely disjunct populations has been widely debated (Manconi and Pronzato, 1996, 2007, 2008; Pinheiro and Calheira 2020). By having gemmules capable of remaining viable for years, it is believed that all gemmuliferous species have the ability to colonize all continents, such as *Sanidastra yokotonensis* Volkmer-Ribeiro & Watanabe, 1983, with known occurrence in Italy and Japan (Manconi and Pronzato 1996). However, the distribution of species from the Neotropical Region goes against this trend, as they present rates of endemism of up to 91% (Pinheiro and Calheira 2020). From the 67 neotropical species, merely six were recorded beyond South America's boundaries, specifically those with few morphological characters, possibly belonging to species complexes (Pinheiro and Calheira 2020). One of these neotropical species was *T. pennsylvanica*, now identified as *T. manauara* n. sp., which reinforces the need to review South American sponge species with distributions that stretch to other continents.

CONCLUSIONS

Our results showed that *Tubella* specimens identified as *T. pennsylvanica* in the Brazilian Amazon belonged to a new species, that should henceforth be referenced as *T. manauara*

n. sp. The species of neotropical sponges that display broad distribution need to be thoroughly revised, including the North American and Indian material of *T. pennsylvanica*, as we might be dealing with a species complex. Much of the taxonomic information regarding neotropical freshwater sponges was gathered decades or centuries ago and needs to be re-evaluated with modern technologies that improve taxonomic analysis. We thus suggest a thorough taxonomic review of South American sponges with widespread distributions and that have had their status as species for more than half a century without revision. These revisions are likely to reveal sponge species complexes and redefine conservation priorities.

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