GEOLOGICAL AGE OF THE WETLAND ECOSYSTEMS OF CUATROCIÉNEGAS, COAHUILA, MEXICO – A NEW HYPOTHESIS.

EDAD GEOLÓGICA DE LOS ECOSISTEMAS DE HUMEDALES DE CUATROCIÉNEGAS, COAHUILA, MÉXICO: UNA NUEVA HIPÓTESIS.

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ABSTRACT

The famous ecosystems of Cuatrociénegas in Coahuila, Mexico, are considered as very ancient environments with an evolutionary history spanning several million years, in the case of prokaryotic microbes even hundreds of millions of years. The hypothesis of this great geological age of the ecosystems is based on investigations of the flora and fauna but in particular on molecular investigation of the microbiota of the recent stromatolites with great affinities with marine species. This paper aims to bring existing models (in particular the “marine isolation hypothesis”) with respect to the ancient origin of ecosystems of Cuatrociénegas to a critical analysis and offers an alternative hypothesis that postulates a more recent origin to most aquatic communities of Cuatrociénegas. The new hypothesis explains that parts of the prokaryotes that built the stromatolites were introduced to the Valley of Cuatrociénegas probably through aquatic birds not before the Pleistocene (or even Holocene). In contrast to the “marine isolation hypothesis”, the present new model is congruent with recent geochemical, isotopic and hydrochemical studies of water of Cuatrociénegas.

RESUMEN

Los famosos ecosistemas de Cuatrociénegas en Coahuila, México, se consideran ambientes muy antiguos con una historia evolutiva que abarca varios millones de años, en el caso de los microbios procarióticos, incluso cientos de millones de años. La hipótesis de esta gran edad geológica de los ecosistemas se basa en investigaciones de flora y fauna, pero en particular en la investigación molecular de la microbiota de los estromatolitos recientes con grandes afinidades con especies marinas. Este artículo tiene como objetivo llevar a los modelos existentes (en particular, la “hipótesis del aislamiento marino”) con respecto al origen antiguo de los ecosistemas de Cuatrociénegas a un análisis crítico y ofrecer una hipótesis alternativa que postula un origen más reciente de la mayoría de las comunidades acuáticas de Cuatrociénegas. La nueva hipótesis explica que partes de los procariotas que construyeron los estromatolitos se introdujeron en el Valle de Cuatrociénegas probablemente a través de aves acuáticas no antes del Pleistoceno (o incluso del Holoceno). En contraste con la “hipótesis del aislamiento marino”, el nuevo modelo actual es congruente con los recientes estudios geoquímicos, isotópicos e hidroquímicos del agua de Cuatrociénegas.

INTRODUCTION

The Cuatrociénegas Valley in the east of the Chihuahuan Desert (Fig. 1) has been for decades known as one of the greatest hotspots of biodiversity. The reason is the large number of endemic species as well as their unique microbial communities with living freshwater stromatolites. The relatively small valley of approximately 1000 km^2 contains more than 70 endemic species of flora and fauna and is biologically the most diverse site in North America with respect to endemism (Stein et al., 2000).

Almost all authors who have investigated the various taxonomic groups postulated a great geological age of the particular ecosystems of Cuatrociénegas. While botanists saw the origins of the flora (especially the endemic forms) millions of years ago in the Tertiary (Johnston, 1941; Powell and Turner, 1974; Turner and Powell, 1979; Rzedowski, 1978, 1991 and others) researchers of the microbial communities estimate a much longer evolutionary history that began 160 million years ago in the Mesozoic or even earlier (Souza et al., 2006; Souza et al., 2008; Moreno-Letelier et al., 2012, Souza et al., 2018). According to these authors microbial communities of marine affinities come directly from Mesozoic marine environments and have survived in Cuatrociénegas up to the present day. The argument is based mainly on molecular research of the prokaryotes where large numbers of bacteria show biological affinities with marine or brackish-water bacteria.

With respect to invertebrates it is also prevalent the idea that the communities are very old. Taylor (1966), who called Cuatrociénegas mollusks as "... the most spectacularly endemic fauna of freshwater snails known in the Western Hemisphere..." concluded his research on gastropods: "No direct fossil evidence is available for judging the length of isolation of the endemic snails of the Cuatrociénegas area. If degree of taxonomic divergence is proportional to isolation, then the ancestry of some of the fauna reaches deep into the Tertiary, or Mesozoic".

Also W. L. Minckley, one of the great figures in the investigation of Cuatrociénegas, underlines the supposed geological antiquity of biota at this locality, especially aquatic environments with mollusks and crustaceans mentioning: "... yet some of the species in each taxon studied are highly differentiated from their living relatives and must date from extreme antiquity" (Minckley, 1969).

Also, endemic taxa of the herpetofauna and fish species were interpreted as relicts with a "long term isolation of the valley since at least early Tertiary or late mesozoic time" (Meyer, 1973). This author, who analyzed a palynological profile from marshy spring in Cuatrociénegas, concluded that principally the vegetation has not changed in the last 30,000-40,000 years, and added: "The diverse and highly-endemic aquatic fauna inhabiting this valley is also evidence for environmental antiquity and stability…since perhaps the Tertiary..." (Meyer, 1973 p. 994).

In fact, structures like stromatolites, often called "living fossils", and the large number of endemic species of flora and fauna, as well as systematically isolated groups of microorganisms transmit at first glance an image of ancient communities. Finally the geomorphology of the Valley itself as an island enclosed by high cretaceous mountains reinforces this impression of a place isolated for a very long time.

However, to take existing model to a critical analysis with respect to the ancient origin of ecosystems of Cuatrociénegas to a critical analysis and offer an alternative hypothesis that postulates a more recent origin of most aquatic communities of Cuatrociénegas are the main objectives of this article.

MATERIAL AND METHODS

This paper aims to bring about existing hypotheses with respect to the ancient origin of ecosystems of Cuatrociénegas to a critical analysis and finally, develop an alternative hypothesis. Therefore the most of these considerations belongs methodically to geobiology and covers various disciplines including botany, zoology and microbiology. A special focus is given to the geological age and origin of the stromatolites and other microbialites ecosystems in Cuatrociénegas.

To do that, an exhaustive literature survey was done including publications on the Cuatrociénegas aquatic ecosystems. Particular emphasis was placed on the geological development of the basin. Both hypotheses were confronted with the main results of these studies and then checked for congruence with these data.

RESULTS AND DISCUSSION

The Marine Isolation Hypothesis.- The basis of the supposed Mesozoic (or even Precambrian) origin of the prokaryotic communities of Cuatrociénegas comes from the molecular investigations of the stromatolites and other microbialites from the last two decades. Recent microbialites are organo-sedimentary structures closest to the fossil stromatolites. The stromatolites are considered the first ecosystems of the earth and therefore are the focus of recent ecological and evolutionary studies (Centeno et al., 2012). The biological constituents of stromatolites of Cuatrociénegas (Fig. 2) in the form of bacteria and archaea were (and are) studied by various scientists which developed a hypothesis that part of the biota (and of the sea water) of Cuatrociénegas has been trapped since the Mesozoic or even earlier ("marine isolation hypothesis", Souza et

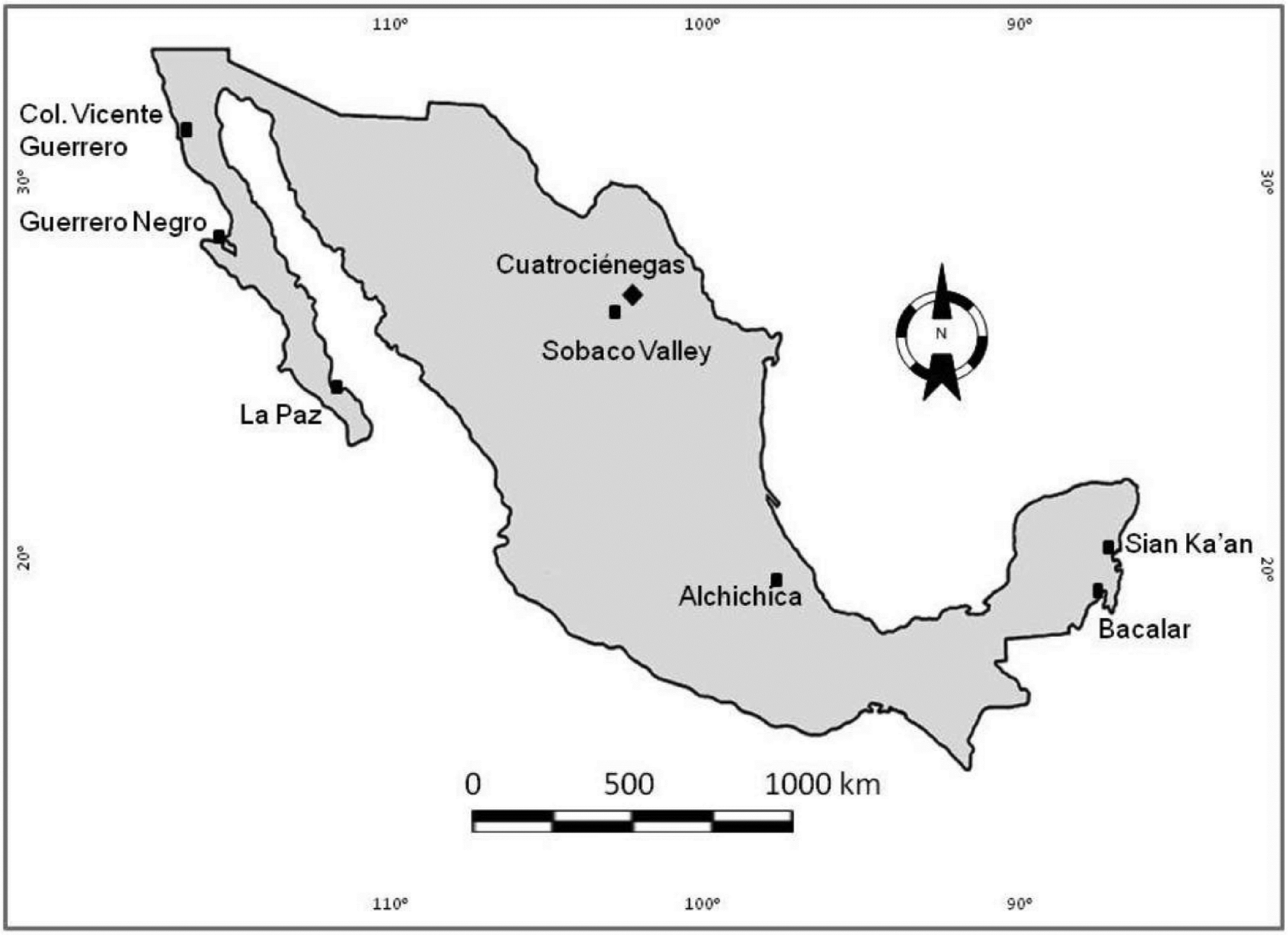

Figura 1. Geographic location of the Valley of Cuatrociénegas, Coahuila and other sites with microbialites in Mexico (Map: Ulises Romero Méndez).

al., 2006; 2008; Moreno-Letelier et al., 2012; Souza et al., 2018). It should be mentioned that this construction is based only on biological affinities of some of the bacteria of Cuatrociénegas with marine forms but lacks any geological, geohydrological or paleontological evidence.

In the most recent publication Souza et al. (2018) stated that "…*These native or 'endemic' species have evolved from ancestors that came to the area in two waves. The oldest colonization event happened 680 million years ago…* [and]*…The most recent one took place while dinosaurs roamed the Earth about 160 million years ago, when geological events opened again the Basin to the ancient Pacific Ocean*".

In the Late Proterozoic, 680 million years ago, the area that it now call Coahuila was near the South Pole and there is no evidence from these periods. Even 160 million years (Jurassic period) ago no basin could be "*opened again"* because there was no basin at all in the area until the Laramide Orogeny formed it in the Eocene, 55-35 m. y. BP (McKee et al., 1990; IMTA, 2005; Molina-Garza et al., 2008).

Considering this scheme about the geological history of Cuatrociénegas an isolation of marine waters for 100 million years or more seems highly unlikely because to the basin (and also all the neighboring valleys) did not exist until the Eocene. Even the preservation of an ecosystem so fragile as stromatolites/microbialites from the Eocene is also highly unlikely.

New geochemical investigations on aquifers and water from the springs of Cuatrociénegas report that the origin of these is a mixture between recharge of the mountains and waters of the aquifers containing mantle hydrothermal fluids that ascend the deep faults caused by asthenospheric upwelling (Johannsson et al., 2004; Wolaver et al., 2013; Mamer and Newton, 2017). The solutes of the Cuatrociénegas waters are mainly SO_4 and HCO_3 with more than 2.0 grams per liter of TDS (Johannsson et al., 2004). Therefore, most of the waters of the springs and wetlands of Cuatrociénegas are not "freshwaters" *sensu stricto*. There is no evidence of trapped Mesozoic or older waters and the authors mentioned explicitly state that the aquifers were recharged with precipitation during the Pleistocene and Holocene. Similar results were already suggested by Cardona et al. (2007) and these authors explained the supposed missing "ocean" (i.e. the central point of the hypothesis of marine isolation!) with evaporation of groundwater in a closed basin under a semiarid climate. These authors mentioned that "…the evaporation of groundwater could represent the missing "ocean" that some biologists are looking for…" (Cardona et al. 2007, p. 6). Paleoclimatic research postulates such conditions in the Chihuahuan Desert (North of Mexico, Bolson de Mapimí) in the early Holocene, not before 8000 years BP (Metcalfe, 2006). In fact, in Cuatrociénegas there are no evidences of trapped Mesozoic (marine) or older water, neither from the authors of this hypothesis nor from other investigations.

Even a possible preservation of marine waters trapped in layers does not automatically guarantee the preservation of biota for nearly 100 (or even 680) million years. In the cases reported by Souza et al. (2006) of supposed survival of bacteria trapped in Permian evaporates and Cretaceous shales it does not mean that these organisms survived from the Permian - as suggested by Souza et al. (2006, p. 6566) - rather that fossil cellulose of bacteria was preserved in inclusions in the mineral halite (NaCl) (Vreeland et al., 1998; Inagaki et al., 2005; Griffith et al., 2008). The bacteria did not survive from Permian but parts of the organic matter were preserved during this extensive period. The preservation of organic matter for hundreds of millions of years is definitely something amazing or even spectacular but ultimately they are fossils, similar to mineralized bones, inclusions in amber or other fossils.

The first concrete doubts of the great geologic antiquity of the ecosystems of the gypsum dunes and its endemic flora of Cuatrociénegas were published by Czaja et al. (2014a). The authors have demonstrated the impossibility of a high geological age of an ecosystem so fragile as terrestrial gypsum dunes and have postulated that the formation of the dunes took place in Holocene. They presented a model in which the recent geological structure of the ecosystem of the dunes coincides with a rapid adaptation of the endemic flora of Cuatrociénegas during the Holocene. Even today it is very common among biologists, especially botanists, to equate a great number of endemic species with a high geological age of the communities. The key point is the erroneous consideration of many organisms in Cuatrociénegas a

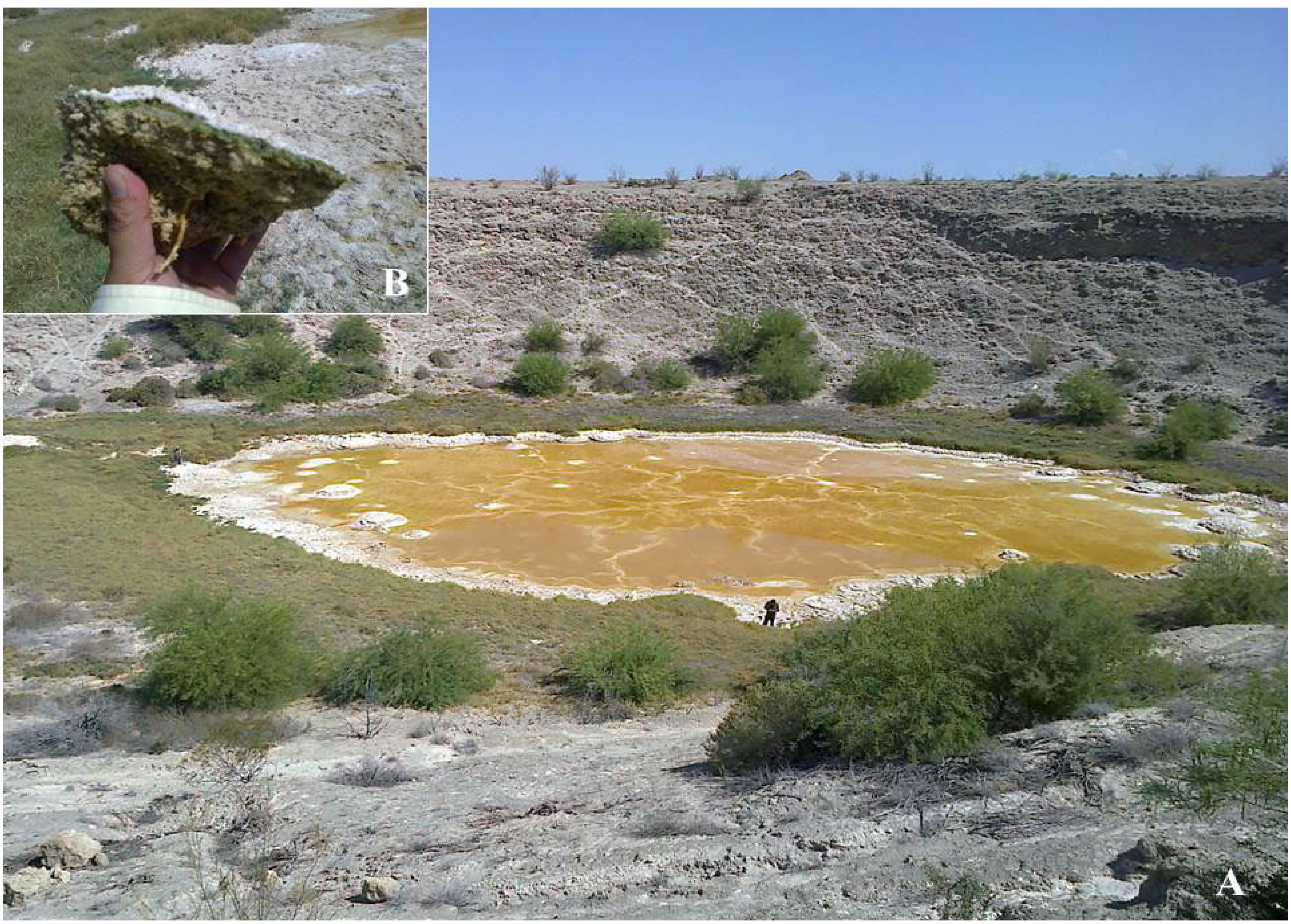

Figura 2. A: Poza "*Caracol*" with microbial mats (B), Sobaco Valley, Coahuila, Mexico (Photo: José Luis Estrada-Rodríguez).

priori as "paleoendemism" with a long evolutionary history instead of neo-endemism (Czaja et al., 2014a). The diversification of many groups, probably caused by abrupt environmental changes of climate and geomorphology during the Pleistocene/Holocene, is typical for formation of such neo-endemic forms. Frey and Lösch (2010) reported cases of formation of meta-populations even within just a few generations.

Hershler (1985), who had investigated the aquatic gastropods of Cuatrociénegas, also postulated a much more recent origin of the endemism of these mollusks. Hershler, contrary to Taylor (1966), Minckley (1969) and Parodiz (1969) mentioned a possible rapid evolution of the gastropods of Cuatrociénegas which had probably begun in the late Cenozoic or later (Hershler, 1985). To reinforce his position, the author mentioned the small scale of endemism at the level of subfamilies and gave several examples of rapid evolution of freshwater snails known from other locations. Nevertheless, the considerations of Hershler regarding the more recent origin of the gastropods did not have great resonance.
Also, the aforementioned pioneer of investigation in Cuatrociénegas, M.L. Minckley, noted that beside the supposed elements of "extreme antiquity" there is another group of many species (especially fish) with little differentiation from adjacent populations (Minckley, 1969). With the advancement of research in Cuatrociénegas and neighboring regions it has been gradually discovered that many species of other groups are not as isolated as previously thought. Especially the recently discovered new paleontological sites near Cuatrociénegas (see below) showed that this valley was in the Pleistocene/Holocene one of many places with similar aquatic ecosystems, including microbialites/ stromatolites in the Pleistocene/Holocene (Czaja et al., 2014b; 2014c; 2015; 2017a; 2017b).

The new hypothesis.- The most powerful argument against the "marine isolation hypothesis" is neither geological nor hydrogeological or evolutionary considerations but the existence of an alternative hypothesis that explains the same phenomenon (marine origin of part of the microbiota of Cuatrociénegas) much more simply and plausibly as well as congruent with the mentioned geo- and hydrological investigations.

According to the new hypothesis presented herein, part of the microbiota of the stromatolites of Cuatrociénegas (and also many invertebrates) has marine affinities because it really comes from the marine/brackish environment. But this marine microbiota ecosystem was not preserved since the Mesozoic Era, like the "marine isolation hypothesis" supposes, instead it was established first in the latest Pleistocene/Early Holocene in the pools (pozas) of Cuatrociénegas and in the neighboring valleys (paleo-lakes). Prokaryotes, responsible for the stromatolites and other microbialites of Cuatrociénegas, were introduced by birds probably from the Gulf of Mexico, Caribean, or the Pacific coast (including associated marginal marine environments such as estuaries or lagoons). The introduction took place most probably in the early or middle Holocene when increased aridity caused a reduction in the size of the lakes and at the same time increased salinity and alkalinity in the small water bodies of Cuatrociénegas and other similar places. Increasing salinity and carbonates saturation in the paleolakes developed a marine like environment that favored the colonization of marine/brackish microbes in a continental water body.

There are no paleontological investigations in Cuatrociénegas itself, but recent findings in neighboring valleys have led to a new perspective to this problem that further reinforces the new hypothesis. In sub-recent sediments of these neighboring valleys several species of gastropods that today are endemic in Cuatrociénegas were found (Czaja et al., 2014b; 2015; 2017a; 2017b). Apparently, in the Early and Middle Holocene there were many sites similar to Cuatrociénegas in the region. These sites contain also contein fossil and (one site) even recent microbialites (Figs. 2a, b) similar to the living forms from Cuatrociénegas. It is noteworthy that also foraminifera such as *Ammonia beccarii* and diatoms such *Campylodiscus clypeus* of marine/brackish origin have been found as fossil in these sites (Czaja et al., 2014b). Similar "marine" foraminifera and diatoms species, which now are abundant in the Gulf of Mexico and the Pacific coast, were also reported from Cuatrociénegas (Bachhuber and McClellan, 1977; Winsborough et al., 2009). Cases of marine like microorganisms in inland areas are known from all continents and are always related to avian transport (Almogi-Labin et al., 1995; Riedel et al., 2011 and others). Riedel *et al*. (2011), who investigated the Aral Sea and several Holocene lakes in West Siberia, mentioned that "...Avian-mediated colonization of lacustrine ecosystems by foraminifera is not an exception, but a regular process". In North America, marine/brackish foraminifera from Estancia Valley were described where the geological situation is very similar to that of Cuatrociénegas, including gypsum dunes (Bachhuber and McClellan, 1977). Also in this case the presence of marine forms was explained by the distribution through birds. Obviously, when the conditions in water bodies of paleolakes have approached or exceeded the salinity of the marine environments, these were (and are) very quickly colonized by marine organisms such as foraminifera, diatoms and no doubt that also prokaryotes are able to survive in these environments. It is certainly no coincidence that some of the endemic gastropods of Cuatrociénegas are halophile species and show a morphologic affinity with marine forms (particularly the genera *Assiminea, Juturnia* and other). Wesselingh et al. (1999) concludes his investigations on two genera of gastropods with the conclusion: "The actual and fossil distribution of the aquatic gastropods… indicate that avian dispersal was an important dispersal mechanism in the geological past". On the importance of birds as distributors Darwin (1859) wrote more than a century and half ago in his masterpiece "The origin of the Species":

"*The wide distribution of fresh-water plants and of the lower animals…apparently depends in main part on the wide dispersal of their seeds and eggs by animals, more especially by fresh-water birds, which have great powers of flight, and naturally travel from one piece of water to another*."

Cuatrociénegas include 144 species of birds (Pisanty et al., 2013) and is one of the resting/foraging places of the migration routes of many migratory birds. According to Wesselingh et al. (1999) there are generally two ways in which birds distribute living organisms: internally, in the digestive tract, and externally, attached to feathers or feet or in clay attached to the feet. They are many investigations on birds as transporters of algae, phytoplankton, snails, bivalves, ostracods, aquatic plants and other organisms (Atkinson, 1972; 1980; Boag, 1986; Almogi-Labin et al., 1995; Wesselingh et al., 1999; Riedel et al., 2011; Palacios-Fest, pers. communication). It is more than evident (but difficult to proof) that the birds together with these organisms also distributed microbes. (Pathogenic microorganisms associated with migratory birds are now one of the many dangers for human society). However, the occurrence of the microorganisms of marine/brackish origin in (saline) "freshwater" environments is a clear evidence in itself.

Although an introduction of the microbiota in Cuatrociénegas through birds was not specifically mentioned in previous papers, Souza et al. (2006) mentioned the possibility of air transport "...via deposition of water droplets or airborne particulate matter". But this possibility was rejected (in favor of the "marine isolation hypothesis") due the great geographic distance and limited rainfall in the region. Although that the aforementioned dispersion of microorganisms and aquatic plants over large distances through birds are known for a long time in the case of Cuatrociénegas, long-distance transport is not required because the Gulf of Mexico and the Caribbean are relatively close by. In northern Mexico countless paleolakes have existed in the transition from Late Pleistocene to Holocene that began to dry-out with increasing aridity during the Holocene (Catto and Bachhuber, 2000; Palacios-Fest et al., 2002; Castiglia and Fawcett, 2006; Metcalfe, 2006; Chavez-Lara et al. 2012; Czaja et al., 2014 and others). Lake to lake communication is a likely venue to introduce microorganisms across northeastern Mexico.

Where do the stromatolites of Cuatrociénegas come from?

Although sites with stromatolites are rare worldwide, they exist in Mexico not only in Cuatrociénegas (Fig. 3), but in several other places (Fig. 1). Recently, it was discovered in the Laguna Bacalar, Quintana Roo, Yucatan, a large area with freshwater stromatolites covering more than 10 km in length (Gischler et al., 2008, 2011). Another location with microbialites in Yucatan is Muyil, in the Sian Ka`an Biosphere Reserve (Centeno et al., 2012). From Guerrero Negro,

Figura. 3. Poza Azul with living stromatolites in Cuatrociénegas, Coahuila, Mexico (Photo: José Luis Estrada-Rodríguez).

Baja California Sur, microbialites were described by Kunin et al. (2008) and Johnson et al. (2012). Also, stromatolites are known for the State of Puebla (Alchichica Crater Lake) stromatolites are known (Kazmierczak et al., 2011). All of these locations have in common a hypersaline environment with a high content of carbonates. Gischler et al. (2008, 2011) was able to prove the importance of carbonate saturation in Laguna Bacalar. In areas of the Laguna with a lower content of $CaCO_3$ microbialites were not recorded. Hypersalinity and carbonate saturation conditions are also characteristic for the stromatolite ecosystems of Cuatrociénegas.

The key to the recent distribution of stromatolites and other microbialites for many authors is the salinity. Monty (1977) , as well as Arp et al. (1999) noted that the Precambrian stromatolites were restricted to hypersaline or intertidal marine environments. Furthermore, according to these authors, the Precambrian oceans had at least twice as much content of salt than modern seas. Shortly before the start of the Phanerozoic the quick decline of these ecosystems presumably began due to the rapid appearance and diversification of grazing and boring invertebrate which today prevent or difficult the growth of the stromatolites in marine environments (Willis and McElwain, 2002). Inland freshwater itself contains countless microbes that are able to form microbialites depending on the water chemistry. Unlike freshwater, the marine water is undersaturated with critical ions and this explains the low abundance of marine stromatolites compared to lacustrine environments (Dr. Joachim Reitner, pers. communication). This explains the abundance of non-marine prokaryotes, microbialites at Cuatrociénegas reported by Souza et al. (2006).

All recent stromatolites are relicts and most of them now inhabit alkaline and hypersaline niches like coastal lagoons and salt lakes in the interior of continents. In Northern Mexico innumerable water bodies of different sizes emerged during and after the Pleistocene glaciations. The vast majority of these lakes dried up after the establishment of the recent weather conditions, ca. 4000 BP (Metcalfe, 2006).

In the search for the origin of the stromatolites of Cuatrociénegas there are, at least, two possibilities:

1. Avian introduction from Atlantic or Pacific coasts (lagoons)

2. Avian introduction from one or more of the other freshwater lakes or ponds

Investigations on prokaryotic communities of microbialites of Mexico seem to favor the first possibility. Gischler et al., (2008) identified more similarities between microbial structure and community among freshwater microbialites of Laguna Bacalar and Cuatrociénegas, than with the marine stromatolites. Also the comparison between the microbial composition of the stromatolites by Centeno et al. (2012) demonstrated that the microbialites of Cuatrociénegas and of the Yucatan Peninsula have, despite the distance of more than 2500 km, large generic similarities. According to these authors, the microbialites that develop in similar abiotic conditions show similar prokaryotic communities. This also means that transfers of microorganisms between localities with similar conditions decrease the problems of adaptation of microbes to new environments.

The stromatolites of Yucatan were dated with ^{14}C and have an age of 7-9 thousand years BP, the highest of all recently dated stromatolites. The results of the cyanobacterial microbialites of Alchichica Crater-Lake, Puebla are also similar, where these stromatolites are dated between 1.1 and 2.8 thousand years (Kazmierczak et al., 2011). The authors had not postulated a preservation of the microbes and water for hundreds of millions of years but they mentioned that the Alchichica alkaline lake reflects hydrochemically Precambrian sea conditions.

Therefore, it can be assumed that the microbes that later formed the stromatolites of Cuatrociénegas had been introduced previously by aquatic birds probably from a freshwater/brackish water lagoon. Although microbial communities show a similarity with those of Laguna Bacalar, Yucatan, it is likely that there were several steps of introduction (now dried) to Cuatrociénegas. Considering the age of dated stromatolites of the Americas and paleoclimatic research in Northern Mexico, we can assume that the time of introduction of the prokaryotes was the Middle or even Late Holocene. The dating of the Stromatolites of Cuatrociénegas is still pending but also far dated recent stromatolites in Mexico are not older than the Holocene.

CONCLUSIONS

The diverse ecosystems of Cuatrociénegas have a much more recent origin than was assumed to date. Many of these communities (stromatolites and dune gypsophytes) are very fragile and vulnerable ecosystems and were established supposedly not before the Late Pleistocene, probably in early Holocene. Not much older are the gastropods that lived a rapid evolution in Cuatrociénegas due to great climatic and geomorphological changes during the Pleistocene. The current hypothesis postulates that parts of the prokaryotes of the microbialites were introduced to the Valley of Cuatrociénegas through aquatic birds probably from coastal sites with stromatolites. The fact that the microbialites (and also snails) of Cuatrociénegas occur in sites regularly visited by migratory birds support the new hypothesis.

Even without applying the principle of parsimony, the new hypothesis explains the origin of aquatic ecosystems in a more congruent manner with the geologic and biologic observations, in contrast to the "marine isolation hypothesis". Recent geochemical, isotopic and hydrochemical studies support our interpretation. This new hypothesis, that still lacks some direct (paleontological) evidences, is a starting point for further studies on the aquatic ecosystems of Cuatrociénegas.

For a long time Cuatrociénegas has been called "The Mexican Galapagos". Thus, "nomen est omen", it appears that the diversity of many ecosystems of Cuatrociénegas are not the product of a long evolution but rather the result of a rapid adaptive radiation just as the famous fauna in the case of the volcanic Galapagos Islands. It should be emphasized that the new hypothesis does not question the results of molecular investigations of the stromatolites of Cuatrociénegas but opposes the interpretation that the long evolution of the prokaryotes happened in Cuatrociénegas since the Mesozoic. This hypothesis does not in any way diminish the importance or singularity of Cuatrociénegas in the Chihuahuan Desert. On the contrary, the results emphasize the vulnerability of a fragile ecosystem like the pools and springs of this beautiful and important place.

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REFERENCES

Almogi-Labin, A., Siman-Tov, R., Rosenfeld, A. and Debard, E. 1995. Occurrence and distribution of the foraminifera *A. beccarii tepida* (Cushman) in water bodies. Recent and Quaternary of the Dead Sea Rift, Israel. *Marine Micropaleontology 26:* 153-159.

Arp, G., Reimer, A. and Reitner, J., 1999. Calcification in cyanobacterial biofilms of alkaline salt lakes. *Eur. J. Phycol*. *34(4):* 393–403.

Atkinson, K.M. 1972. Birds as transporters of algae. *Br. Phycol. J. 7(3):* 319–321.

Atkinson, K.M. 1980. Experiments in dispersal of phytoplankton by ducks. *Br. Phycol. J. 15*: 498.

Bachhuber, F.W. and McClellan, W.A. 1977. Paleoecology of marine Foraminifera in pluvial Estancia valley, central New Mexico. *Quaternary Research 7(2):* 254-267.

Boag, D.A. 1986. Dispersal in pond snails: potential role of waterfowl. *Can. J. Zool*. *64(4):* 904–909.

Cardona, A., Gutiérrez-Ojeda, C., Martínez-Morales, M., González-Hita, L., Mata-Arellano, I., Pérez-Morán, A., Aldama, A.A., Aparicio, J. and Mejía-González, M.A. 2007. Geochemical groundwater evolution in Cuatrocienegas closed semi-arid basin: origin of the missing saline water. Memorias del IAH 2007. Groundwater and Ecosystems, Lisbon, Portugal. 6 pp.

Castiglia, P.J. and Fawcett, P.J. 2006. Large Holocene lakes and climate change in the Chihuahuan Desert. *Geology 34(2):* 113–116.

Catto, N.R. and Bachhuber, F.W. 2000. Aeolian geomorphic response to climate change: an example from the Estancia Valley, central New Mexico. In Mclaren, S. and Kniveton, D., eds., Linking Climate Change to Land Surface Change. Kluwer Academic Press, 171-192 pp.

Centeno, C.M., Legendre, P. Beltrán, Y., Alcántara-Hernádez, R.J., Lidstrom, U.E., Matthew, N., Ashby, M.N. and Falcón, L.I. 2012. Microbialite genetic diversity and composition relate to environmental variables. *FEMS Microbiol. Ecol*. *82(3):* 724–735.

Chavez-Lara, C.M., Roy, P.D., Caballero, M.M., Carreño, A.L. and Lakshumanan, C. 2012. Lacustrine ostracodes from the Chihuahuan Desertand inferred Late Quartenary paleoecological conditions. *Revista Mexicana de Ciencias Geológicas 29(2):* 422–431.

Czaja, A., Estrada-Rodríguez, J.L. and Flores-Olvera, H. 2014a. The gypsum dunes of Cuatrociénegas Valley, Mexico – a secondary Sabkha ecosystem with gypsophytes. In: Khan, M.A.; Böer, B.; Öztürk, M.; Al Abdessalaam, T.Z.; Clüsener-Godt, M.; Gul, B. (Eds.) Tasks for Vegetations Science Vol. 47, Sabkha Ecosystems Vol. IV: Cash Crop Halophyte and Biodiversity Conservation, Springer, 81–92.

Czaja, A., Estrada-Rodríguez, J.L. and Romero-Méndez, U. 2014b. Freshwater mollusks of the Valley of Sobaco, Coahuila, Northeastern Mexico – a subfossil ecosystem similar to Cuatrociénegas. *Boletín de la Sociedad Geológica Mexicana 66(3):* 459–469.

Czaja, A., Palacios-Fest, M.R., Estrada-Rodríguez, J.L., Romero-Méndez, U. and Alba-Ávila, J.A. 2014c. Inland Dunes mollusks fauna from the Paleolake Irritila in the Comarca Lagunera, Coahuila, Northern Mexico. *Boletín de la Sociedad Geológica Mexicana* 66*(3):* 541–551.

Czaja, A., Estrada-Rodríguez, J.L. and Romero-Méndez, U. 2015. A new species of the genus *Mexipyrgus* Taylor, 1966 (Caenogastropoda: Truncatelloidea:

Cochliopidae) from late Holocene spring deposits in Viesca, Coahuila, Mexico. *The Nautilus 129*: 163–168.

Czaja, A., Estrada-Rodríguez, J.L., Romero-Méndez, U. and Orona-Espino, A. 2017a. Two new subfossil species of springsnails (Hydrobiidae: Pyrgulopsis) from north Mexico and their relation with extant species from Cuatrociénegas. *Boletín de la Sociedad Geológica Mexicana 69:* 199–208.

Czaja, A., Estrada-Rodríguez, J.L., Romero-Méndez, U., Ávila-Rodríguez, V., Meza-Sánchez, I.G. and Covich, A.P. 2017b. New species and records of phreatic snails (Caenogastropoda: Cochliopidae) from the Holocene of Coahuila, Mexico. *Archiv für Molluskenkunde 146(2):* 227–232.

Darwin, Ch. 1859. The origin of the species. Oxford University Press, Oxford (1998). 439 pp.

Frey, W. and Lösch, R. 2010. Geobotanik: Pflanzen und Vegetation in Raum und Zeit. Spektrum Akademischer Verlag Heidelberg. 600 pp.

Gischler, E., Gibson, M.A. and Oschmann, W. 2008. Giant Holocene Freshwater Microbialites, Laguna Bacalar, Quintana Roo, Mexico. *Sedimentology 55(5):* 1293–1309.

Gischler, E., Golubic, S. Gibson, M.A., Oschmann, W. and Hudson. H.J. 2011. Microbial Mats and Microbialites in the Freshwater Laguna Bacalar, Yucatan Peninsula, Mexico Advances in Stromatolite Geobiology. *Lecture Notes in Earth Sciences 131, Springer:* 187-205.

Griffith, J. D., Willcox, S., Powers, D. W., Nelson, R. and Baxter, B. K. 2008. Discovery of abundant cellulose microfibers encased in 250 Ma Permian halite: a macromolecular target in the search for life on other planets. *Astrobiology 8(2):* 215–228.

Hershler, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissoacea) of the Cuatro Cienegas Basin, Coahuila, Mexico. *Malacologia 26:* 31–123.

IMTA (Instituto Mexicano de Tecnologia del Agua). 2005. Estudio hidrogeológico de los acuíferos el Hundido y Cuatrocienegas, Coah, 292 p.

Inagaki, F., Okada, H., Tsapin, A.I. and Nealson, K.H. 2005. The paleome: a sedimentary genetic record of past microbial communities. *Astrobiology 5(2):* 141–153.

Johnson, M.E., Ledesma-Vázquez, J., Backus, D.H. and González, M.R. 2012. Lagoon microbialites on Isla Angel de la Guarda and associated peninsular shores, Gulf of California (Mexico). *Elsevier Sedimentary Geology 263:* 76-84.

Johannsson, K.H., Cortés, A. and Kilroy, K.C. 2004. Reconnaissance isotopic and hydrochemical study of Cuatro Ciénegas groundwater, Coahuila, México. *Journal of South American Earth Sciences 17(2):* 171–180.

Johnston, I.M. 1941. Gypsophily among Mexican desert plants. *J. Arnold Arboret. 22(2)*: 145-170.

Kazmierczak, J., Kempe, S., Kremer, B., López-García, P., Moreira, D. and Tavera, R. 2011. Hydrochemistry and microbialites of the alkaline crater Lake Alchichica, Mexico. *Facies 57(4):* 543-570.

Kunin, V., Raes, J., Harris, J.K., Spear, J.R., Walker, J.J., Ivanova, N., von Mering, C., Bebout, B.M., Pace, N.R., Bork, P. and Hugenholtz, P. 2008. Millimeter-scale genetic gradients and community-level molecular convergence in a hypersaline microbial mat. *Mol. Syst. Biol. 4:* 198.

Mamer, E.A. and Newton, B.T. 2017. The relationship between the Cuatrociénegas gypsum dune field and the regional hydrogeology, Coahuila, Mexico: New Mexico Bureau of Geology Open-file Report, 589.

McKee, J.W., Jones, N.W., and Long, L.E. 1990. Stratigraphy and provenance of strata along the San Marcos fault, central Coahuila, Mexico. *Geological Society of America Bulletin, 102(5):* 593–614.

Metcalfe, S.E. 2006. Late Quaternary environments of the northern deserts and central transvolcanic belt of Mexico. *Annals of the Missouri Botanical Garden 93(2):* 258-274.

Meyer, E.R. 1973. Late-Quaternary paleocology of the Cuatro Ciénegas basin, Coahuila, Mexico. *Ecology 54(5):* 982-995.

Minckley, W.L. 1969. Environments of the Bolsón of Cuatro Ciénegas, Coahuila, México. *Science Series, University of Texas, El Paso, Texas, 2:* 1-65.

Molina-Garza, R.S., Chávez-Cabello, G., Iriondo, A., Porras-Vásquez, M.A. and Terrazas-Calderón, G.D. 2008. Paleomagnetism, structure and 40Ar/39Argeochronology of the Cerro Mercado pluton Coahuila: Implications for the timing of the Laramide orogeny, in northern Mexico. *Revista Mexicana Ciencias Geológicas 25:* 284-301.

Monty, C.L.V. 1977. Evolving concepts on the nature and the ecological significance of stromatolites. In: Fossil Algae (ed. E. Flügel). *Springer:* 15–35.

Moreno-Letelier, A., Olmedo-Alvarez, G, Eguiarte, L.E. and Souza V. 2012. Divergence and phylogeny of Firmicutes from the Cuatrociénegas Basin, Mexico: a window to an ancient ocean. *Astrobiology 12(7):* 674-

684.
Palacios-Fest, M.R., Carreno, A.L., Ortega-Ramírez. J.R. and Alvarado-Valdez, G. 2002. A palaeoenvironmental reconstruction of Laguna Babicora, Chihuahua, Mexico, based on ostracods palaeoecology and trace element shell chemistry. *J. Paleolimnol. 27(2):* 185–206.

Parodiz, J.J. 1969. The Tertiary non-marine Mollusca of South America. *Annals of the Carnegie Museum 40:* 1-242.

Pisanty, I., Sosa, C.P. and Gálvez, G. 2013. Agriculture, Water Mismanagement and Ecosystem Transformations in the Cuatrociénegas Valley in the Chihuahuan Desert, Mexico. *Drought in Arid and Semi-Arid Regions*. 199-216.

Powell, A.M. and Turner, B.L. 1974. Aspects of the plant biology of the gypsum outcrops of the Chihuahuan Desert. In: Wauer, R.H. and D.H. Riskind (eds.). Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and México. Sul Ross State University. Alpine, Texas. 315–325 pp.

Riedel, F., Kossler, A., Tarasov, P. and Wünnemann, B. 2011. A study on Holocene foraminifera from the Aral Sea and West Siberian lakes and its implication for migration pathways. *Quaternary International 229*: 105-111.

Rzedowski, J., 1978. Vegetación de México. Editorial Limusa, Mexico. 432 pp.

Rzedowski, J., 1991. El endemismo en la flora Fanerogamica Mexicana: Una apreciación analítica preliminar. *Acta Botánica Mexicana 15:* 47-64.

Souza, V., Espinosa-Asuar, L., Escalante, A.E., Eguiarte, L.E., Farmer, J., Forney, L., Lloret, L., Rodríguez-Martínez, J.M., Soberón, X., Dirzo, R. and Elser, J.J. 2006. An endangered oasis of aquatic microbial biodiversity in the Chihuahuan desert. *P.N.A.S. 103(17):* 6565–6570.

Souza, V., Eguiarte, L.E., Siefert. J. and Elser, J.J. 2008. Microbial endemism: does phosphorus limitation enhance speciation? *Nature Reviews Microbiology 6(7):* 559-564.

Souza, V., Moreno-Letelier, A., Travisano, M., Alcaraz, L.D., Olmedo, G. and Eguiarte, L.E. 2018. The lost world of Cuatro Ciénegas Basin, a relictual bacterial niche in a desert oasis. *eLife 7:* 1–17.

Stein, B.A., Kutner, L.S. and Adams, J.S. 2000. Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, Oxford.

Taylor, D.W. 1966. A remarkable snail fauna from Coahuila, Mexico. *The Veliger 9*: 152-228.
Turner, B.L. and Powell, A.M. 1979. Deserts, gypsum and endemism. In: Arid Land Plant Resources. International Center for Arid and Semi-arid Land Studies. Texas Tech. University. Lubbock, Texas. 96-116 pp.

Vreeland, R.H., Piselli, A.F., McDonnough, S. and Meyers, S.S. 1998. Distribution and diversity of halophilic bacteria in a subsurface salt formation. *Extremophyles 2(3):* 321–331.

Wesselingh, F.P., Cadée, G.C. and Renema, W. 1999. Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera. *Geologie en Mijnbouw 78:* 165–174.

Willis, K.J. and McElwain, J.C. 2002. The evolution of plants. Oxford University Press. Oxford. 378 pp.

Winsborough, B.M., Theriot, E. and Czarnecki, D.B. 2009. Diatoms on a continental ''island'': Lazarus species, marine disjuncts and other endemic diatoms of the Cuatrocienegas basin, Coahuila, Mexico. *Nova Hedwigia*, *Suppl. 135*: 257–274.

Wolaver, B.D. Crossey, L.J., Karlstrom, K.E., Banner, J.L. Cardenas, M.B., Gutiérrez- Ojeda, C. and Sharp Jr. J.M. 2013. Identifying origins of and pathways for spring waters in a semiarid basin using He, Sr, and C isotopes: Cuatrociénegas Basin, Mexico. *Geosphere 9(1):* 113–125.