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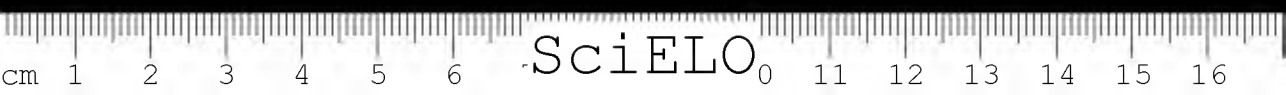
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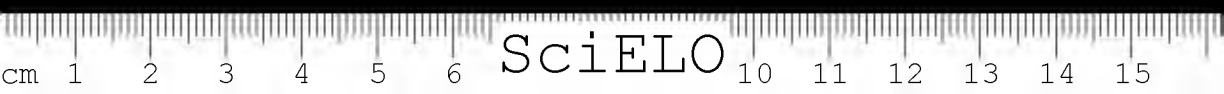
VOL. 3. LENNOLOGIA

RIO DE JANEIRO, GB

Na capa: *Encontro das águas — rios Negro e Solimões.*







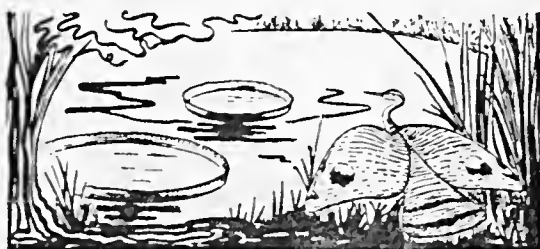
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SÔBRE A

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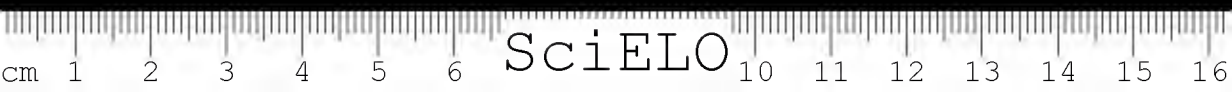
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APRESENTAÇÃO

De 6 a 11 de junho de 1966, na cidade de Belém, Estado do Pará, Brasil, foi realizado o Simpósio sobre a Biota Amazônica, organizado pela Associação de Biologia Tropical, com a colaboração do Conselho Nacional de Pesquisas do Brasil, tendo JOSÉ CANDIDO DE MELO CARVALHO como Presidente Executivo.

O Simpósio homenageava especialmente o Museu Paraense "Emílio Goeldi" que comemorava seu 100.º aniversário.

Ao se iniciarem os trabalhos, achavam-se inscritos no Simpósio 16 países representados por 97 instituições, 256 pesquisadores inscritos para apresentação de trabalhos que perfaziam um total de 22 conferências e 198 contribuições originais. Associaram-se como observadores, até esse dia, 103 pessoas. Nos dias que se seguiram, até o encerramento, o total geral de frequência dos inscritos foi a 611 pessoas. As contribuições originais também aumentaram para 227.

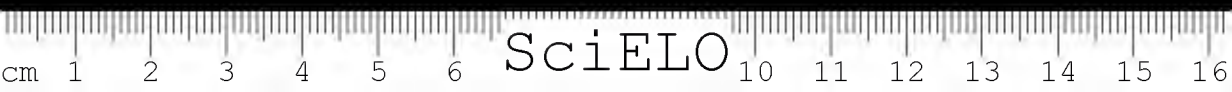
Resolvemos editar estas Atas em 7 volumes, cada qual correspondendo a uma das seções do Simpósio: Geociências, Antropologia, Limnologia, Botânica, Zoologia, Patologia e Conservação da Natureza e Recursos Naturais; serão todos publicados pelo Conselho Nacional de Pesquisas do Brasil, que assumiu a responsabilidade global da edição, da mesma forma como promoveu a realização e apoiou a execução do Simpósio.

Em relação ao Programa do Simpósio distribuído na ocasião e, ainda, ao próprio desenrolar das reuniões de cada Seção, as Atas não incluem necessariamente todos os trabalhos, retirados que foram alguns por motivos vários.

Este terceiro volume corresponde à Seção III (Limnologia) que teve como coordenador HARALD SIOLI (Max-Planck-Gesellschaft, Plön); consta de um total de 226 páginas, 60 figuras no texto e 4 encartes, e divulga 17 trabalhos, dos quais duas conferências. O índice do volume aparece a seguir pela ordem alfabética do sobrenome dos autores, primeiro as conferências e depois as comunicações.

HERMAN LENT

Julho, 1967



ÍNDICE DO VOLUME 3: LIMNOLOGIA

	<i>Pág.</i>
MARLIER, G.	
Hydrobiology in the Amazon region (Conferência)	1
SIOLI, Harald	
Studies in Amazonian waters (Conferência)	9
BECK, JR., William M.	
Comparative limnology of the streams of Florida and the upper Amazon basin	51
BONETTO, Argentino A.	
La superfamilia Unionacea en la cuenca amazonica	63
CARVALHO, Antenor Leitão de	
Novos dados para o conhecimento de <i>Phreatobius cisternarum</i> Goeldi (Pisces, Pygidiidae, Phreatobiinae)	83
CASTEX, Mariano N.	
Bases para el estudio de las rayas de agua dulce del sistema ama- zonico. Nuevas sinonimias de <i>P. motoro</i> (M. H., 1841)	89
CORRÊA, Diva Diniz	
Nemertinos de água doce da região amazônica	93
FITTKAU, Ernst-Josef	
On the ecology of Amazonian rain-forest streams	97
KLAPPENBACH, Miguel A.	
<i>Eupera primei</i> sp. n. de la región del rio Ucayali, Peru (Molusca, Pelecypoda)	109
KLINGE, H.	
Podzol soils: a source of blackwater rivers in Amazonia	117

	Pág.
LEENTVAAR, P.	
The artificial Brokopondo Lake of the Suriname river. Its biological implications	127
MEDEM, Federico	
El género <i>Paleosuchus</i> en Amazonia	141
OLTMAN, Roy E.	
Reconnaissance investigations of the discharge and water quality of the Amazon	163
PARAENSE, W. Lobato	
Moluscos Planorbídeos da Amazônia	187
SATTLER, Werner	
Primeiros resultados de pesquisas etológicas em invertebrados límnicos da Amazônia	195
SCHWASSMANN, Horst O.	
Orientation of Amazonian fishes to the equatorial sun	201
UNGEMACH, Harald	
Sobre o balanço metabólico de íônios inorgânicos da área do sistema do rio Negro	221

HYDROBIOLOGY IN THE AMAZON REGION

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The Amazon watershed is the greatest river basin of the tropical world. It has an extension of 6,5 million square kilometers (i.e. 2,5 millions square miles). Its water flow is the highest in the world and has been computed by Katzer to be near 120,000 cubic meters per second at the mouth during the dry season.

A look on the hydrographical map edited by the Brazilian Institute of Geography (1953) shows clearly the importance of the river network on the structure of the Amazonian region. But the best way to visualize the part played by water in the Amazonian environment, is to fly by Catalina plane over the river from Belém to Manaus. Then the interdependence of soil and water appears without a doubt.

The history of this watershed has been told many times and Professor SIOLI recently gave a summary of the succession of geologi-

cal events which led to the shape of the country we presently know.

The actual fluvial basin is the remain of the huge freshwater lake which extended over the whole "planície" above the region of Óbidos, during the second half of the Tertiary and the first part of the Pleistocene. This lacustrine stage thus lasted a comparatively short time and the present river network lasted still less.

The geographical conditions of the Amazon plain bring about some important consequences, from the viewpoints of Limnology and Biology. One of these is the great extension of the brackish waters in the mouth of the river itself and also on the coast of the Ocean. This has formed an almost ideal starting point for the invasion of the freshwaters of the region by sea animals.

The most conspicuous of these are the Cetaceans. Two species of Dolphins have adapted themselves completely to freshwater condi-

tions in the Amazon; they are the great "pink" dolphin, or Boto, *Inia geoffroyensis* (Blainville) and the lesser grey dolphin or Tucuxi, *Sotalia pallida* (Gervais).

Other very typical sea animals are the shark, the saw-fish and some stingrays, of which the first two are probably marine individuals making migration far into the river (as far as Manaus and Iquitos) while the rays are certainly wholly adapted to a freshwater life.

Among the bone-fishes also some marine families are now completely at home in the Amazonian freshwaters such as the Needle-fishes, the Soles etc.

These marine families have also representatives in some other freshwaters, particularly in the Tropics, but we think that nowhere such an array of marine animals found their way in a freshwater fauna in which a rich true freshwater fauna also exists. (We must not forget the presence of a shark in lake Nicarágua, of Dolphins in India and China, of stingrays in the freshwaters of several tropical countries).

Among the Invertebrates of marine origin, we may mention the Nemertine *Siolineus turbidus* Ev. du Bois Reymond, found by Prof. Sioli in the Tapajós and which belongs to the Order Heteronemertina. As the other freshwater Hete-

ronemertines "*Nemertes*" *polyhople* and *Planolineus exsul*, found respectively in lake Nicarágua and in the Botanical garden of Buitenzorg, *Siolineus* shows strong marine affinities and its presence in the Tapajós points to a recent evolution of this species from a formerly marine environment. Another interesting worm of recent marine origin is the Polychaete *Lycastis siolii* Diniz Corrêa found by the same collector in the Tapajós. This species must be, according to CORRÊA (1948) not an old marine relict, but a "young" marine immigrant.

As the knowledge of the freshwater fauna is still in its infancy, it is likely that many more instances of such marine invasions will be found in the future. Very different conditions prevail for instance in Africa where most of the continent is high above sea level and where marine migrants do not enter the freshwaters very far inland.

Another geographical condition of great importance and having both direct and indirect consequences, is the very small slope of the Amazon and its great affluents and the very flat nature of the basin. The river itself has a slope of 1/100,000. But as the rainfall is very high and seasonal in the highest reaches of the Amazon, proper and its affluents, the level fluctuates

tuations are very powerful (They may reach 15 meters annually in Manaus on the lower Rio Negro).

At high water time, the waters of the Amazon and of its big affluents flow over the banks and flood the neighbouring land, entering the forests and backing up the waters of the minor affluents. These, in turn, swell and enter the surrounding country. This huge inundation area is thus accessible to the river animals which invade the formerly terrestrial environments where they feed and probably spawn. This explains how fish can find very favourable life conditions during the high water times. We know that this occurs also in several other tropical regions as in the African big rivers (principally the Niger and the Nile) and in the South Asian sub-continent when the Mekong shows very important level fluctuations. But all these countries are very much more populated and deforested in such a manner that fish doesn't find as favourable feeding grounds as in the huge Amazonian forest.

This third geographical feature of biological importance is the absence of old lakes in the Amazonian plain. All the hitherto known amazonian lakes belong to one or two types, both of which are shallow and very young.

The first type is the "varzea lake" which is a lake in continuous or periodical relation with the Amazon or with a white water affluent and receives water from these rivers either by a permanent "furo" or by the periodical invasion of its effluent at high water time.

The second of these types is the "terra firme" lake which flows into the Amazon by a long effluent. It may swell into a large lake when its effluent is dammed by the high waters of the Amazon but it never receives white waters from the latter.

Both types of lakes are thus very dependent of the river itself and it is thus not surprising that no real lake fauna could be evolved in them, comparable with the particular lake fauna of Africa, for instance.

The fishes of these lakes are those of the rivers, or may be a little less numerous. But these lakes are very important spawning grounds for many of the river fishes most of which have migratory habits. These fish migrations in the amazonian waters are well known (the piracema) and are probably obligatory for the success of reproduction of most species (as it is for most Indian Carps in the Asian Continent). If this is confirmed, the scarcity of lake and pond species able to spawn in confined con-

ditions may be an obstacle to the use of Amazonian fishes for fish culture.

In fact one could think that after the lapse of thousands of years, or after tectonic movements take place, the Amazonian region will be very rich in lakes, as so many deep drowned valleys are known to exist in this basin. We know, personally, no lake out of reach of the rise of the Amazon or its affluents and which could have an independent existence from that of the rivers.

The orographic conditions of the basin have another result. No true lakes, with the classical characters of the deep lakes, can be found. From the theoretical considerations developed by LÖFFLER, we should expect that a deep lake in this equatorial forest of climate Af and Am would be oligomictic; it means that it would mix and circulate at irregular intervals, owing to the great stability due to the high water temperature.

In fact most of the lakes studied by BRAUN and the author were of the polymictic type, being too shallow to develop a great stability. Of course this limnological condition has very important consequences on the nature of the fauna.

Apart from its freshwater fauna directly from marine origin, the Amazonian freshwaters harbour an

extraordinary rich freshwater fauna. It is yet not well known, except for some particular groups and we may suppose a great number of species remain to be found.

Let us consider the class of Fishes to which many studies have been devoted. It is well known that a great part of the aquarium fishes are of south american and particularly amazonian origin. More than 1500 species of fish have been described from the area, a respectable number considering that it belongs to one watershed only. If we compare it with other freshwaters in the Tropical regions, we see that the river Congo harbours a little more than 500 species (not included the fauna of Lake Tanganyika), the Ganges 300, the Nile 200 etc.

South America has been isolated from North America during the greater part of the Tertiary period and was united with the latter Continent only in the Pliocene. Its freshwater fish fauna is very much endemic, owing to this long isolation and we find that many fish families are peculiar to South America, and have found in the huge Amazonian tertiary lake and the subsequent water network an ideal distribution area. Such are the Gymnotids, many Siluroid families and the greater part of the Characids.

From the point of view of the chemical and physical conditions, the amazonian waters represent, as is well known, one of the following three types. The "white" waters rivers are loaded with a rather great quantity of silt, which they collect in the crossing of the Andes. Such are the Amazon proper, the Madeira; compared with other amazonian rivers these waters are relatively rich in salts. This assessment is, of course, to be taken with some caution.

According to SIOLI, the total hardness (expressed in German degrees) of the Amazon around Santarém, varies between 0.65 and 1.27. This compares very well with the hardness of river Congo near Stanleyville, which is around 1.4 but is well below that of the river Nile at Cairo, which reaches 5.0.

The second type are the "clear" water rivers, coming from much older ranges which are the central brazilian plateau and the Guyana plateau. These do not give rise to great mineral transport and very soon these rivers loose their load and carry only crystal-clear waters (river Tapajós). These contain variable quantities of dissolved salts but generally lower quantities than the white waters (according to SIOLI the Tapajós has a total hardness of 0.31 to 0.82, German degrees). Their pH is also general-

ly low when the rivers do not cross geological deposits particularly rich in calcareous salts as are the Carboniferous layers of the Middle Tapajós.

As the anorganic nutrient content of all waters flowing in the Tertiary layers of the Série das Barreiras is always very low and as the limestone rich layers of the Carboniferous period are of a reduced extension we may safely assume that the principal source of dissolved nutrients is the Andean and Subandean region where the Amazon proper and some large white-water affluents have their headwaters.

The "black" waters have a brown colour given to them by the leaching of the humic soils in the forest swamps called Igapos. These waters are generally rather transparent, very poor in salt and of a very low pH (4.4 and even less).

From the biological point of view, we must point here to the influence of these chemical properties of the waters on their fauna. As an instance we find many fish species in the black water rivers, even if they are less numerous than the white waters species. But it is generally admitted that such low pH values around 4 would preclude even the existence of fishes.

Indeed it is difficult to understand how the hemoglobin of these

animals can be saturated with oxygen in the presence of such acidic waters and how the blood can get rid of its dissolved CO_2 . Anyway it seems, according to the experiences of WILLMER, that the effects of water acidity are less pronounced in warm than in cold water fishes.

A last characteristic of the Amazon rivers is to be found in the cycle of production of plankton in the lakes formed on the banks on in the course of the affluents of the river.

It has been found by the author that the primary productivity in the waters of the white water lakes may undergo an annual cycle according to the fluctuations of the lake level and its relations with the Amazon. It is, of course, easy to understand knowing the relative riches of these white waters, that their invasion in the lakes may bring about a renewal of the nutrient resources of the environment. This renewal is followed by an increase of the phytoplankton standing crop.

We thus arrive at the conclusion that one of the most important of the factors in the amazonian environment is related to fluctuations of the white waters and the penetration of these waters in the lakes. Knowing this, we understand how imperative it is for the limnologist and the fishery expert

to have a good hypsometric survey of the Amazonian basin with the contour lines very close to each other.

It has been said above that nutrients brought by the waters are always rather scarce but this seems in disagreement with the great wealth of the fauna one finds in the Amazon basin. This apparent paradox is explained when studying the alimentary regimes of the fish of the rivers and lakes.

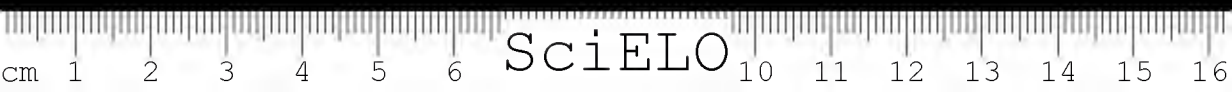
These fishes are found to feed frequently on items which are derived not from the aquatic biological cycle but from the terrestrial environment of these waters, i.e. from the shore forest. Many species feed directly on leaves, seeds, fruits or on terrestrial insects or other invertebrates which take their subsistence in the riparian vegetation. It is thus the forest which maintains the fish fauna at its present high level. All alterations to this littoral forest could mean the disappearance of most fishes and of a valuable food resource for the human population.

This points to the necessity of respecting the littoral forest while planning development and agricultural schemes in Amazonia, considering the Hylaea as a most valuable element even in the aquatic resources of the country. Any attempt to fell and burn the forest without due care to replace the

burned or exported nutrients would mean a loss of productivity in the waters.

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STUDIES IN AMAZONIAN WATERS

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(With 10 text-figures)

As no other country, no other landscape in the world, the Amazonian region is formed and characterized by its amount of waters. The Amazon is not only the mightiest river on earth, but also the final collector of the largest network formed by innumerable creeks, rivers and streams, which drain an area of about 7 million square kilometers situated in a very wet climate and covered by the most extensive, continuous, tropical rain-forest.

Thus it is no wonder that the history of the studies of the Amazonian waters starts with the history of the discovery and conquest of the whole country of Amazonia itself, that its very beginning coincides with the first expeditions of the Spanish and Portuguese discoverers and "conquistadores".

While Marco Polo travelled on foot or on animals back on ancient

roads and paths to the fabulous Middle Kingdom, while the Boers penetrated South Africa, and while pioneering settlers of North America made their way to the Far West, both on their four-wheelers of the traditional stile of Central — and Northwestern Europe, while Siberia was conquered by the mounted Cossack posses, while Arabs crossed Arabia, the Sahara and the Near East on camel-caravans, while the great discoverers of Central Africa made their "Safaris" with a more or less numerous train of barefooted negro-carriers — the Amazonian region was discovered, opened and conquered for Christian-European colonization and civilization, from the late Middle Ages up to recent times, by expeditions and travellers, who used the long and numerous waterways as the only practicable

possibility to penetrate the endless, dense jungle.

By this way, the waters of Amazonia were the first of the factors which compose the Amazonian landscape and with which the pioneers came into contact, and the knowledge of the water-courses was a *conditio-sine-qua-non* for success of any colonization scheme.

The history begins with the strange adventure of Don Francisco de Orellana, who, in February 1541, started from Quito, in the high Andes, with an expedition, lead by Gonçalo Pizarro, in search of the land of "El Dorado" and of cinnamon. With 4000 Indians and 220 Spaniards they went eastward, down the mountains to the moist and warm lowlands of the unknown land. But they found neither El Dorado, the legendary gilded king in the silvery town of Manoa, nor the cinnamon-trees. Instead, the expedition ran short of food and got into extreme emergency. Pizarro and Orellana separated, and the latter, driven by famine, continued with his men in eastern direction in vain search for food. On the banks of the "Rio de los Omáguas", now Rio Napo, on its confluence with the Rio Aguárico, he ordered to build a boat, a "bergantim", for still exploring some stretches down the river. By the end of 1541, Capitán Francisco de Orellana embarked in it toge-

ther with 55 Spanish soldiers and two fratres, one of them being FREY GASPAR DE CARVAJAL, who became the chronicler of the voyage.

They went down that river, hoping to come back within a few days. But also there they could not find anything to eat, and the only possibility that remained for Orellana and his weakened men was to continue the voyage on board of that boat, down the river with the current which somewhere was to flow into the ocean. And Orellana decided to do so.

So there began one of the most adventurous and remarkable voyages ever made by man which led to the discovery of that enormous river which at first, received the name of "Rio de Orellana".

Frey Gaspar de Carvajal wrote down what happened during the trip, but he was a typical child of his time and a representant of his profession. He reported what happened on board, what the Spaniards did and how they suffered and invoked the Holy Virgin etc., but practically nothing stands in his narrative concerning the characteristics of the river or the landscape. He always describes more and more only the hunger, the attacks on Indian villages which became less rare and finally very numerous as they descended the river, and where they killed the Indians who did not achiev to flee,

and how they burnt the houses of them. Is it a wonder that the natives got more and more hostile, the more the discoverers came down the river? The communication-system of the Indians, consisting of messengers and bush-drums, had the fame of robbers and killers go ahead of the desperate Spaniards...

Only the report on the discovery of the Rio Negro, in the eve of St. Trinity of 1542, written by FREY GASPAR DE CARVAJAL, is worth reading for us. He wrote: "On the same day, starting from there and continuing our voyage, we saw the mouth of another big river, on the left side, which entered that one in which we navigated, and of water as black as ink, and therefore we gave to it the name of Rio Negro. It ran so much and with such ferocity that for more than 20 léguas (110 km) it made a strip in the other water without mixing itself with that one."

These are the laconic words by which, for the first time in history, the biggest tropical black-water-river has been made known to European civilization.

The voyage of Orellana and his men turned more and more a flight down the river, a flight from hunger and the hostile Indians. Finally, on August 26th, 1542, the mouth of the Amazon was reached. FREY GASPAR DE CARVAJAL writes:

"We came out of the mouth of that river between two islands, separated from each other by 4 léguas (22 km) of width of the river, and the whole, as we have seen above, has from one side to the other more than 50 léguas (275 km), while the fresh water enters into the sea more than 25 léguas (137,5 km). The tides grow and fall 6 to 7 braças (10 — 11 1/2 m)."

The greatest river of the world was discovered — strange to see, from its headwaters at the feet of the Andes to the ocean. But almost nothing about it had been observed but its colossity, its shores which were inhabited by very numerous "savages", and the existence of some affluents, one of them with remarkably black water.

It took some time, till the voyage made by Francisco de Orellana, was followed by the next expedition which shall only be touched.

Pedro de Orsua started from Cuzco in 1560 and descended the Rio Yutaí into the Yuruá, and from this river at 5° S into the Amazon. But not even a report of this voyage has been left.

Much later on, Juan de Palácios came from Quito down the Rio Napo, but he reached only the "Provincia de los Encabelados" where he was killed by the natives.

Only in 1636, i.e. almost 100 years after Francisco de Orellana,

there started, from Quito, two priests together with 6 soldiers on the next voyage. They succeeded in repeating the achievements of the discoverer and finally reached Grão Pará, where the Portuguese had already a fortified "praça", which in the following time, developed to what is now the city of Belém.

This voyage gave rise to the famous expedition of Pedro Teixeira, a Portuguese general in Grão Pará, in 1637-38, who was the first to ascend the river from Belém to Quito and then return the same way.

At that time, the lower Amazon up to the Tapajós had already been well known, not only to the Portuguese, but also to the Dutch and the British, who had started to build fortresses and to occupy parts of the country. Pedro Teixeira had already fought those intruders and gone up the Amazon and the Tapajós for punishing the natives and catching slaves. By such experiences, he was well prepared for that great, new enterprise for which he took with him a total of around 2000 persons in 47 canôas "of good size".

There exist two reports on that expedition, the one by ALONSO DE ROJAS, the other one by P. CRISTOBAL DE ACUÑA S. J., which are in part identical, in part complete each other mutually. Father Cristobal de Acuña had been ordered,

by the Vice-Rey del Peru to accompany Pedro Teixeira on his way back to Pará, while Alonso de Rojas seems not to have participated in the expedition. The most visible result for our interests — which do not coincide with the political aims of that expedition — is the first map of the Amazon, idealized and, probably, designed by the pilot of Pedro Teixeira's fleet.

But not only that first map is worthy of note for us, the reports contain so many excellent observations of peculiarities of our big river and its surrounding landscape — naturally also mistakes — that for reasons, I shall explain afterwards, it seems to me worth while dedicating more time to them and to cite some parts in extenso.

It is already another spirit, different from that of Frey Gaspar de Carvajal, when Father CRISTOBAL DE ACUÑA writes in his preface that they arrived in Pará, on December 12th, 1639 "after having transpassed the mountains which feed the beginning of the great river, and having travelled on its waves till the mouth of 80 léguas (440 km) width, after having written down with special care all what is notable, after having determined its height and annotated the names of the affluents, having verified the peoples who live on the banks, seen the fertility and admired the re-

sources, having experienced the climate, come into contact with the natives and, finally, after not having neglected what all there happened and of what they had been witnesses."

We may say that, with the chroniclers of Pedro Teixeira's voyage, there began the exact and objective observation, the study in a modern sense, of Amazonia.

CRISTOBAL DE ACUÑA soon starts to discuss the origin of the Amazon: "Some people want the Marañón as source with its beginning in the Cordilleras de Guanuco de los Caballeros, 70 léguas (385 km) from the "Ciudad de los reys", with the lake Lauricocha; other ones want the sources of the Rio Macoá and with them the Caquetá as its origin." But this is rejected by Father Acuña, and he means that in a distance of 8 léguas (44 km) from Quito, between the mountains Guamamá and Pulca, there are two lakes, 20' below the equator-line, from which, in direction to the south, the Amazon has its origin.

According to him, the length from the spring to the mouth into the sea is 1356 léguas castelhanas (7458 km), "well measured". Running in wide curves, the amplitude and width are very different from 1 — 2 léguas (5,5 — 11 km) and partly much more, to 80 léguas (440 km) in the mouth. The

narrowest place has a little more than 1/4 léguas (1,4 km), at 2 2/3° S and 360 léguas (1980 km) from the "lake" (what probably must be taken for the sea). — From the mouth to the Rio Negro, in a distance of almost 600 léguas (3300 km), the main channel is always at least 30 — 40 braças (50 — 65 m) deep; at some places one does not find any ground. Above the Rio Negro the depth varies among 20, 12, well above 8 braças (35; 20; 13 m), but it is always deep enough for boats. There are innumerable islands, commonly of 4 — 5 léguas (22 — 28 km), other ones of 10 and 20 léguas (55 and 110 km) etc., and there are also many very small ones, which serve the natives for the plantations while on the larger ones, they have their settlements. "These small ones, sometimes also the greater islands or a great part of them are inundated every year by the river which fertilizes them in this way with its mud so that they can never be called sterile even if there is claimed from them the same production of corn and mandioca in many subsequent years."

There are many fishes "which the natives catch with incredible abundance every day in the river. King of all fishes, however, and by which the whole river from the source to the mouth is inhabited, is the "Peixe boi" ("ox-fish"),

which has only the name of a fish, for there is nobody who, eating it, does not think it to be real meat. It is of the same size like a 1 1/2 years old calf and, if it had horns and ears, its head would not differ from a calf's one. Its whole body is covered with rather short hairs like soft bristles, and it moves in the water with two short arms, which, looking like shovels, serve it for sculls. Under these "arms" the female has its teats, which it gives to the young ones, it has born. The warriors make so strong shields of the very thick leather that, if the leather is well curried, no bullet can perforate them. This fish lives only on herbs, which it grazes like a real ox, and thus its meat gets so highly nutritious and has such a good taste that a man becomes more satisfied and stronger by a small amount of it than by double the quantity of goat-meat. It cannot stay under water for a long time, and so it lifts its snout out of the water for taking breath, wherever it is swimming. And thus this fish promotes its total extermination, because it enables its own enemy to find it very quickly; the Indians become aware of the animal and follow it in small canoes, waiting that it will lift its head out of the water, in order to draw a deep breath, and then they kill it with their har-

poons which they make of mussels."

This description of the manati is very exact, and till Alfred Russel Wallace, who, in 1848 — 1852 made a voyage on the Amazon and the Rio Negro, there was nobody to excel it.

The number of water-turtles must have been enormous at that time: "They (the Indians) catch these turtles in such a quantity that there is not even one of those fences" (in which the Indians store the turtles alive) "which would not contain turtles in a number from 100 upward".

ACUÑA describes also Indian fishing methods, as fishing with timbó, or harpooning with arrows, equipped with a swimmer, which they throw with their hands. Interesting is his description of the electric eel: "Many fishes have special peculiarities, e, g. one, the Indians call Peraque, has the shape of an enormous eel or better of a small Conger. And the one who touches this fish, begins to tremble all over like attacked by shivers of Malaria, and it lasts as long as there is a contact between the fish and this person, stopping immediately when loosing the fish."

Naturally, since it was one of the main interests of his time, ACUÑA speaks of enormous riches in gold, "for all rivers and springs etc., which run from the Andes to

the Amazon at a stretch of 600 léguas (3300 km), come from areas which are the richest in silver and gold on earth."

After him, the climate is "temperate", and the winter is not caused by changes in the position of the planets and the sun, which rises and sets always at the same hour, but by floods which impede agriculture and the harvesting of fruits of the earth for some months. There are no "rotten airs", and "if there were no plagues of mosquitos which in many zones are so innumerable, one could call the river at the top of one's voice an enlarged paradise."

In his narrative he gives a circumference of 4000 léguas. (22000 km) to the whole Amazon Region, and his report contains many details about the affluents of the Amazon, and the Rio Negro called his great interest. At the mouth it is 1 1/2 léguas wide (8,25 km). Its black water fills half the width of the bed of the Amazon and accompanies it for more than 12 léguas (66 km) where one can clearly distinguish between the water of the Amazon and the one of the Rio Negro, till it is mixed up into the turbid water of the Amazon. Here we also find the first mention of the connexion with the Orinoco, the famous anastomose through the Cassiquiare: "One arm which that river" (the Rio Ne-

gro) "sends out through which, after informations, one comes out in the Rio Grande in the mouth of which, in the northern ocean, are the Dutch. . .".

This Rio Grande should be the Rio Doce or more probably, the Rio Felipe, but ACUÑA affirms intensively that it is not the Orinoco. The other chronicler of Pedro Teixeira's expedition, ALONSO DE ROJAS, however, has a different opinion, and he writes that "there are people who think this river to be the famous Orinoco."

Acuña and Rojas have been unanimous that the rivers and the whole country are very rich, that the soils are very good ones, that there are many nations of "bárbaros", and that all together is by far larger and richer than whole Peru. This opinion of infinite riches, has not yet died out completely, and it has only been corrected by scientific studies in the last few decades. May be that their reports contain some intentionally added political influence, because ACUÑA was a Spaniard and the lower Amazon belonged to Portugal while both nations were interested in the still unoccupied western part of Amazonia. ROJAS even beats Acuña in his enthusiastic description of the splendor and the riches of the country: "The discoverers of the Amazon maintain that its campos seem to be paradises, its islands

gardens, and that, if art would support the fertility of the soil, these parts would be well treated paradises and gardens...". "The river is abounding in fishes, the mountains are extremely rich in game, the air is overabundant in birds, the trees are full of fruits, the campos give very rich crops, and the earth is full of mines." And he tells of an enormous number of Indians — who, later on, after the conquista, diminished very rapidly so that Antônio Vieira writes in the 17th century that, within 30 years, more than 2 millions of the Indians on the lower Amazon and on the coast till São Luís do Maranhão were killed...

This circumstance does not belong to our theme, but I had found it in the old reports and I did not want to withhold it from you, because there may be some ecological background in the fact that in the following time during the European occupation and introduction of European methods of treatment of the land, of agriculture, of exploitation of the nature etc., the number of the neo-Brazilian and the surviving Indian population always remained extremely low and even today it does not exceed two millions in the whole States of Amazonas and Pará and the Territories of Roraima, Rondônia and Amapá together, i. e. in an area of more

than 2 1/2 million square-kilometers...

As already mentioned, all main points of posterior studies of Amazonian waters are already touched in the reports on Pedro Teixeira's expedition, written by ACUÑA and ROJAS, as e. g.:

Cartography and Hydrography (map by the pilot of the fleet and descriptions of a great number of affluents);

River anastomoses (first mention of the connexion with the Orinoco);

Morphology of the Rivers (width and depth);

River-types (black-water of the Rio Negro);

Rôle of the Várzea (fertility by annual flooding);

Nutrient-household and Ecology of the whole Region ("very good" soils anywhere, number of native population).

To continue the history of studies of Amazonian waters, it is now more instructive not to report simply in a chronicle sequence, but to follow up the development of each of those different topics.

After the first map of the Amazon according to the pilot of Pedro Teixeira's fleet, which contained the course of the Amazon itself and the mouths of many of its tributaries, it is only natural that the most intelligent and broad-

minded among the early missionaries and travellers tried their best to contribute to a more exact and more complete knowledge of the big river-system.

One of the next original and famous maps of that time, in fact the 5th map of the Amazon at all, was the one by Pater Samuel Fritz, S. J., of the year 1691.

Further on, not only the missions, but also the governmental authorities were more and more interested in better maps of our region, and there appeared maps, not only from the main river with more details, but also from some affluents.

When in 1743/44 Charles Maria de la Condamine, who had been sent to the equatorial region of South America for measuring the first 3 degrees of a meridian, came down the Amazon from Quito to Pará, he designed a map of the Amazon too, and so did other travellers of that period. The knowledge of the immense Amazonian river-system grew more and more, and also in Europe there were printed new maps of that region, but it shall not be said that each new map, which appeared, signified a progress. So it happened that, for giving their maps a more impressive and more complete appearance, the designers also mixed fantasy into the known facts which were not too numerous.

Also the voyages of the first scientific explorers of Amazonia did not too much to improve the cartography of our region. The travellers described, often excellently, the geographical conditions, the flora etc., corresponding to their special interests and knowledges, but new measurements of the rivers were very scarce.

A systematic mapping of the affluents of the Amazon started only in the second half of the last century, when some of the scientific travellers dedicated a good part of their time and energy during their trips to this purpose. The common method, they used, was the survey by the help of a watch and a compass when they travelled in boats on the rivers. I cite here only the excellent map of the Rio Xingu, made by Dr. O. CLAUSS on the occasion of the ethnological expedition of Karl von den Steinen; it contains exact geographical coordinates for many points, indications of the width of the river, wherever possible, and even some profiles of the river-bed.

Perhaps the most important progress in the knowledge of the courses of a good deal of tributaries to the lower Amazon was achieved by the French explorer, Henri Anatole Coudreau and his wife, Olga Coudreau, who, after having lived and worked in the Guianas for more than 10 years, began to explore

systematically those rivers in the last decade of the 19th century. HENRI COUDREAU visited first the southern affluents Tapajós, Xingu and Tocantins — Araguaya, then he turned to the northern side, to the Yamundá and the Trombetas, where he died at the end of 1899. After his death, Olga Coudreau continued the work of her husband, travelling to the Rio Cumina, Curuá, Mapuera, Maycuru and finally to the Rio Canumã. The results were always published with the corresponding maps in a series of books.

Naturally, also some captains or pilots of the river-steamers, who, during the famous “golden rubber time” penetrated the Amazonian interior as far as possible, had drawn maps of their rivers: as an example I am going to show you a map of the upper Rio Juruá, designed by Comandante Hilliges from the little steamer “Marapata”.

One other important map, we must not forget, is the one of a certain part of the lower Amazon, made by PAUL LE COINTE, because it did not restrict itself only to the very bed of the river but it included the environment of that section of the Amazon, too: all the paranás (side-arms) and the shore-lagoons, the Várzea-lakes, and also the edges of the terra firme towards the wide valley of the Ama-

zon are indicated in that map. For the first time one could get now an idea of the morphology of the valley of the lower Amazon, which was formed by the activity of the river with its erosion and sedimentation in seasonal floods and drier periods.

Finally, all what was known about the topography of the river-courses and about the Hydrography of the whole Amazon system found its expression partly in outline maps, compiled in different countries, partly in special maps of single rivers, the best of them being collected and published in a now classical book “Hydrographia do Amazonas e seus afluentes” by AUGUSTO OCTAVIANO PINTO in 1930. The first volume contains the most detailed descriptions of all Amazonian rivers, while the second volume is a collection of the best river maps of those years.

All these maps, made with relatively rough methods, were, of course, however, subject to many omissions and inaccuracies, which could not be avoided by the lack of well-determined coordinates, and because of the impossibility to establish a triangulation system over a jungle-covered flat area of some million of square kilometers.

This situation changed, when, during the last war, the United States Air Force started to make the first aerial photographic map-

ping of the lower Amazon and parts of the courses of some tributaries, an enterprise, which was later on continued by Brazilian institutions as the Petrobrás etc. A great part of Amazonia is now mapped in this way, and since about two decades, we have now really authentic maps with the exact courses of the rivers, of always greater areas of this large country shown e. g. in the Atlas do Brasil 1:1 000 000 of the Instituto Brasileiro de Geografia e Estatística, or also in the World Aeronautical Chart, also 1:1 000 000, edited by USAF. By the use of aerial photographs, the former difficulties of mapping the Amazonian rivers were overcome, and the history of Amazonian river cartography has come to an end. The substratum for the "Studies in Amazonian Waters" was known, and new problems came into the centre of interests.

Only one principal difficulty still remains, namely the presentation of the extension of the Várzea-lakes of the Amazon, because they shrink considerably in the dry season while, in the rainy season, the water of the flood of the river covers many times the whole valley of the lower Amazon between the two edges of the "terra firme".

And one other feature, which is highly desirable, is not yet indicated in these maps, i.e. these edges

themselves of the terra firme to the Várzea filled valley of the Amazon, and eventual "islands" of terra firme within the same among the recent river alluvions of the Várzea.

But these details do not belong any more to a cartographic representation of strictly only the river courses, being of greatest importance, however, for an understanding of the morphology and the development in recent-geological periods, of the valley of the Amazon.

For those, who want to study in detail the history of Amazonian cartography a recently published descriptive catalogue "A Cartografia da Região Amazônica" by ISA ADONIAS, which lists all maps of this country, published between 1500 and 1960, is highly recommended.

The geomorphological problems of the Amazonian rivers have been detected in their significance for an understanding of the development of the surface of Amazônia to its present structure, only in relatively recent times. One exception are the river anastomoses which exist in South America among different river-nets and which are treated first and very intensively by ALEXANDER VON HUMBOLDT in his "Voyage aux régions équinoxiales du nouveau continent". It is a famous fact that he was the first civilized per-

son to *prove* such a connexion, that between the Orinoco and the Amazon system by the Cassiquiare, by passing it in May 1804; Humboldt, however, is not the discoverer of it: Acuña already, as we heard, had notice about it, and it also appeared in maps of the year of 1778. And Humboldt himself writes that the President of the Mission in San Fernando de Atabapo had given him the route, he had to follow from the Orinoco through small blackwater rivers and finally by bringing the canoe over a strip of land of only 4000 toises (7,8 km) of length to the Caño Pimichin which leads to the Rio Negro, and then back to the Orinoco through the Cassiquiare. Humboldt followed this way and writes: "On the first stretch on the course from east to west, it" (the Orinoco) "forms the famous bifurcation which has been denied by the geographers so many times and the position of which I was the first to be able to determine by astronomical observations..." Humboldt also describes two further connexions between these two river systems, namely one arm of the Cassiquiare, which under the names of Itinivini and Conorichite brings "white" water of the Cassiquiare into the Rio Negro, and another one from the Rio Negro up the Cababuri (= Cauaburi) to the Baria and down this river into the Cassi-

quiare. The geomorphological implications of these river-connexions were finally discussed by GOUROU in 1950.

In this century, JAGUARIBE DE MATOS has occupied himself with the studies of the connexions of the Amazon system with other river systems in South America. He found that there are such anastomoses — besides those, described by HUMBOLDT — between the Japurá and the Magdalena, the Uaupés and the Guaviare, the Gainia and the Inírida, within the net of the Rio Branco, between the Mapuera and the Essequibo, and in the south between the Guaporé and the Paraguai, the Tapajós and the Paraguai, this last one in the centre in South America. All these anastomoses are, however, very small and shallow, except the one between the Guaporé and the Paraguai, which is a bit deeper in the rainy season. — But even small boats are not able to navigate on them.

The connexions among different rivers show that the relief of the surface of the earth in our region must be old, that it must have been strongly levelled while no important catastrophic geological events must have happened here for a long period. All *intense* geological activity in South America is concentrated on the range of the An-



Fig. 1 — *Aerial photograph showing the rectangular structure of the earth's surface in Amazonia.*



Fig. 2 — *Delta of the Rio Branco into the Rio Negro (phot. SIOLI).*

des, which is in steady movement, while the rest of the continent remains relatively calm, i. e. without any volcanic activity, without any

remarkable uplift or sinking of the crust of the earth; so far as we know, even no stronger earthquake was reported in all eastern parts

of South America during the whole period of European colonization.

Besides this interest for geomorphology, the anastomoses among so many South American river systems are of importance for zoogeographical studies, because they enable also the purely aquatic fauna to penetrate from one river-net into the other ones.

An observation concerning the phenomenon of river-anastomoses, as considered in respect to the geomorphological viewpoints and the development of the network of the river-courses, was only made by STERNBERG less than two decades ago. As we said, there had not happened any great or, still less, catastrophic movements of the earth's crust, but there were tectonic, probably eustatic movements even in recent times, by which a strong fracturation was caused. This fracturation, also proved by recent geophysical prospectings, which were made by Petrobrás, broke the earth's crust into pieces of more or less rectangular shape and gave it a structuration, which determined strongly the general directions of the river courses. STERNBERG reconstructed the fractures in a map by following the orientation of the main stretches of the river courses. The result, shown in STERNBERG's map, may seem a bit theoretical or even arbitrary, but I think the last doubts will disappear

when regarding an aerial photograph, made somewhere in the vicinity of Manaus, which can be bought as a postcard in Manaus (Fig 1). In this picture one can clearly distinguish that this structuration consists of a system of lines, crossing each other rectangularly.

Another phenomenon of Amazonian river morphology, linked with geomorphological peculiarities of our region and with hydrological features of Amazonian rivers, e.g. currents and sediment load, is the formation of internal deltas, which was first discussed by HUMBOLDT. We find such "deltas of affluents" or "deltas of confluency", e.g. at the mouth of the Japurá into the Solimões, of the Rio Branco into the Rio Negro (Fig. 2), or at the southern end of the Estreitos de Breves into the Rio Pará (Fig. 3).

That region of the Estreitos de Breves and its current conditions were described by HARTT, 1897/98 and especially by HUBER, 1903; and TASTEVIN reported on the delta of the Japurá in 1929. The most recent study on Amazonian internal deltas is the one of GILBERTO OSÓRIO DE ANDRADE. These deltas occur when the affluent of so-called "white water", has a heavy sediment load, and when the collector-river cannot remove the added load, because of general or local current conditions, so that this

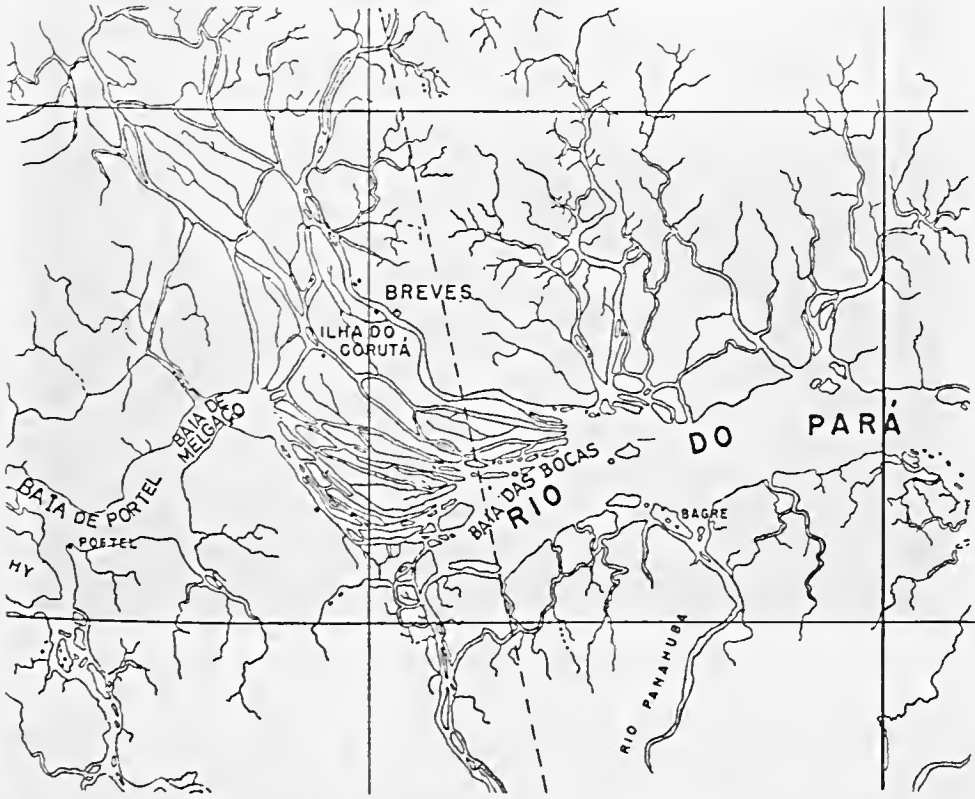


Fig. 3 — Internal delta of the "Estreitos de Breves" into the Rio Pará (From: Preliminary Map, Amazon Delta, 1 : 500 000, 1943).

load is accumulated near the mouth of the affluent, dividing it into many arms and having it grown, so that the affluent reaches out into the bed of the collector-river.

The most striking feature of many Amazonian clear-and black-water rivers, however, is the shape of their lower courses, their "mouth-bays". The river water covers there enormous areas, the width of which is, at all, in no proportion

to the sizes and the discharge of the upper courses. The shores generally consist of pure white sand-beaches behind of which rises the terra firme, often in form of cliffs of different heights. The shore-line is neither more or less straight, nor consisting of alternating stretches of erosion and sedimentation banks, but it is jagged and, seen from above (Fig. 4) the whole river section looks like an artificial reservoir. Even where such a river



Fig. 4 — *Rio Arapiuns, lower course with the shape of an artificial reservoir (phot. SIOLI).*

is meandering, as in Fig. 5, the meanders are those of a valley, not of a river-bed.

Such a morphology of lower courses cannot have been elaborated by the respective rivers under their actual conditions, with their practically stagnant water in the mouthbays; they can only be understood as “drowned valleys” what was pointed out first by DENIS, 1927, interpreted them as true freshwater rias. The cause of this drowning of Amazonian river valleys, which is observed up to the affluents of the middle Solimões, where we still find large mouth-

“lakes” as that of Coari, Tefé etc., can easily be deduced from the known rising of the ocean level after the glacial period. If, besides that fact, a regional sinking of the continent crust must be taken into consideration, is not easy to prove. That there must have happened some up- and/or downward movements of the earth’s surface can be seen from the fact, that in the region between the lower Tapajós and the lower Xingu the affluents of the Amazon have no mouthbays, while east and west of that zone we find those typical drowned valleys.

All these affluents with such mouthbays obey in their courses one typical scheme (Fig. 6).

After a "normal" upper course, commonly in the arquean complexes of granites and gneisses of Central Brazil or of the Guianas, and after passing the strips of paleozoic marine sediments and of diabase eruptions, the rivers reach the Amazonian depression, filled with the relatively soft sediments of the tertiary freshwater inland lake, the so-called "series of the barreiras". Here the river valleys suddenly widen, but their first section is filled with many, generally elongated, islands, built up by recent river alluvions. Only after pas-

sing that "sedimentation zone" in which by the slowing down of the current in the widened bed, they deposit their sediment load, the rivers reach the open mouthbays. The water is now decanted, very transparent, and, stretching out over an enormous profile of the river bed, it loses its current almost completely. Side erosion is caused only by the activity of the waves, which attack the cliff of terra firme during the highwater season, thus enlarging the river bed still more. But there is no depth erosion, on the contrary, bottom-samples and eco-soundings in the lower course of the Rio Arapiuns, e. g. revealed a layer of very soft,



Fig. 5 — *Rio Arapiuns, meanders of the drowned valley* (phot. SIOLI).

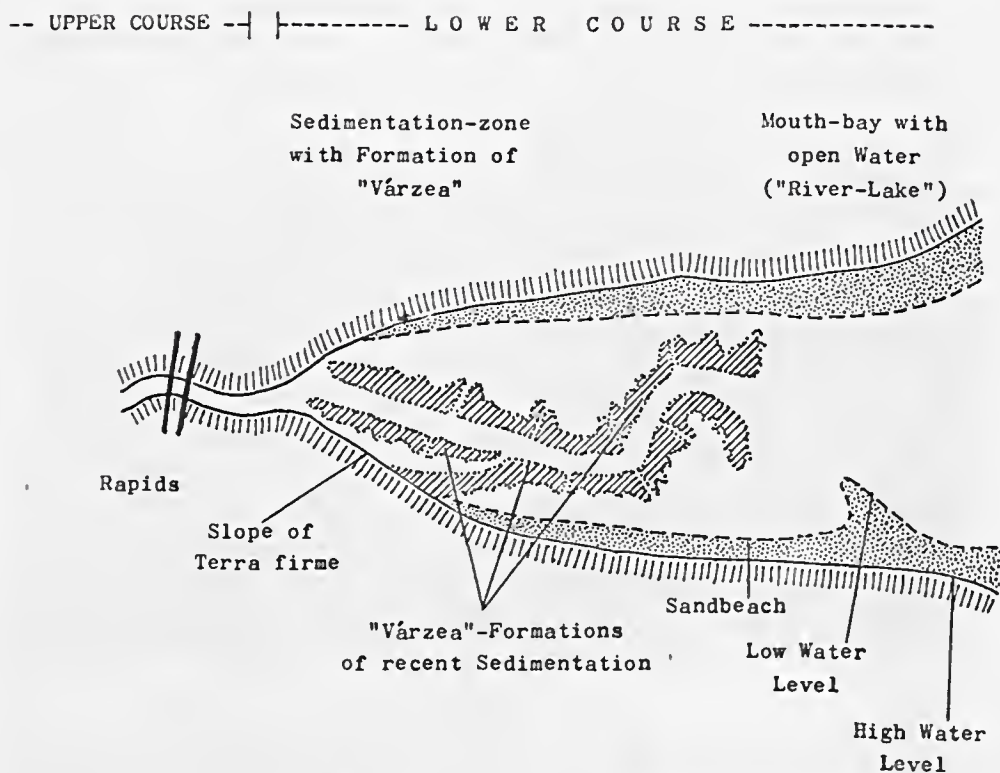


Fig. 6 — Scheme of the lower courses of Amazonian affluents.

muddy and fine sediments, 3 — 4 m thick (Fig. 7) typical for lakes, and which cannot be accumulated under the flowing water of rivers. Also phytoplankton develops in the open water of mouthbays, even in such quantities as to form waterbloom. So, the lower sections of these Amazonian tributaries, their "mouthbays", must limnologically be considered more as lakes than as rivers.

The best term will certainly be that of "Amazonian river-lakes".

In the literature (LE COINTE, 1954, DE O. ANDRADE, 1958, DE C. SOARES, 1959) these mouthbays, the sections of drowned valleys of Amazonian affluents, are also called "lagos de terra firme", "terra firme-lakes" (contrary to the "lagos de Várzea", "Várzea-lakes"), namely because of their opening into a white-water river, where the sediments of that turbid, suspension-rich water have blocked by deposition of fresh alluvial lands the originally widely opened funnel-

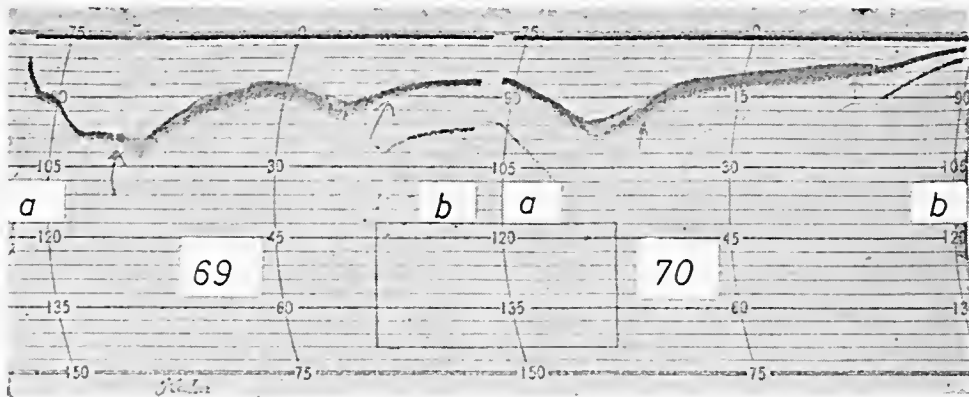


Fig. 7 — Echograms of the lower Rio Arapiuns, showing the layers of soft "lake" - sediments.

mouths, letting only a narrow channel as an outlet for water of the tributary.

Also the valley of the Amazon itself, where does not be such a great, open and more or less stagnant water area as in the described affluents, must be understood as an originally "drowned valley". The clear- and black-water rivers brought so little amounts of suspended particles with their water that they built up with these particles in the lower courses, after the drowning of them, only a more or less restricted sedimentation zone which is still growing, by continuing sedimentation, in direction to the river mouth but which has not yet reached it. The Amazon, however, is a turbid "white water" river, i. e. its water contains a greater quantity of suspensoids (50 — 150 mg/l), and by deposition of this material it has completed, sin-

ce a long time, the filling of its wide drowned valley with its own recent alluvions, which now form the "Várzea", the floodlands of that river. And not enough that the whole drowned valley has been occupied by the "sedimentation zone", not letting any space for wide and open mouthbays as in the case of clear- and black-water rivers, the river alluvions of the Amazon have been accumulated even outside its mouth into the ocean, along the Guiana coast, where the Amazon water is conducted along the continent shore by the Brazil-Current of the Atlantic Ocean. There they are extended in front of the terra firme as a strip of swampy, floodable land, a continuation of the lower Amazonian Várzea, in a width of up to more or less 80 km and reaching to French Guiana.

Related to the phenomenon of the drowned valleys is the great depth, found in some places in the bed of the lower Amazon. SPRIX & MARTIUS were the first to measure the depth in the gorge of this river at Óbidos, where they found 83 m. The recent eco-soundings of the American group (U. S. Department of the Interior Geological Survey Information Office, 1964) in the lower Amazon found several, at least 10 places with a depth of 90 and more meters. But if the "mouthbays" of affluents are indeed drowned valleys, it may be possible that there also persist great depths and that the original bottom of the riverbed may be ma-

intained, if no products of side-erosion or deposition of "lake-sediments" filled it up in the meantime. Really, a sounding, made by hand with a line in the Rio Negro below Manaus, south of the island Marapatá, where the river is so wide that there was no notable current, indicated a depth of... 102 m. And later eco-soundings revealed the profile of the ancient river on that place as a deep, almost cañon-like valley, as shown in Fig. 8 (SIOLI, unpublished).

The morphological peculiarities of Amazonian rivers which we described and interpreted — except that of the river courses along fracture lines — are consequences of

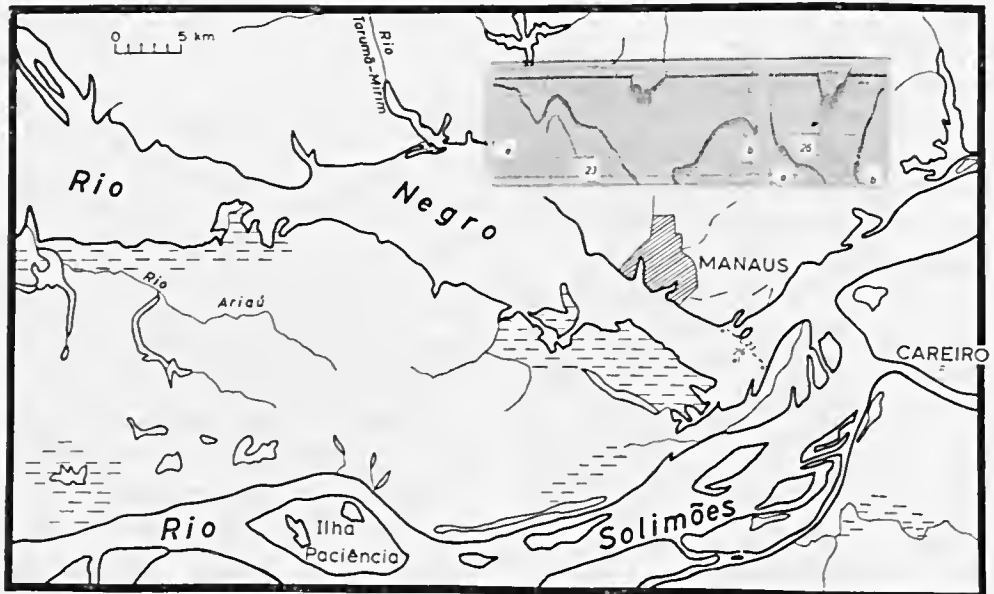


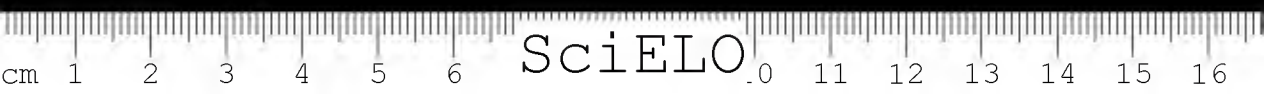
Fig. 8 — Echograms of the Rio Negro, indicating a greatest depth of around 100 m.

the flatness of the country, the very small gradient of the rivers in it (the Amazon having only ≈ 1 cm/1 km between the mouth of the Rio Negro and the ocean) and the very ancient and "old" i. e. levelled relief of the country, even in many headwater regions.

In spite of that small gradient, the current speed of the Amazon is really high, varying in the lower Amazon in an average of 1 to 2 miles per hour ($\frac{1}{2}$ — 1 m/sec.) in the dry season, and 2 to 4 miles per hour (1 — 2 m/sec.) in the flood season. This high current speed at a given gradient naturally depends on the relation: water quantity/friction on the surface of the riverbed, or: perfile through the riverbed/contact-line of the water with the bedground. The greater the water quantity, flowing down the river, the smaller is, relatively, the friction-zone between the running water and the surface of the riverbed. How much water, now, is flowing down the Amazon?

The discharge of the Amazon was, till very recent years, only estimated but not exactly determined. The first estimate, however, made by KATZER (1897), which unfortunately, has almost been forgotten and is not mentioned in modern literature treating especially this question, has been astonishingly precise. KATZER found that the discharge of the Amazon into

the ocean is around 120 000 m³/sec. in the dry season, an amount which might be multiplied in the highwater season. PARDÉ (1936), basing on calculations about rainfalls, evaporation etc. came to much smaller amounts, namely only 90 000 — 110 000 m³/sec. as annual average. But finally, the recent determinations with most exact methods, made by that American group (U. S. Department of the Interior Geological Survey, 1964; OLTMAN, O'R. STERNBERG, AMES & DAVIS, 1964; STERNBERG & PARDÉ, 1965) gave as result an average of 218 000 m³/sec. all over the year, a figure, which could not better confirm the indication of KATZER! This means that the Amazon is by far the mightiest river of the world, having 5 times the water of the Congo and 12 times of the Mississippi, and carrying 15 to 20% of the water which *all* rivers of the world together conduct into the oceans. Corresponding to that mass of water is the extension of the estuary of the Amazon, where Orellana and his chronicler CARVAJAL already admired the width of the mouthfunnel. Special studies about currents in and displacement of the mixing zone of fresh and sea-water and of other limnological conditions in the estuarine section of the Amazon were made by EGLER & SCHWASSMANN (1962, 1964).



The enormous mass of water of the Amazon, running down the wide and deep riverbed with strong current, does not carry in its turbid "white" water only a certain amount of suspended particles, but it also moves the bed load on its bottom, the quantity of which can-

not yet be determined. It appears in sandbanks, which change their height and position by the shifting of the movable material. Where it wanders, however, on the bottom of the riverbed, it forms gigantic "ripplemarks", true sanddunes of up to 190 m length and 8 m height

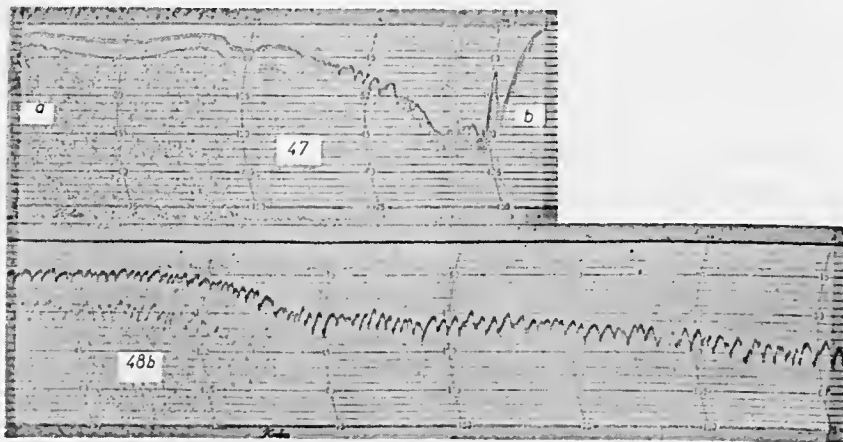
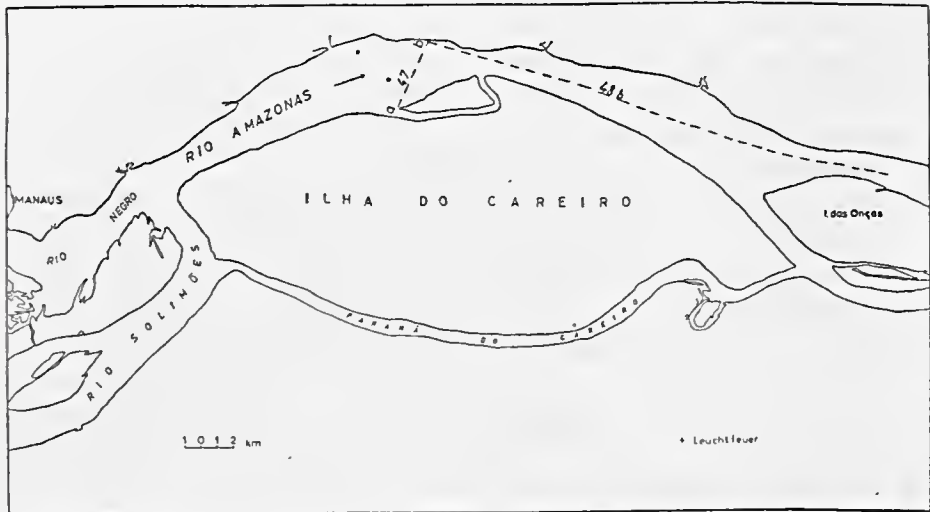


Fig. 9 — Giant "ripplemarks" (sand dunes) on the bottom of the Amazon below the confluence with the Rio Negro. Echogram of a longitudinal section of the riverbed.

as to be seen in Fig. 9 which shows a longitudinal profile, taken by eco-sounding of the Amazon below the mouth of the Rio Negro (SIOLI, 1965).

We spoke already of turbid "white" water, of clear water and of black water rivers, and with these expressions we mentioned the classical river types of Amazônia. We also heard above what CARVAJAL had written about the black water of the Rio Negro, when Orellana and his men had seen it first, and how ACUÑA and ROJAS had described that strange water, too. The first scientist to discuss the phenomenon of blackwater rivers was, however, ALEXANDER VON HUMBOLDT, who did not only describe the appearance of such rivers, together with some biological peculiarities of them as e. g. lack in crocodiles (*Caiman spp.*) and in black-flies (*Simulidae*), and who cited the opinion of the people that these black waters do not turn the stones brown and that white rivers have black, black rivers have white shores, but who asked already for the origin and the reasons for that black water! He writes (HUMBOLDT, l. c., vol. 3, pp. . . . 264-266): "In the widely extense river-system that we travelled — and this circumstance seems to me very striking — the black waters occur preferably only in the stretch near the equator...; but in that

whole area, white and black waters occur in the forests and on the savannahs simultaneously one near the other, in a form that one does not know to what circumstance one shall contribute the coloration of the water... If one asks the Indians about the reasons for this strange coloration, their answer is, . . .: they repeat the fact in other words. If one addresses oneself to the missionaries, they speak as if they had the severest proofs for their conjecture, "the water colours when it runs over the roots of Sarsaparille". The Smilacaceae are, indeed, very common at the Rio Negro, Pacimony and Cababury, and their roots give, soaked in water, a brown, bitter, slimy extractable mater; but how many *Smilax*-bushes have we seen at places, where the waters are completely white! How is it possible that in the swampy forest through which we had to carry our pirogue from the Rio Tuamini to the Caño Pimichin and to the Rio Negro, we waded through the same stretch of land, now through creeks with white, now through other ones with black water?... Very near the equator, indeed, the vegetation is, because of the quantity of rains, stronger than 8 — 10 degrees to the north and to the south; but in no way it can be maintained that the rivers with black water have their origin pre-



ferably in the most dense and shadowy forest. On the contrary, very many "águas negras" come from the open grasslands which extend from the Meta on the other side of the Guaviare to the Caquetá. . . . The colour derives, without any doubt, from coaled hydrogen. One can observe a corresponding appearance on the manure-water which our gardeners prepare, and on the water which flows out of peat-pits. Cannot, after this, be assumed, that also the black rivers. . . are coloured by a compound of carbon and hydrogen, by a plant-extract-matter? . . . The colouring matter seems to be in very small amounts in the water; for, boiling water from the Guinia or the Rio Negro, I do not see that it turned brown like other liquids which contain much hydrocarbon".

At the times of Humboldt and later on, one distinguished only two types of Amazonian rivers: white and black ones. But we have in fact three different types (SIOU, 1951, 1964), namely

Rivers with turbid yellowish, so-called "white" water, with a transparency between 10 and 60 cm, as the Amazon, Rio Madeira, Rio Branco;
rivers with more transparent water of yellowish to green and olive-green colour and a

transparency between 60 cm and 4 m, to be called "clear" water rivers, as the Tapajós, the Xingu and the majority of small creeks in the terra firme high forest;

rivers with transparent but olive-brown to darker even reddish-brown water, looking like black coffee in the river bed, in a glass like weak tea, with a transparency of 1 — 2m, so-called black-water rivers (as described above), as the Rio Negro (the "classic" black water river), Rio Cururu, and certain creeks coming from areas with a special vegetation which grows on a certain soil type.

These three types of running waters in Amazonia result from characteristic landscapes, i. e. from the geomorphological and/or mineralogical-pedological conditions in the headwater areas.

White waters are bound to more or less mountainous terrain in the region of their origin, with an irregular relief, where erosion furnishes the sediment load of the water (mainly the Andes or their foot-hills, or also the Parima-system on the Venezuelan border).

Clear water rivers have their catchment areas in the less rugged, really strongly flat reliefs of the old massives of Central Brazil and

the Guianas, or in the tertiary sediments of the Amazonian terra firme plains, with their characteristic brown loam soils.

The black water rivers come equally from very flat regions; the Rio Negro, for example, rises on a very old peneplain. That is the reason for the little contents of suspended matter, but not for the brown colour of those waters. As shown above, HUMBOLDT already discussed the origin of that brown colour. One thought also that the colour had its origin in the decaying organic matter of the flooded jungle, of the so-called igapó-forests. This possibility has not been refuted nor proved —, but it could be shown (SIOLI, 1954a, 1955b) that the black water is coloured by dissolved or colloidal humus substances which are linked with a

special soil type, namely, bleached white sands, covered by a special vegetation, the caatinga-forest of the upper Rio Negro, the “campinas” near Manaus and certain “campos” as e. g. around the Rio Cururu. These bleached sands revealed themselves as tropical lowland podzols, first indicated by chemical analyses of the black waters, later proved by pedological investigations (SIOLI & KLINGE 1961, KLINGE 1965).

As we see, there are physical factors (relief) as well as chemical ones (soils) in the headwater regions which create the types of running waters in Amazonia. And we can make even a scheme of the combinations of the physical and chemical factors which are necessary for the formation of the river types:

TABLE 1
Factors of the headwater zones which determine the types of Amazonian rivers

	Mountain-slopes (as primary supplier of the suspended matter)	± Even relief of the earth's surface	Podzol soils (as supplier of the colouring humus substances)	Other soils
White waters	+	—	—	+
Clear waters	—	+	—	+
Black waters	—	+	+	—

Such a connexion respectively exclusion also clarifies the phenomenon that black waters are very

uniform in regard to their chemisms, that also white waters do not show too great divergences, at

least in the pH values, but that clear waters present the very greatest differences in pH and in the contents of inorganic ions:

black waters: pH 3.8 — 4.9

white waters: pH 6.2 — 7.2

clear waters: pH 4.5 — 7.8

The lower pH-values (around 4.5) of the clear waters occur in creeks in the region of the "Série das barreiras", a bit higher ones (around 5) in creeks of the arguean granite-zones of the upper Rio Negro, while the great clear water rivers have pH 6 to 6.7. The highest pH-values are found in the strips of carboniferous origin north and south of the lower Amazon, with occurrences of limestone and gypsite-deposits. Already this spread of the pH-values and the distribution of the clear waters over the most different geological zones of Amazonia show that the clear waters are only a collective name of chemically (and biologically) very heterogenous waters and that they possess only the scarcity of suspended matter as common characteristic.

The described river types are not always clearly distinct from each other. In nature we find transitions of all degrees between white waters and clear waters, and between clear waters and black waters. Also one and the same ri-

ver sometimes can change its "type" periodically or occasionally with the seasons or even with every single rainfall. Much less than a lake, a river is determined in its characteristics by its own, internal laws, being only a product of its surrounding landscape, mainly in the headwater zone, its water is chemically spoken the "urine of the landscape". Thus, we now see that the river types are not abstractions, "ideas" of rivers, but more or less rough descriptions of sections of the framework of causes and effects of the eco-system, which constitutes a landscape (STOLI, 1965d).

Rivers, however, do not receive only their qualities from the surrounding landscape, they are also able to build around them their typical landscape. We saw already the scheme of the course of the clear water rivers, with the "normal" upper course, the sedimentation zone and the mouthbays with the sandbeaches.

Also the Amazon, as greatest white water river, has built *its* river landscape, a schematic cross section of which we see in Fig. 10 (STOLI, 1964b).

The wide valley of the river between the terra firme slopes, carved out probably during the glacial period and then drowned, was filled in the meantime with recent river alluvions which form the

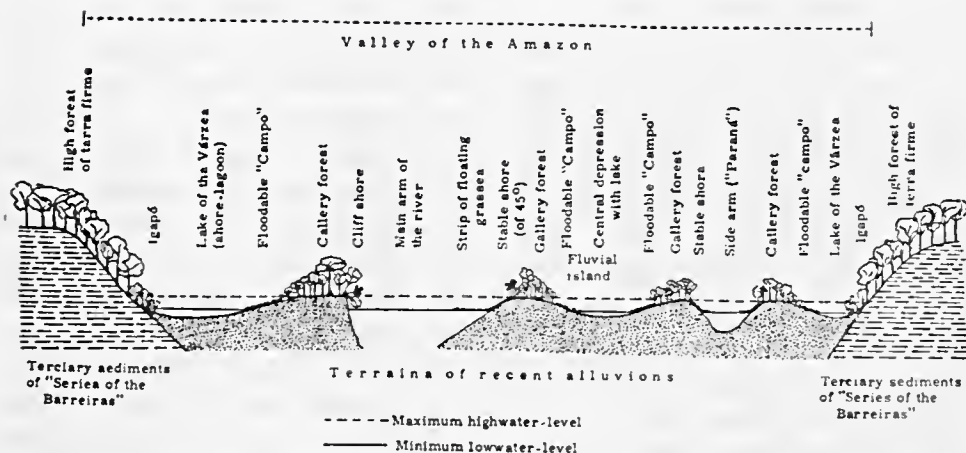


Fig. 10 — Schematic cross-section through the Lower Amazon valley; height exaggerated (From: SIOLI, 1964 b).

floodlands of the so-called "Várzea". The Várzea is covered with a special vegetation type, different from the high forest of the shores of clear and black waters. This may be taken as an indication that the Várzea-forest is growing on soil with (chemical or other) qualities different from the behind terra firme soils. Our schematic cross section is derived from the conditions at the lower Amazon. But the more we go up the Amazon, the Solimões, the more we approach the foreland of the Andes, the more vanishes the difference between Várzea and terra firme, the more the vegetations become equal. ACUÑA already characterized the Várzea of the lower Amazon as a very fertile land, of which the Indians profit with their plantations and which is fertilized

annually by the flood of the Amazon which every time lets behind a new layer of fresh sediments. After FITTKAU (unpublished), the Várzea must now be understood as an extraneous element in the lower Amazonian landscape, as an appendix-like prolongation of the pre-andean strip of material which originated from the fresh, and relatively nutrient-rich products of the weathering crust of the mountains and has been washed down, by the waters, from the slopes of the Andes and deposited first near their feet, in their foreland. From there, these "fertile" sediments had been transported down the white water rivers where they were deposited and eroded on the way probably several times before they built the Várzea of the

lower Amazon, from where they will finally be taken to the ocean.

Perhaps the most important chapter of the studies in Amazonian waters is that of the chemistry of rivers and, still more, of creeks, because it did not only reveal some peculiarities of the waters themselves — important as they are for an understanding of their biology, inclusive their rôle for the distribution and expansion of certain human diseases — but it showed relations between water chemistry and geology/mineralogy as well as pedology of the head-water areas, and finally it led to first insights into the nutrient-household of whole Amazonian landscapes, to the ecology of the rain-forest.

The first chemical analyses ever made of Amazonian waters are those by KATZER by the end of the last century (KATZER, 1897, 1903): "A short time ago, one knew almost nothing about the quality of the water of the Amazon. Only by the studies of the last time, there has been proved that the water of the giant river is, in chemical aspect, of *extraordinary purity*. The same is true, partly in still higher degree, for its affluents as far as they were analysed for this purpose so that, indeed, the rivers and streams of lower Amazonia belong to the *purest waters of the world*."

And, after KATZER, the waters of many springs and the ground water in the lower Amazon region are of the same quality.

During the last 20 years this statement has been confirmed by a lot of chemical analyses of waters from many parts of Brazilian Amazônia, from the Zona Bragantina, east of Belém, to Benjamim Constant at the Peruvian border, and from the southern limit of the Hylaea near the upper Tapajós River to the Campos of Rio Branco and the frontier-mountains of Venezuela in the north. While the water of the main river, the Amazon itself, is already extremely poor in its ionic content, as KATZER and later determinations showed, the same condition is true in a still higher degree in most parts of Amazônia, where the natural waters may be compared best with "a little bit contaminated distilled water". In the area of the so-called "Series of the barreiras", i. e. of the terciary (pliocene to pleistocene) deposits of the then enormous Amazonian freshwater-inlandlake, in the arquean complexes of Central Brazil and of the Guianas, with their granitic gneissic rocks, in the zone of cretaceous (?) sandstones around the Rio Cururu (near the Serra do Cachimbo), the waters of the creeks and springs and of eventual lakes are all of that quality and of surprisingly

low pH-values. But we have also some other regions in Amazônia, where the waters are not so poor and acid, even if these zones are of relatively small extent in lower Amazônia, namely restricting themselves to the narrow strips of carboniferous marine sediments,

with limestone and gypsite deposits, north and south of the lower Amazon, to the "islands" of diabase eruptions, and to the area of a miocene sea-transgression in the Zona Bragantina, east of Belém — Pará, the so-called Formation Pirabas.

TABLE 2
Chemistry of Amazonian Waters

pH.....	4.2 — 5.5	4.0 — 6.6	5.2 — 7.8
HCO ₃ 'mval/l.....	0.00 — 0.04	0 — 0.174	0.026 — 6.311
Ca'' mg/l.....	0 — +5	0 — 18.4	2.6 — 204
Mg'' mg/l.....	0 — 0.38	0 — 5.6	—
Na' mg/l.....	0.847 — 2.530	0.245 — 2.060	—
K' mg/l.....	0.534 — 1.52	0.143 — 1.000	—
Li' mg/l.....	—	0 — 0.160	—
Fe'' + Fe''' γ/l.....	0 — 143	0 — 250	0 — 1.200
Mn'' γ/l.....	0 — 82	0 — 212	0 — 160
Al''' γ/l.....	0 — 488	0 — 314	0
Cl' mg/l.....	0 — 3.5	0 — 2.5	0 — 16.5
SO ₄ '' mg/l.....	0.000 — 0.480	0 — 2.690	0 — 556.7
P (PO ₄ ''') γ/l.....	0 — 50.2	0 — 110	0 — 42
N (NO ₃ ') γ/l.....	0 — + 200	0 — + 150	0 — + 550
N (Kjeldahl) γ/l.....	138 — 724	0 — 2.620	—
Si diss. mg/l.....	± 0.5 — 4.5	0.502 — 6.650	1.5 — 22.4

Table 2 shows the extreme values of the results of very many water analyses of the cited regions. It is obvious that the chemistry of the waters is neatly related with the geological, i. e. mineralogical underground of the region, it comes from. Naturally, that had to be expected, but in Amazônia those relations are surprisingly evident, thanks to the large-scale geological structure of our region. Based on that experience, e. g. even the delimitation of the extension of the miocene marine transgres-

sion of the Formation Pirabas in the Zona Bragantina once was tried, and I think, with certain success.

Where there are some lakes in Amazônia — and they are practically all shore-lakes of some rivers — their water is also related to the geology of the surrounding and, naturally, via the river, of the headwater zone of the same. The limnology of such lakes was first studied by BRAUN (1952), more recently by MARLIER (in press a, b).

The most interesting example for that relation between shore-lakes and their river and the head-water region of the same, we saw already in the Amazon itself, the *Várzea* of which is a landscape-strange element in lower Amazônia. The water of the *Várzea*-lakes, however, is of double quality. In part, it comes from the Amazon, when the river, with the rising flood, overflows into the lagoons where it diminishes its turbidity by decantation of the suspended particles, while getting more or less stagnant; from behind, from the slopes of the terra firme, however, those *várzea*-lakes receive very poor, clear and acid water, which often prevent the Amazon water from reaching the terra firme shore of the *várzea*-lakes.

A consequence of the chemically richer Amazon water, which becomes decanted in parts of the *Várzea*-lakes, is that the waters with the greatest primary production of phytoplankton are to be found here. In the turbid "white" water rivers, light penetration is too small for allowing an autochthonous high primary production; in regard to the alimentation of the biota, living in them, these rivers are dependant biotopes. I. e. they depend on the introduction of organic matter, of phytoplankton from the shore-lakes and from the

mouthbays of clear water rivers for the beginning of the food-chain. On the other hand, we find in the *várzea*-lakes the upper layer sometimes thick green from water-bloom, and the pH, during the clear day, risen to almost 10 by the consumption of CO₂ by the photosynthetic processes of that enormous mass of algae.

It is no wonder that just in and around those *várzea*-lakes there is also the most intensive concentration of higher animal life, from fishes to enormous amounts of water birds. In the white water rivers, as e. g. in the Amazon, as well as in the lakes and in the sedimentation zones of great clear water rivers, we have, however, another biotope of good primary productivity. These are the floating meadows of grasses etc. which develop in calm river stretches and inlets on the water surface, thus being independant from the turbidity of the water and profiting only from the inorganic nutrients in the water through the floating roots.

Also the mouthbays of great clear water rivers, as the Tapajós and the Xingu, are, as I said, places of primary production of phytoplankton. Sometimes we can there observe even waterbloom, too, but never in such a quantity as in the cleared-off Amazon water of the *várzea*-lakes. The limiting factor must be sought in the inor-

ganic nutrient content of those great clear water rivers, which generally come from the old massives of Central Brazil and from the Guianas, and not in scarcity of light, as is the case in the white water bodies.

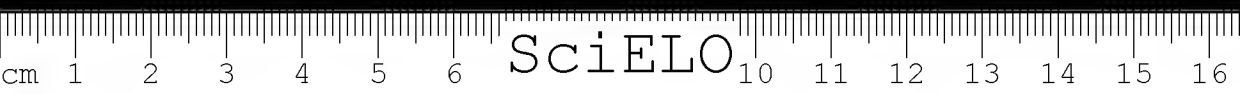
And where we have the acid and chemically extremely poor "black" water, even in so great and lake-like mouthbays like in the lower Rio Negro, the chemical poorness and the dark colour of the water combine for reducing the primary production to extreme low values. Those large black water rivers have the general fame to be hunger-rivers, also for the human population, living on the banks, caused by the scarcity of fishes and waterfowl etc. Where there are igapó-forests on their banks, these, with their litter etc., must be the main source of organic matter to start the food chain in them.

General characteristics of the chemical properties of Amazonian waters, also in relation to soil conditions, were examined and discussed by KLINGE & OHLE, 1964.

The water of the Amazon itself, as well as of the Rio Negro, was also investigated especially by GESNER, who compared these rivers with the Orinoco. After him, the electrolytical conductivity in Amazonian waters is generally very low, in clear water rivers still by far lower than in the Amazon itself,

but rises with the pH, when this exceeds ± 5 . Below that value, the conductivity rises again with a falling pH-value. The Amazon has its highest conductivity in the uppermost part of its course; downward it diminishes by "dilution" with the waters of low conductivity of the affluents. The oxygen content in the Amazon water is around 70% of saturation, having the lowest value during the high water period. For the phosphate content, the sediments of the Várzea act as a buffer system.

We have now seen in which way the chemistry of the water in Amazônia is related to the geology-mineralogy of the underground of their headwater areas and, already before, how it indicates some processes which occur in the soils, e. g. podzolisation. But we must consider yet, what the chemical poorness of the waters tells about the ecology of the landscapes from which they come. This is possible, because the landscapes with their relief, their soils and their vegetation etc. are interposed in the circulation of the water on earth and determine the quality of the waters, which pass them. GALENUS already knew about this connexion when he said: "Tales sunt aquae quales terrae quas percurrent." The water, which appears in springs and then forms creeks and rivers, comes, in the last



end, only from the rain, which falls on the bottom and partly flows away on the surface, partly penetrates the soil before reaching the groundwater, where it eventually comes into contact with the subsoil and finally drains into the springs. Passing the soil and being in contact with the deeper underground, it enriches itself with ions, which originate there from weathering- and soilforming-processes. When — as in the Amazonian hylaea — the earth's surface, under the influence of a humid climate, is covered by a climax vegetation, the mass of which is constant during long periods, none of the ions liberated in the soil by these weathering etc. processes from the reserves, is additionally accumulated in the vegetation cover or in the upper soil layer where, with time, such an accumulation would provoke salting, but all will be washed out and appear in the springs and creeks where the ions can be analysed, qualitatively and quantitatively. And if we find so little ion content in the waters — a part of which must even still be contributed by the influx of the rains — as we do in the already mentioned zones of Amazônia, we are enforced to conclude that also the soils must be very poor in those ion reserves, among which the macro- and micro-nutrients for the plant growth are of special in-

terest for the understanding of the "budget" of the high rainforest as well as for prospects of a practical utilization of those areas for eventual future agricultural or silvicultural purposes. The general chemical poorness of the waters indicates an equally general poverty of the soils, and when we find these covered by high forest, the existence of the forest is not to be explained by a supposed "fertility" of the soil, but by the fact that the forest lives in a short-circuited circulation of the mineral nutrients within the living and dying organic matter, more or less isolated from the soil. The forest uses the soil more as a mechanical substratum for the trees than as a source of nutrients.

The minerals, contained in the forest matter, have there been accumulated during centuries or thousands of years. If now, the forest is cut down and burnt for giving space for a plantation, these minerals, and among them the nutrient-salts, are liberated at once in the ashes. But already the next rains will wash the greatest parts of them away — as once was found occasionally when examining creeks in the area of the "Series of the barreiras", in lower Amazônia —, only small amounts still remain for the crop and will be carried away with the harvest. It is a general experience that a new "roça"

in the jungle gives good harvests only during two, exceptionally three years. Then the soil is exhausted, the mineral reserves of the former jungle-cover have disappeared.

The conclusions as to the "fertility" of the soils which have been drawn from the results of chemical analyses of waters from the greatest parts of the Amazonian region were simultaneously and later on confirmed by soil-analyses and by practical experiences which all contradict the former idea of a never ending fertility of our region.

These findings are, however, neither a reason for being shocked, nor for despair in regard to a beneficial contribution of Amazônia to the food-economy of the growing population of Brazil. It only says that care must be taken not to waste uselessly the resources of our country and that new methods, which correspond with the ruling ecological conditions in Amazônia, must be applied and even still created by studies in loco instead of importing only methods and machinery and ideas from highly industrialized countries, in which these were developed, generally under completely different conditions. All must be done to avoid a devastation of Amazônia which may easily happen because the ecological equilibrium is really

unstable and very vulnerable in consequence of the shown lack of buffering nutrient reserves. There exist already enough examples of devastated landscapes in other tropical countries of South America and also of Africa. Investigations of the waters may also help to contribute some knowledge for the purpose of avoiding dissipation of singular riches and benefits contained in the Amazonian nature. That is also one aim when elaborating a budget of inorganic nutrients for catchment areas of whole river systems, as Dr. UNGEMACH is just doing, or when establishing an ecological subdivision of this huge country, as is tried by Dr. FITTKAU. These two scientists are going to report on their work during this symposium.

And so we learn that the studies of Amazonian waters are also linked with the observation about the supposed fertility of the Amazonian soil, mentioned by ACUÑA & ROJAS.

Finally, I should like to say that it was only along very general lines and under omission of many studies and works that have been done, that I tried to give an idea of the points of view under which Amazonian waters were observed, described and analysed, from the very first contact of Europeans with them on the occasion of the

discovery of the mightiest river of the world, to the concept of the waters being parts of greater sections of the biosphere, what are the landscapes, and of using them, too, as indicators for other, more general ecological conditions in the nature of this big country.

SUMMARY

There is no other region in the world in which the water plays an equally decisive rôle, in the formation and in the character of the landscape, as it does in Amazonia. The wet climate created, in the enormous lowland, the greatest and vastest river-system on earth.

Already the discovery, the conquest and the colonization of our region were connected with the water-courses so that their knowledge was, from the beginning, of vital importance for the Spaniards and Portuguese when they made themselves rulers of the new country. The studies in Amazonian water started therefore with the mapping of the water-courses; the improvement of that task was concluded only in recent time with the elaboration of the modern maps based on aerial photographs.

The chroniclers of the expedition of PEDRO TEIXEIRA in 1637/38 — the first one to ascend and to descend the Amazon in a planned trip from the mouth to the Andes —,

ACUÑA & ROJAS, however, were observers with such a wide look that they perceived, in principle, almost all aspects which the Amazonian waters later on offered to the scientific curiosity of mankind. Besides of the cartography — and of the hydrobiology which will be treated, in this symposium, in a special paper given by MARLIER — those reports already touched the following complexes:

Anastomoses between different river-systems (by the mention of the connexion between the Rio Negro and a river which leads to the ocean);

Morphology of the rivers (by giving dates about widths and depths);

River-types (by the description of the black water of Rio Negro);

Peculiarity of the *Várzea* in the complex of the Amazonian landscape (by the observation of its periodical fertilization by the annual floods);

Nutrient-content and Ecology of the whole region (by the judgement — even being an enormous one — of the quality of the soils).

River-anastomoses between different fluvial systems have been scientifically proved for the first

time by HUMBOLDT who navigated through the Cassiquiare. Today, more connexions between the Amazonian and other Southamerican river-systems are known.

In the Morphology and Hydrology of the Amazonian rivers the following problems occupy the greatest interest: the profiles of the beds of the big rivers, the lake-shaped lower courses of many affluents, and the discharge of the Amazon. The first measurements of great depths (e. g. in the "gorge" of Óbidos, SPIX & MARTIUS found 83 m) were proved and even surpassed by recent eco-soundings in the Rio Negro (~ 100 m) and in the lower Amazon. The bed-ground of the lower Amazon consists of load-matter which is moved down the river of giant "ripplemarks", of true dunes. The lower courses of many affluents which are disproportionately widened and transformed even in "Terra firme — lakes", have been recognized, first by DENIS, as drowned valleys; limnologically, the sections of river-courses are more alike to lakes than to rivers. The discharge of the Amazon, exactly measured only recently, is of 218 000 m³/sec in the annual average, i. e. 1/6 to 1/5 of the water-mass which all rivers of the earth together empty into the oceans.

The following river-types were established in Amazonia: rivers

of "white" (turbid) water, of clear (transparent) water, and of black" water (transparent but brown coloured). The types depend on landscape-factors in the headwater-zones (relief, climate, vegetation cover), but they are not absolutely distinct from another and permanent, but they may be connected by intermediate types, or they may even periodically or occasionally change within the same river.

The Várzea, the floodland, of the lower Amazon which is so different from the Terra firme in the quality and fertility of the soil and in the vegetation, is explained as the product of geologically recent filling of the drowned valley of the Amazon with the river-alluvions; it is therefore, after FITTKAU, a prolongation, along the course of the white water of the Amazon, of the sediment-matter from the pre-andean strip of land, an appendix to the same through Lower Amazonia. This sediment-matter from the pre-andean strip differs, by its geological-mineralogical origin and its age, in its geological qualities from the soils of the arquean and terciary Terra firme zones of the lower Amazon.

The nutrient-content was concluded by chemical analyses of rivers, creeks and ground-waters. Already the first analyses made by KATZER showed a surprising pover-

ty in dissolved salts. Later analyses of waters from different geological zones confirmed that general chemical poverty with only few exceptions, e. g. in the carboniferous strips. Such chemical poorness of the running waters is an expression of a corresponding poverty, of the soils of the headwater zones, in the same ions, among them also in nutrients for the vegetation. The chemistry of the water revealed itself, by the way, as an excellent indicator for getting a first idea of the Amazonian landscape-ecology, too, especially of the nutrient-household of the ecosystem of the Amazonian Terra firme with the high rain-forest.

SUMÁRIO

PESQUISAS EM ÁGUAS DA AMAZÔNIA

Não há nenhuma outra região no globo na qual a água faz um papel igualmente decisivo, na formação e no caráter da paisagem, como na Amazônia. O clima úmido fez desenvolver-se, naquela enorme planície baixa, o maior e mais extenso sistema potâmico do mundo.

Já o descobrimento e a conquista e a colonização da nossa região eram ligados aos corpos d'água de forma que o conhecimento destes foi, desde o início, de importância primordial para os espanhóis e portugueses quando se fizeram novos donos deste país. As pesquisas

em águas amazônicas começaram, pois, com o mapeamento dos cursos de água cujo aperfeiçoamento concluiu-se somente no tempo atual com a elaboração dos mapas modernos, baseados em aerofotografias.

Porém, já os cronistas da primeira expedição, da de Pedro Teixeira em 1637/38, a qual planejadamente subiu e desceu o Amazonas desde a foz até os Andes, ACUÑA e ROJAS, eram observadores de uma visão tão vasta que eles notaram, em princípio, quase todos os aspectos que as águas amazônicas ofereceram, nos tempos posteriores, à curiosidade científica dos homens. Além da cartografia — e da hidrobiologia que se tratará, neste simpósio, numa conferência especial — aqueles relatórios já tocaram nos seguintes complexos:

Anastomoses entre diferentes sistemas fluviais (pela menção do conexo entre o Rio Negro e um rio que desemboca no oceano);

Morfologia dos rios (pelas indicações sobre larguras e profundidades);

Tipos de rios (pela descrição da água preta do Rio Negro);

Peculiaridade da Várzea no conjunto da paisagem amazônica (pela observação da fertilização periódica pelas inundações anuais);

Conteúdo em nutrientes e Ecologia da região inteira (pelo julgamento — aliás errôneo — da qualidade dos solos).

Anastomoses entre rios de sistemas potâmicos diferentes foram provados cientificamente pela primeira vez por HUMBOLDT quando navegou pelo Cassiquiare. Hoje conhecem-se mais ligações entre o sistema amazônico e outros sistemas fluviais sul-americanos.

Na Morfologia dos rios amazônicos, dois problemas destacam-se no interesse dos geógrafos e limnólogos: os perfis dos leitos dos grandes rios, e os cursos inferiores, lagoiformes, de muitos afluentes. As primeiras determinações de profundidades grandes (na "garganta" de Óbidos, SPIX & MARTIUS encontraram 83 m) foram provadas e até superadas por recentes sondagens de éco, no rio Negro (~ 100m) e no Baixo Amazonas; o fundo do leito do Baixo Amazonas revelou-se como consistindo de material que se desloca em forma de "ripple-marks" gigantescos, de verdadeiras dunas. Os cursos inferiores de muitos afluentes, alargados desproporcionalmente e transformados até em "lagos de terra firme", reconheceram-se, primeiramente por DENIS, como sendo "vales afogados"; limnologicamente, estas seções de cursos de rios assemelham-se mais a lagos do que a rios.

Como tipos de rios amazônicos estabeleceram-se os de rios de água "branca" (barrenta), de água clara (transparente) e de água preta. Os tipos dependem de fatores de paisagem nas regiões das cabeceiras (relêvo, clima, cobertura vegetal), porém não são absolutamente distintos um do outro e permanentes mas podem ser ligados por tipos intermediários, ou até podem variar periodicamente ou casualmente para o mesmo rio.

A Várzea do Baixo Amazonas, tão diferente, na qualidade e fertilidade do solo e na vegetação, da terra firme, explica-se como produto de colmatagem geologicamente recente do vale afogado do Amazonas, sendo desta forma, segundo FITTKAU, uma prolongação, ao longo do curso da água branca do Amazonas, do material sedimentar da faixa pré-andina, um apêndice à mesma através da Baixa Amazônia. Este material sedimentar da faixa pré-andina difere, pela origem geológica e pela idade, nas suas qualidades pedológicas, dos solos das camadas do arqueano e do terciário da terra firme do Baixo Amazonas.

O conteúdo em nutrientes concluiu-se de análises químicas de águas de rios e igarapés e de água freática. Já as primeiras análises feitas por KATZER revelaram uma surpreendente pobreza em sais dissolvidos. Análises posteriores de

águas de diferentes zonas geológicas provaram esta pureza química geral, havendo somente poucas exceções, p. e. nas faixas do carbonífero. Tal pobreza das águas correntes é uma expressão de pobreza correspondente, dos solos nas cabeceiras, nos mesmos iônios, entre eles também em nutrimentos para a vegetação. O quimismo das águas, pois, mostrou-se como excelente indicador para ganhar uma primeira idéia também da Ecologia da paisagem amazônica, especialmente do metabolismo de nutrimentos do ecossistema da terra firme amazônica com a floresta alta pluvial.

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COMPARATIVE LIMNOLOGY OF THE STREAMS OF FLORIDA AND THE UPPER AMAZON BASIN

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(With 7 text-figures)

The long history of lake limnology has made possible comparative regional studies based on a period of many years. A typical example of this is the expedition made by BRUNDIN (1956) to the high mountain lakes of the southern Andes for the purpose of comparing these lakes with the equivalent lakes of Northern Europe. As was pointed out by BECK (1956), limnology has been taught in North America largely in schools located in lake regions with a consequent lack of emphasis or even minor efforts with regard to streams. Most studies of streams in North America have been made by federal or state agencies for the purpose of determining water quality in connection with pollution abatement, fisheries resources, the effects of impoundments, etc. Most of this work either ends up in the files of the aforementioned governmental agencies or is occasionally

distributed in the form of mimeographed reports. These reports are frequently an accumulation of results gathered individually by engineers, chemists, bacteriologists, and biologists with the result that most lack the integrated approach of a true limnological survey, geology being the one factor most frequently neglected.

The following quotation from HUTCHINSON (1963: 689) reflects to a large degree what has been stated above: "The whole subject of rivers, now ordinarily though not philologically subsumed in limnology, appears to him [the author] as a marvelous foreign territory explored by workers whose audacity is admirable in view of the difficulty of getting a theoretical grasp of the subject."

The many excellent publications of SIOLI, FITTKAU, and KLINGE & OHLE give a rather thorough understanding of the limnology, in

its total aspect, of the streams of Amazonia. My own work with the streams of Florida has extended over a period of 25 years and is sufficient, I believe, for a comparison of the streams of the two areas in question.

I wish to express my sincere gratitude to the Association for Tropical Biology and the National Academy of Sciences for making possible my participation in this Symposium.

FLORIDA AND ITS STREAMS

The geology of the State is of primary importance in Florida limnology. Florida is underlain entirely by limestones, marls and sands of tertiary and quarternary origin which is very similar to the geological background of certain areas of Amazonia. One striking difference is the presence of considerable quantities of dissolved phosphorus

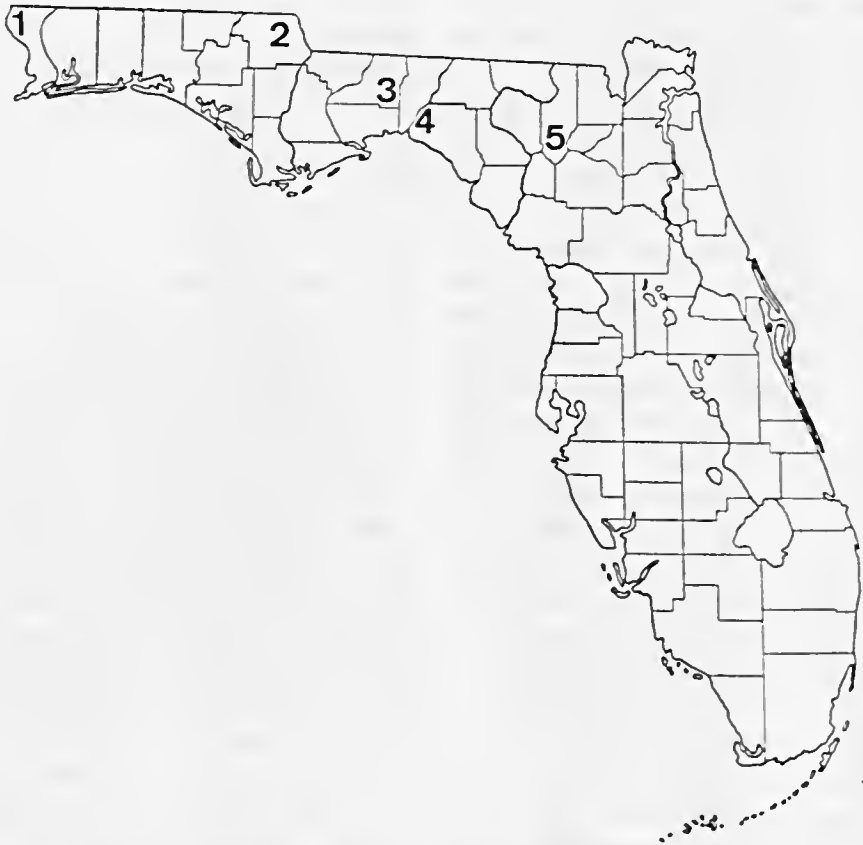


Fig. 1 — Florida (1 — Perdido River; 2 — Chipola River; 3 — St. Marks River; 4 — Aucilla River; 5 — Santa Fe River).



Fig. 2 — *Alapaha River, during normal or low flow.*

tes in most of the waters of Florida.

With the exception of the extreme western panhandle, Florida is an area of Karst topography typified by innumerable sink-holes, lakes of solution origin, disappearing rivers (Figs. 1-3), numerous springs, and areas with no streams at all. According to the geologists, Pleistocene deposits due to changes in sea level have concealed a Karst topography even more striking than that of the classical region.

It is in the area of topography that another striking regional difference occurs. Florida has a maximum elevation of about 400 feet with stream gradients in some

areas sufficient for the formation of rapids but no surface waterfalls over four feet in height.

According to COOKE (1963), Florida is divided distinctly into five topographic regions (Fig. 4). An additional topographic area was delineated by BECK & BECK (1959) and designated as the Relict Area. This area is one of special interest to the biologist as it consists of cool, shaded ravines in which are found many species of plants and animals representing either species confined to that area or relict populations of species not found elsewhere south of the Piedmont of northern Georgia.

The highest elevations in Florida occur in the Central Highlands and

the Western Highlands while the Coastal Lowlands occupy a major portion of the State of Florida and extend entirely around the coast, ranging in width from a very narrow strip in the extreme western panhandle to their greatest width in the southern portion of the State where the southern third of the peninsula is entirely lowland. The Tallahassee Hills is an area of rolling hills of high pineland and hardwood forests. The term "Marianna Lowlands" is a misnomer since the area is only slightly lower in general elevation than the two adjacent areas. It is, however, one of the most interesting areas with some of the most striking Karst topography in the State and has the only caverns developed for public use.

The climate of Florida ranges from south temperate in the northwestern panhandle to tropical in the Keys. According to PROVOST (undated manuscript), no part of the mainland of Florida is truly tropical despite the presence of many tropical plants and animals (Fig. 5).

Fig. 5 shows several items of special interest with regard to the climate of Florida. Foremost is the influence of the proximity of the Gulf Stream to the east coast, extending the subtropical and Floridian regions much farther up the east coast than they extend up



Fig. 3 — Alapaha River, in flood.

the west coast. The subtropical region delineates the range of the large bromeliad, *Tillandsia utriculata*, and the West Indian land crab, *Cardisoma guanhumii*.

The 58.° January isotherm represents roughly a zone of intergradation between southeastern and Floridian, subspecies in the field of herpetology. Thus in the Floridian region are found most of the species and subspecies of endemic reptiles and amphibians. The 64.° isotherm crosses another area of intergradation between Floridian and South Floridian subspecies of reptiles (CARR, 1940).

Figure 6 is a climatograph based on mean monthly temperatures and rainfall for the Miami (sub-

tropical) area. It will be noted that the climatograph is an almost typical example of a tropical annual cycle involving a hot, rainy season and a cool, dry season. BATES (1864: 31) makes the following statement with regard to the climate of Belém: "A little difference exists between the dry and wet seasons; but generally, the dry season, which lasts from July to December, is varied with showers, and the wet, from January to June, with sunny days."

COMPARATIVE LIMNOLOGY

SIOLI (1964, 1965) presents excellent summaries of the limnological features of Amazonia in which he divides the streams of the area into three basic types. BECK (1965) lists five different types of streams found in Florida. These classifications are listed and compared in Table 1.

The "white" water stream of SIOLI (1964: 1054) is quite similar to the larger rivers of BECK. Ran-

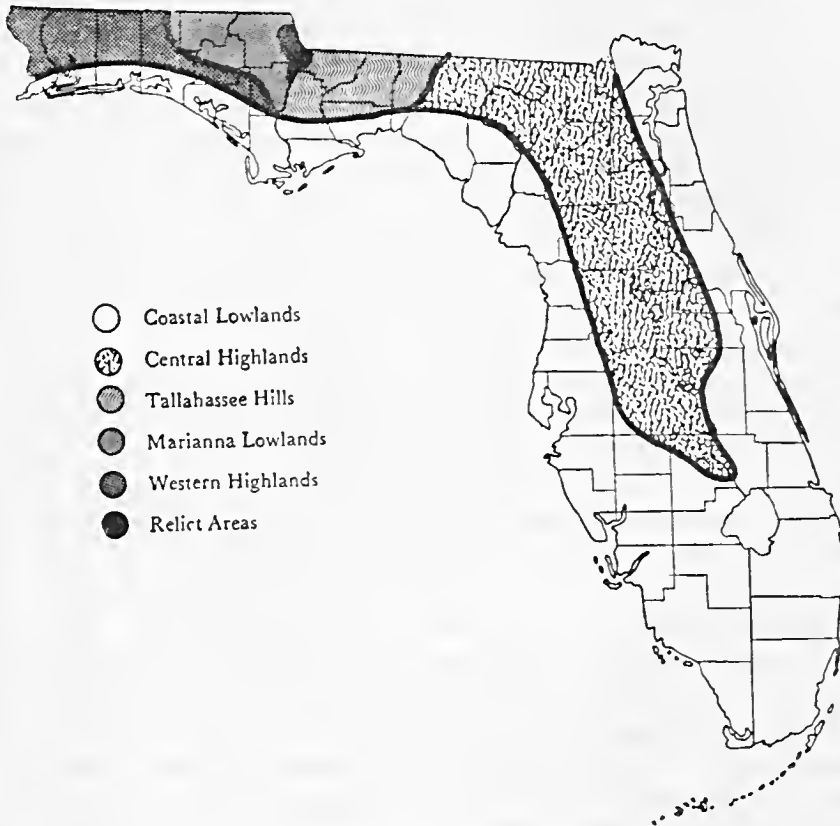


Fig. 4 — Topographic regions of Cooke.

TABLE 1
Stream Classification

<i>Sioli</i>	<i>pH</i>	<i>Beck</i>	<i>pH</i>
1. "White" water.....	6.5—6.9	Larger rivers.....	6.5—6.9
2. "Clear" water.....	6.4—6.65	Calcareous streams.....	7.9—8.2
3. "Black" water.....	3.8—4.9	Sand-bottomed streams.....	5.7—7.4
4. "Black" water.....	-----	Swamp-&-bog streams.....	3.8—6.5
5. -----	-----	Canals of southeastern Florida	-----

ges of pH are identical, probably by coincidence since the figures given for the larger rivers of Florida represent only one stream. With the exception of the St. Johns River which is unique (Numeral 6, Fig. 7), these larger rivers are quite similar chemically and physically. The values selected for comparative purposes in Table 1 are for the Apalachicola River (Numeral 3, Fig. 7) which has been studied more thoroughly than the others. Larger rivers, such as the Escambia, Choctawhatchee, Apalachicola and Ochlocknee, are all interstate streams rising in the hills of Alabama and Georgia, and all are consistently turbid due to a suspension of Montmorillonite clay giving these waters a whitish or slightly yellowish appearance and reducing light penetration to a major degree.

The second category of SIOLI, the "clear" water stream, is somewhat comparable to the calcareous stream of BECK although uniformly lower in pH. The calcareous stream originates entirely, or to a major degree, from springs although ge-

nerally there are lateral contributions of colored swamp or lake drainage. Consequently, though the water is very transparent, it often has a yellowish color.

The "black" water stream of SIOLI is apparently quite similar to both the sand-bottom and the swamp-and-bog streams in Florida (Table 1). Although I consider these two types of Florida streams distinctive, the only real difference is found in the extremely low velocity of the swamp-and-bog stream and in chemical differences associated with this lowered velocity (extremely low pH, alkalinity, hardness; extremely high color due to "humic acids"). Despite the higher pH limits of the sand-bottom stream in Florida, it is still comparable to the "black" water stream of SIOLI due to its high color.

The canals of southeastern Florida are listed in the publication of BECK (1965) as a stream type although they are not streams in any true sense of the word. At most times these canals have a distinct

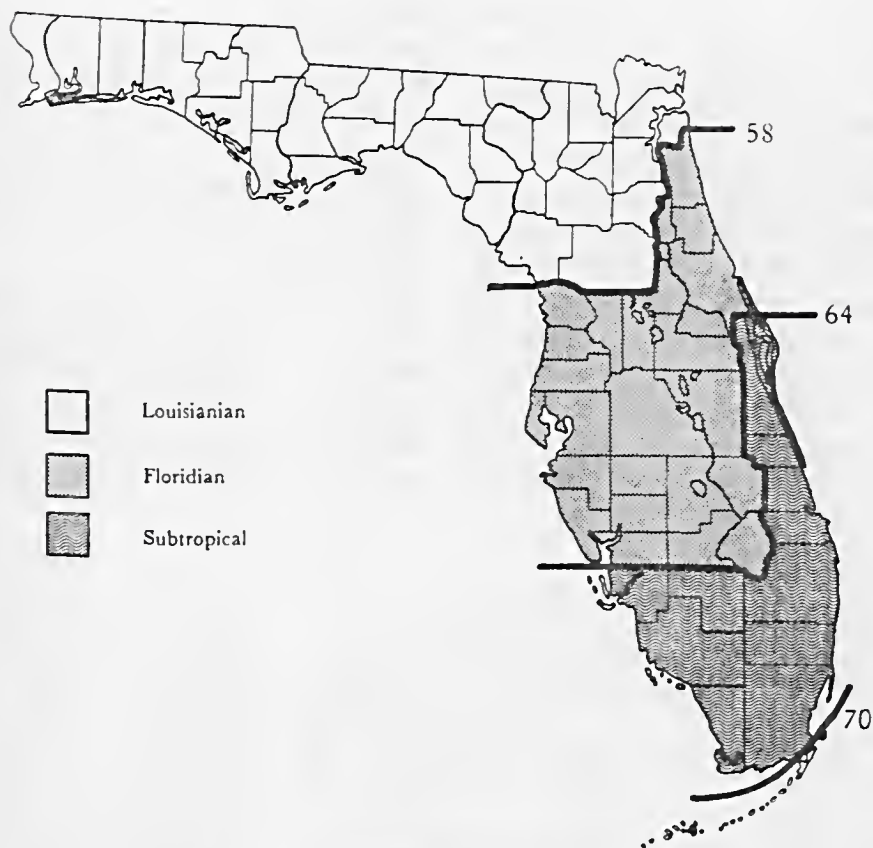


Fig. 5 — *Climatic regions of Provost.*

seaward flow although at other times there may be no movement of the water at all. They are listed as a stream type simply because they are all that remain of the former streams along some 140 miles of the coast of southeastern Florida.

It would thus appear that both Amazonia and Florida possess three basic, comparable types of streams with a certain amount of intergradation among the different types.

FITTKAU (1964) discusses limnological features of the rain-forest streams of the upper Rio Negro basin. The most unusual feature of these streams is their remarkably low concentration of dissolved electrolytes. The stream forming the western boundary of Florida, the Perdido River (Numeral 1, Fig. 1), is quite similar chemically to the rain-forest streams. Table 2 compares certain factors in these streams. It will be noted that these streams

are distinctly acid, may have very high free carbon dioxide content and are very low in hardness, alkalinity, and chlorides. FITTKAU attributes the paucity of life in the rain-forest streams to the extreme poverty of electrolytes and the lack of light due to the dense rain-forest canopy. While the Perdido River is neither as densely shaded nor quite as low in dissolved electrolytes, it is not a particularly productive stream. In areas where vegetation occurs, growths of aquatic

plants, which may support quite a rich and varied invertebrate fauna, are generally confined to small areas. Most of the stream bottom consists of coarse, shifting sand and is inhabited only by the larger species of burrowing dragonflies and mayflies.

At this time no attempt will be made to compare the biology of the streams of Amazonia and Florida due to the fact that relatively little has been published thus far concerning the biology of the

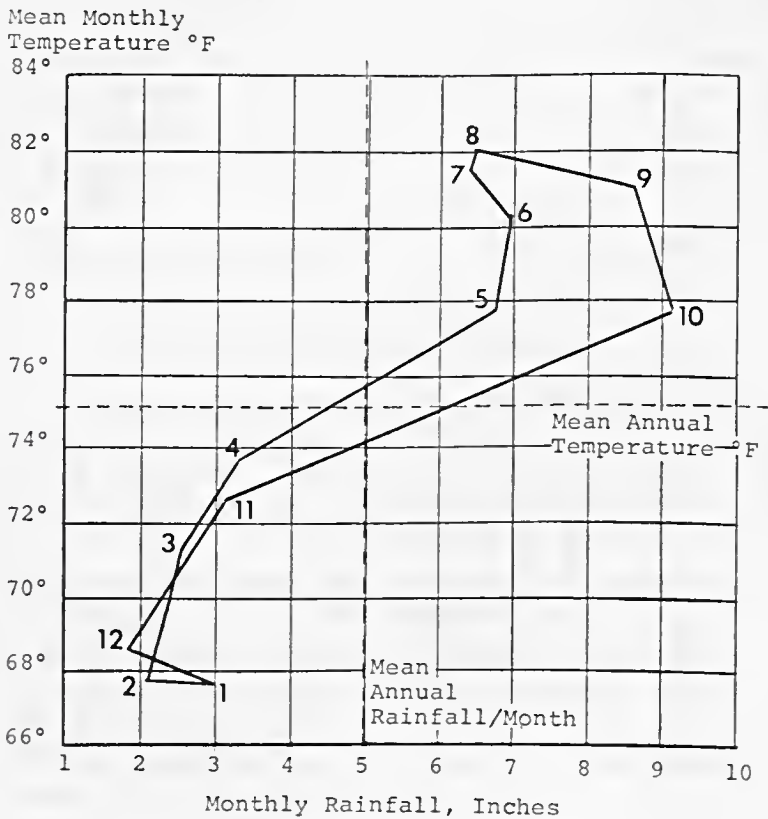


Fig. 6 — Climatograph: Miami area.

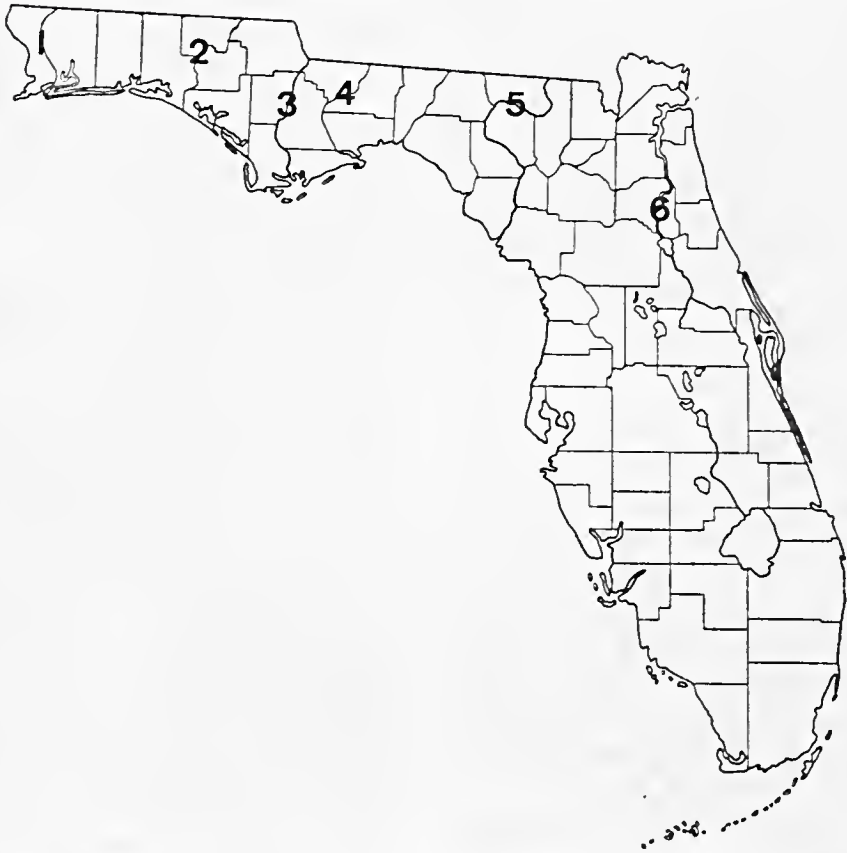


Fig. 7 — Florida, larger rivers: (1 — Escambia River; 2 — Choctawhatchee River; 3 — Apalachicola River; 4 Ochlocknee River; 5 — Suwannee River; 6 — St. Johns River).

streams of Amazonia despite extensive study of the area performed especially by biologists from *Hydrobiologische Anstalt der Max-Planck-Gesellschaft*, and also because the biota of the streams of Florida has not been thoroughly studied.

In December, 1965, following several months spent in Amazonia, Dr. Fittkau was our guest in north-

ern Florida for a brief period. During this time we spent one day examining streams in our area, mainly sampling for invertebrates. We were truly astonished at the number of different genera in diverse groups of invertebrates that Dr. Fittkau could identify immediately. Many of these, including the Odonata, Trichoptera, Coleoptera, Plecoptera, Ephemeroptera,

mollusks and other smaller groups, possessed genera which I did not realize existed in Amazonia. Although Dr. Fittkau has studied the chironomid fauna of Amazonia for some years, and my wife and I have conducted similar studies in Florida, too little has been published to support any significant comparisons at present.

CONCLUSIONS

Both Florida and Amazonia have three similar, basic types of streams. Although significant differences exist among the three stream types of the two areas in question, there are enough chemical and physical similarities to suggest that the approach of comparative limnology is worthwhile. In both areas, intergradation exists among all stream types.

The most interesting features of the streams of both areas are the factors in which they differ. Foremost among these differences is the high dissolved nutrient concentrations normally found in the waters of Florida in contrast with the extremely low concentrations in the streams of Amazonia. Second is the significantly higher velocity of the upper Amazon streams, supporting groups of invertebrates that have not been found thus far in Florida. One type of stream not found in Florida is the rain-forest stream described by FITTKAU.

These streams are so covered by a canopy of trees that only 0.5 to 1 percent of the total solar radiation at noon reaches them. The Perdido River, compared with the rain-forest streams in Table 2, is quite similar in some respects to those streams.

It is my belief that principles exist in stream limnology just as they do in the limnology of lakes. Unfortunately, it requires more effort to discover them. Ever since the origin of the concept of a lake as a microcosm, the possibilities inherent in the study of a more or less closed system have appealed to a great many students. On the other hand, streams apparently have had less appeal, perhaps due to the extensive variation of limnologic factors in regard to both time and space. This lack of appreciation for or interest in streams is reflected in the recent enactment of the Wild Rivers legislation by the United States government making rivers the last natural resources to be recognized and preserved in their natural state for the benefit of future generations.

Already we have developed a specialized terminology with regard to flowing waters including such terms as rheophile, rheobiont, *Spritzwasserarten*, etc. in addition to many generic names of aquatic organisms beginning with Rheo. or Potamo. Many special items of

TABLE 2
Comparison of Low Electrolyte Waters

Upper Rio Negro	Factors	Perdido River
4.1—5.2	pH	5.3—5.5
4.4—91.5	free CO ₂ mg/L	60—150
0—0.65° DGH	hardness	5—8 mg/L
0—3	ehlorides mg/L	4—8
0—0.5 NO ₃ -N		0.1 NH ₃ -N
0—7	bicarbonates mg/L	10—15

equipment have been developed specifically for work in streams: the fresh water current meter, the electronic oxygen probe (especially the type which measures oxygen only in waters with a minimum velocity of 1 foot per second), the Brundin net, the Catherwood diatometer, the Hestler-Dendy plate sampler and the Tebo sampler. Both the specialized terminology and specialized equipment reflect distinctive aspects of a specialized field and suggest rather precisely where to look for possible universal principles of stream behavior. The following items are offered as being basic to the formation of any principles of stream limnology:

1. A stream is a body of water of geographical significance typified by unidirectional flow.
2. A stream is highly variable in its physical, chemical and biological characteristics with respect to both time and space.

3. These variations are cyclic in nature, the variations depending on both geographic locations and climatic differences.
4. A stream is a function of its entire drainage basin.
5. Water is the most extraordinary of all compounds known to science. Whether in lakes or in streams or indeed in the oceans themselves, water reacts everywhere to the same laws of physics and chemistry regardless of the container in which it is found.

SUMMARY

Streams of the areas in question have many features in common. The basic classification of stream typology as presented by SLOLI (1964, 1965) does not differ greatly from the classification of Florida streams as proposed by BECK (1965).

Although there are some striking similarities in the streams of

the two areas in question, it is in the differences — chemical, physical, biological, and geological — that we find the most striking and informative features. A comparison of both the common and the distinctive features may contribute significantly to a better understanding of comparative regional limnology and further development of that branch of limnology devoted to the study of flowing waters.

Probably more has been published on the limnology of the Upper Amazon than on all the streams of Florida combined. This literature makes possible comparisons between streams of an area in which I have worked for many years and streams of an area which I have never seen. The writings of Sioli, Ohle, Klinge, and Fittkau, in addition to correspondence and personal contact with these workers, have further contributed to an understanding of mutual and unique problems. Dr. Fittkau spent several days with us in December, 1965, and we were astonished at his familiarity with our local stream faunas. He recognized many genera of aquatic invertebrates that we did not realize existed in South America.

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LA SUPERFAMILIA UNIONACEA EN LA CUENCA AMAZONICA

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(Con 10 figuras en el texto)

El conocimiento sistemático de las Nayades de la cuenca del Amazonas resulta bastante pobre aun si lo comparamos con el que se posee respecto al resto de América neotrópica. Tal situación no depende tanto de la falta de trabajos del tipo corriente sino, por el contrario, de la existencia de una gran cantidad de tipos descritos sobre la base de unos pocos ejemplares, muchas veces de pobre conservación, con referencias geográficas imprecisas cuando no con desconocimiento total de su procedencia. A esto debe sumarse la falta de colecciones básicas, los problemas que plantea la gran extensión de la cuenca y, sobre todo, la carencia de trabajos orgánicos y de cierta continuidad, respaldados en métodos adecuados de investigación.

Resulta un hecho bien conocido aunque muchas veces olvidado en los trabajos sistemáticos, que las

Nayades experimentan notables variaciones bajo la acción modificadora del biotopo en que se desarrollan, dando así lugar a formas de reacción sumamente diversas, de modo que no es de extrañarse que los distintos autores, ante ejemplares aislados de tales variaciones, hayan podido distinguir otros tantos tipos diferentes describiéndolos como tales. Tal situación, que es de validez general, ya fue señalada en nuestro caso por HAAS en varias oportunidades y en especial en su trabajo de 1930/31 (19). Recientemente se ha dado a conocer un interesante ensayo estadístico por parte de ZILCH (53), respecto a las especies paleárticas, donde se señala que de 1309 especies descritas sólo resultan válidas 19 de ellas y 58 subespecies. Esto revela incuestionablemente la necesidad de efectuar estudios revisivos en profundidad, tendiendo a la reducción

de la frondosidad sistemática resultante de una modalidad de trabajo puramente descriptiva y de escaso fundamento científico.

A tal efecto venimos ensayando desde un tiempo considerable la aplicación de los caracteres determinativos preconizados por HAAS, fundado en el estudio de la escultura umbonal y del análisis de la forma de la concha joven, combinándolos con los propuestos por ORTMANN, basados en el estudio del "glochidium", la posición de la marsupia en la branquia interna y la forma y estructura de las branquias. A todo ello debe sumarse, lógicamente, el análisis conchológico de amplias colecciones correspondientes a una serie de localidades representativas dentro de los grandes sistemas hidrográficos del continente, tratando de correlacionar tales variaciones con los caracteres del biotopo en que se desarrollan.

Debemos confesar que tal método sólo ha podido ser ensayado parcialmente en el caso de los Unionacea del Amazonas, ya que no hemos podido contar con la cantidad de material suficiente, sobre todo con las partes blandas conservadas, ni con mayores informaciones acerca de los caracteres de las aguas en que fueron obtenidas, lo que ha venido a limitar considerablemente los alcances del trabajo propuesto.

Pese a lo expuesto, se considera de interés dar a conocer el presen-

te ensayo en la convicción de que el mismo ha de ser de utilidad para esclarecer, aunque sea en parte, la complicada maraña sistemática creada en torno a estos moluscos, y que es necesario proveer a una información revisiva actualizada — aun a riesgo de cometer errores — que persistir en una situación como la actual, tan confusa como estéril, y carente de mayor significación científica.

LOS UNIONACEA AMAZONICOS

Los Unionacea de la cuenca amazónica están comprendidos en la familia Hyriidae, que contienen a todos los representantes de Australasia y América neotrópica. Los últimos integran la subfamilia Hyriinae, agrupándose en tres tribus: Prisdontini, Castaliini y Diplodontini (44). Las dos últimas son comunes a todas las grandes cuencas del continente sudamericano, en tanto que la primera sólo se da en el Amazonas y en algunas cuencas más septentrionales, faltando completamente en los ríos integrantes del sistema del Plata.

La tribu Diplodontini comprende sólo el género *Diplodon* Spix, cuyos dos subgéneros *Diplodon* ss y *Rhipidodonta* Mörch, poseen especies en la Amazonia. Castaliini posee dos géneros: *Castalia* Lamarck y *Callonaia* Simpson (10), ambos con representantes amazónicos, siendo el último exclusivo de esta cuenca.

La tribu Prisodontini es descompuesta en los trabajos más actualizados (42) en dos géneros: *Paxyodon* Schumacher y *Prisodon* Schumacher, siendo el último descompuesto en dos subgéneros: *Prisodon* ss y *Triplodon* Spix. En realidad, como se verá luego, se considera que tal ordenamiento requiere considerables ajustes y que, aun a título provisório, los últimos pueden ser llevados a la categoría de géneros.

El rasgo más característico de los Unionacea de la cuenca amazónica está dado por la presencia de un género propio de la tribu Castaliini, el género *Callonaia*, y por contener a los representantes de la tribu Prisodontini, que si bien existen también en los ríos de las Guayanas, son características de este sistema, faltan por completo en las aguas de los grandes potamos que concurren al Río de la Plata.

Cabe destacar que aunque en la cuenca amazónica se dan todos los géneros que existen en la del Plata, poseyendo además algunos exclusivos y otros que faltan en la última, el número de las especies registradas no es mucho mayor, ya que gran parte de los últimos, por no decir su totalidad, son monotípicos. Es decir, que el número de especies realmente válidas, en general, aparece como muy limitado contrastando tal situación con la

amplitud de la extensión geográfica alcanzada por las mismas.

La enorme extensión de la cuenca también se refleja en diferencias distribucionales que, de momento, no parecen muy claras. De mucho interés resultan en tal sentido algunas áreas de engranaje, especialmente las que definen los afluentes que arrancan en puntos próximos a las nacientes del río Paraguay, donde parece producirse el ingreso de algunas especies propias del sistema del Plata, y viceversa, fenómeno este que debe ser reciente o que no alcanzaría todavía una gran extensión sobre ambas cuencas.

Tribu: DIPLODONTINI

Género *DIPLODON* Spix

El género *Diplodon* Spix es el más común y extendido entre todos los Hyriinae, presentando una evidente unidad de conjunto, distinguiéndose claramente de los restantes géneros de la subfamilia. La conformación regular de la concha, la sencillez de la escultura umbonal y del aparato articular de las valvas, son bien característicos y no exigen mayores comentarios. Dentro de este conjunto se distinguen dos subgéneros: *Diplodon* ss y *Rhipidodonta* Mörch, especialmente en base a la forma "larval", aunque también puede sumarse a estos ciertos detalles conchológicos y anatómicos menos claros y defini-

torios. El subgénero *Diplodon* ss, posee "glochidium" parásito, en tanto que *Rhipidodonta* se caracteriza por que las crías se desarrollan directamente, completando en la marsupia la formación de la almeja juvenil, es decir, sin requerir una etapa de vida parásita.

Subgénero *DIPLODON* ss

Diplodon (Diplodon) granosus granosus (Bruguière)

Unio granosa Bruguière, 1792

HAAS al ocuparse de esta especie en su importante trabajo de..... 1930/31 (19), distingue la existencia de tres subespecies, haciendo llegar a la típica desde las Guayanas al estado de São Paulo, en tanto que distingue a *D. granosus elypticus* (Spix) para el río San Francisco y los ríos costeros de Bahía, y a *D. granosus multistriatus* (Lea) para los ríos de la pendiente atlántica del sur de Brasil hasta el estado de Santa Catarina y el Alto Paraná.

Tales distingos no parecen muy claros ni correctos pero, de cualquier forma, pueden ser aprovechados en parte, señalando que lo considerado como *D. granosus elypticus* corresponde parcial o totalmente a simples formas de *D. rhombeus* (Wagner) y reservando el nombre de *D. granosus multistriatus* para el conjunto de formas que se hacen presentes en los

ríos de la pendiente atlántica de Brasil, al sur del río San Francisco, y en el Alto Paraná.

Cabe señalar, además, que entre los materiales estudiados por HAAS, así como por otros distintos autores, no parecen encontrarse ejemplares de esta especie de procedencia amazónica. Por mi parte sólo posee unos pocos ejemplares, mal conservados, que quizás puedan corresponder a esta especie y cuya única referencia es la "Río Amazonas". El hecho llama poderosamente la atención ya que si la especie se extiende desde las Guayanas hasta Santa Catarina y el Alto Paraná, parecería definir un extenso hiatus correspondiente a toda la cuenca amazónica.

Claro está que es posible que esta anomalía pueda atribuirse a las deficiencias de las colecciones existentes, o a falta de una verdadera relación específica entre *D. granosus*, propiamente dicho, y el grupo de especies que se subordinan corrientemente a *U. multistriatus* Lea. Caso contrario debemos admitir que el Amazonas posee condiciones que resultan inadecuadas al desarrollo de *D. granosus*, lo que indicaría que se trata de una especie particularmente estenotopa. El problema merece un adecuado estudio y sólo puede ser resuelto mediante la intensificación de las investigaciones acerca de la especie típica, muy poco conocida, y la

realización de colecciones sistemáticas en la cuenca que nos ocupa.

**Diplodon (Diplodon) rhombeus
rhombeus (Wagner)**
(Fig. 2)

Unio rhombeus Wagner, 1827
Unio rotundus Wagner, 1827
Unio patelloides Lea, 1860
Diplodon enno Ortmann, 1921
Diplodon jacksoni Marshall, 1928
*Diplodon (Diplodon) beskeanus
nordestinus* Haas, 1938

En diversas publicaciones anteriores se hizo referencia al hecho de que *D. rotundus* Wagner y *D. fontaineanus* Orb., pertenecían a una misma especie, la que en su distribución probablemente alcanzaría también al Amazonas. Recientes estudios llevados a cabo en el museo de Senckenberg, Frankfurt, sobre la colección de Ihering, han venido a confirmar tal identidad y a demostrar que la especie se extiende al Amazonas por el norte, llegando por el sur hasta el Alto Paraná y los ríos costeros hasta el estado de Santa Catarina, experimentando a lo largo de tan extenso territorio grandes variaciones conchológicas que dieran lugar a una considerable cantidad de tipos descriptos.

En conjunto, podemos distinguir dos subespecies: *Diplodon rhombeus rhombeus* (Wagner) para el Amazonas, el San Francisco y los ríos de la pendiente del Atlántico comprendidos entre ambas cuencas; y a *D. rhombeus fontaineanus*

(Orb.), que se extiende desde el río Doce y los ríos costeros hasta el estado de Santa Catarina y el Alto Paraná.

La identidad de *D. rhombeus* con *D. rotundus* no deja lugar a dudas, confirmándose así lo expresado por HAAS en su fundamental trabajo de 1930/31. Lo mismo cabe expresar respecto a *D. patelloides* (Lea). Pero, a este conjunto de formas decididamente redondeadas, que HAAS considerara equivocadamente como propias del subgénero *Cyclomya* Simpson — *Rhipidodonta* Mörch, se hace necesario sumar otro, algo más bajas, aunque local y circunstancialmente pueden adquirir perfil redondeado. Entre ellas se encuentra *D. enno* Ortmann, *Diplodon beskeanus nordestinus* Haas y *D. jacksoni* Marshall. El rasgo común que las vincula está dado por un conjunto de caracteres a los que nos hemos referido anteriormente (5), y entre los que se destacan una escultura de variable convergencia, a veces con varias costillas confluentes, una ligera depresión del margen ventral por debajo de los umbones, la forma moderadamente alargada de la concha juvenil con tendencia posterior al crecimiento en altura, el escaso desarrollo del aparato articular de la charnela, la tonalidad azulada-grisácea del nácar y el color pardo oscuro o negro mate del periostraco. Por otra parte, la conformación

del "glochidium" parásito y la posición de la marsupia en la branquia interna (subcentral o ligeramente desplazada hacia adelante) aportan otros tantos elementos diagnósticos complementarios.

Cabe señalar la posibilidad de que *D. ellypticus* (Spix) corresponda también a este conjunto de formas, cuando que en general se lo considerara vinculado a *D. granosus*. En este caso, los otros nombres deberían subordinársele por razones de prioridad.

Diplodon (Diplodon) parodizi
Bonetto

- Diplodon parodizi* Bonetto, 1960
Unio burroughianus Lea, parcialmente en Orbigny, 1834
Unio burroughianus Lea, en Sowerby, 1886
Diplodon charruanus (Orb.), parcialmente en Haas, 1930
Diplodon charruanus (Orb.), en Bonetto, 1953

Esta especie, tan común en aguas del Paraná medio e inferior y del río Paraguay, se hace presente también en los afluentes del Amazonas que nacen en Bolivia, de acuerdo a lo expresado — aunque no muy claramente — por ORBIGNY (41), lo que se deduce del ejemplar que reproduce y comenta SOWERBY (49) * y a lo que hemos podido establecer a través de algunas muestras procedentes del río San Miguel, afluente del Guaporé.

En el resto de la cuenca amazónica parece ser desconocida, lo que

* La referencia de estos autores corresponde a *D. burroughianus* (Lea)

vendría a indicar que se trata de una especie de reciente incorporación a la misma a través de las cabecezas del río Paraguay.

La especie es fácilmente reconocida por su forma moderadamente alargada rematada posteriormente en un ángulo marcado, por el relieve de la escultura con clara convergencia de las costillas centrales, y la posesión de un "glochidium" parásito.

Diplodon (Diplodon) parallelopedon (Lea)
(Fig. 1)

- Unio parallelopedon* Lea, 1834
Unio acutirostris Lea, 1866
 ? *Diplodon trifidus* (Lea), en Ortmann, 1921

En el año 1921 ORTMANN (43) describe, sin proporcionar figura, a lo que considera el verdadero *U. trifidus* Lea, expresando su convicción de que esta especie es amazónica y que la localidad originaria (Buenos Aires), señalada por Lea, correspondería a un error ya que, hasta entonces, no había vuelto a ser encontrada.

En el año 1953, al ocuparnos de la fauna de Nayades del río Paraná (3), señalábamos que esta especie existe, aunque parece ser algo rara, en el Paraná medio.

Por otra parte, el lote original de Ortmann constituido por 6 ejemplares obtenidos por Hase-man en el río Guaporé, cerca de

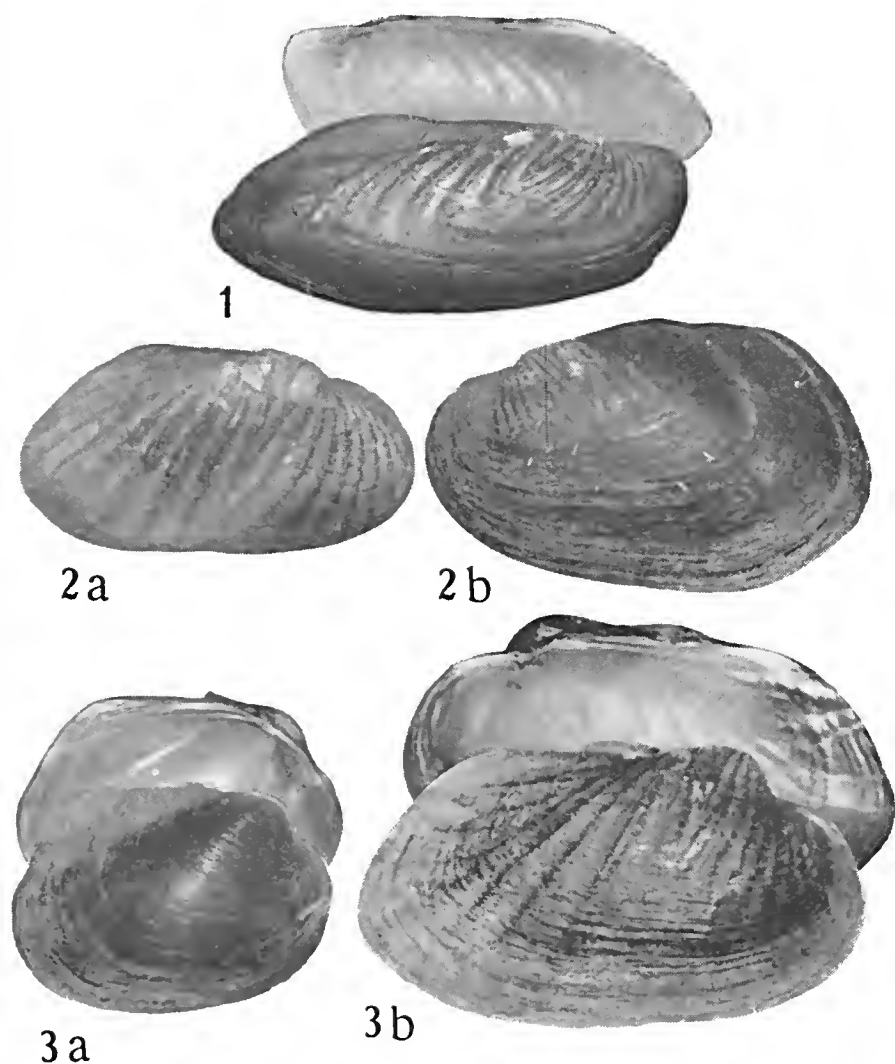


Fig. 1 — *Diplodon (Diplodon) parallelipedon (Lea)*, materiales del Guaporé atribuidos por Ortmann a *D. trifidus (Lea)*; fig. 2 — paratipos de *Diplodon enno Ortmann = Diplodon (Diplodon) rhombeus rhombeus Wagner* (2a: ejemplar de 16mm; 2b: ejemplar de 31mm); fig. 3 — algunas variaciones extremas de *Diplodon (Rhipidodonta) suavidicus (Lea)* (3a: paratipo de *Diplodon garbei Ihering*, Lagoa Juparanã, Espírito Santo, Brasil, ejemplar de 29mm; 3b: paratipo de *Unio hartwrighti Ihering*, Río Amazonas, ejemplar de 16mm).

São Simão, Mato Grosso, Brasil, presenta muchos rasgos particulares que los llevan a diferir consi-

derablemente de *U. trifidus* Lea, especialmente por lo que hace al perfil de la concha joven, al particular

desarrollo de la escultura y a su marcada inclinación hacia atrás. Estudiando las formas jóvenes del lote de Ortmann, se advierte que el perfil se ajusta estrechamente al de *D. parallelopipedon*, y que si bien la escultura posee una mayor acentuación, número de costillas, y parece más inclinada, sus rasgos esenciales son prácticamente los mismos. El color del periostraco, bastante más claro, tampoco constituiría un rasgo excluyente, ya que los ejemplares de Ortmann parecen provenir de aguas lóxicas, en tanto que la totalidad de nuestros materiales del río Paraná y aun del Uruguay, proceden de aguas lénticas. Consideramos que esta misma circunstancia puede explicar las diferencias en la escultura y el perfil de los ejemplares adultos, diferencias estas que, en caso de ser constantes en los materiales amazónicos, podría justificar el distingo de una subespecie.

De cualquier manera, la presencia de *D. parallelopipedon* en estas aguas ya fue señalada por d'Orbigny, quien indicó su halazgo en el río San Miguel de Bolivia, que es tributario del Guaporé. Lamentablemente no nos ha sido posible estudiar los materiales de este autor para establecer mejor la relación de los mismos con los ejemplares de Ortmann que comentáramos anteriormente.

Subgénero *RHIPIDODONTA*
Mörch

Diplodon (*Rhipidodonta*)
suavidicus Lea
(Fig. 3)

Unio suavidicus Lea, 1856
Diplodon hartwrighti Ihering, 1910
Diplodon garbei Ihering, 1910
Diplodon kelseyi F. Baker, 1913
Diplodon obsolescens F. Baker, 1913

Esta es una especie característica del Amazonas, aunque parece extenderse hacia territorios más septentrionales — quizás alcanzando el Orinoco — y también hacia el sur, por lo menos hasta el río Doce, en el Estado de Espírito Santo.

La escultura, la conformación de la concha joven, la presencia de un "glochidium" de desarrollo directo y la moderada pero evidente gravitación de la marsupia hacia la parte posterior, proporcionan generalmente suficientes elementos diagnósticos para su fácil identificación, permitiendo de tal manera aclarar considerablemente los problemas sistemáticos planteados en torno a esta especie y al conjunto de tipos que realmente se le deben subordinar.

Diplodon hartwrighti Ihering corresponde evidentemente a esta especie, por lo menos en lo relativo a los materiales de Ihering procedentes del Amazonas, los que

representan sólo una forma de *D. suavidicus*, algo alargada, angulosa, expandida posteriormente y de charnela muy reducida. *Diplodon obsolescens* F. Baker, correspondería a una simple acentuación de los caracteres de tal variación.

Diplodon garbei Ihering, que fuera considerada por HAAS como sinónima de *D. beskeanus* Dunker — *D. rhombeus* Wagner, debe in-

cuestionablemente ser subordinada a la especie que nos ocupa, como lo evidencia el análisis conchológico y lo confirma el estudio del "glochidium" (7).

Diplodon kelseyi F. Baker, corresponde a una forma de *D. suavidicus* (Lea), que ha alcanzado un considerable desarrollo con engrosamiento de las valvas, modificando ligeramente los detalles del contorno. Pero la concha juvenil se

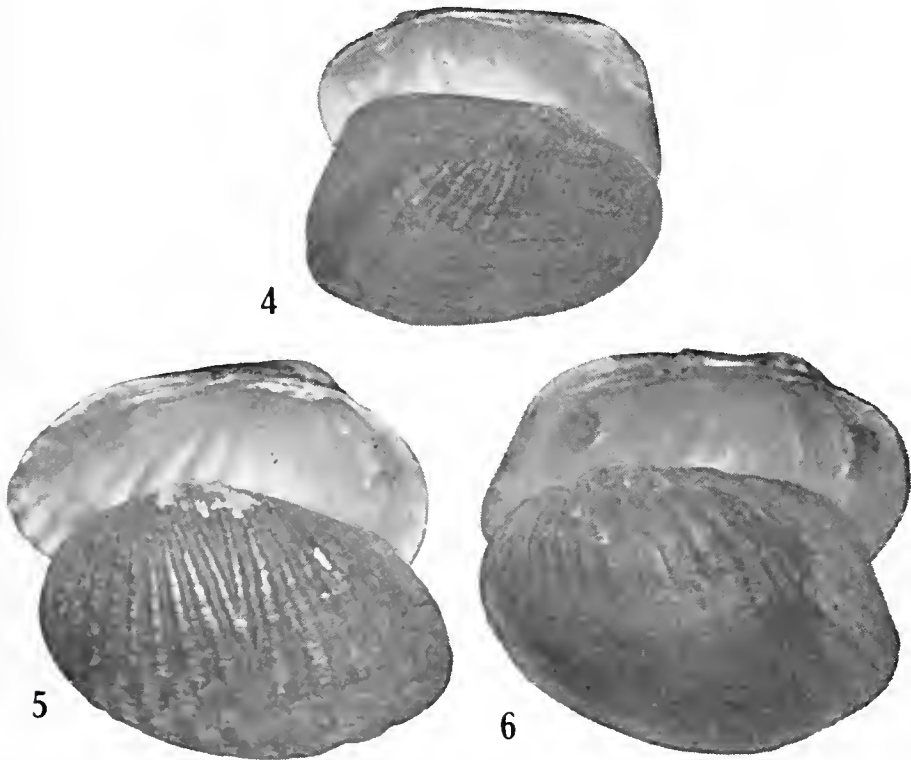


Fig. 4 — *Diplodon* (Rhipidodonta) *hylaeus hylaeus* (Orbigny), río Alto Paraguay (ejemplar de 39mm); fig. 5 — *Diplodon* (Rhipidodonta) *hylaeus pazi* (Hidalgo), laguna adyacente al río Napo, Ecuador, ejemplar de 31mm que reproduce muy bien la forma de *Castalia pazi* Hidalgo; fig. 6 — paratipo de *Diplodon hasemani* Ortmann = *Diplodon* (Rhipidodonta) *hylaeus pazi* (Hidalgo) (ejemplar de 15mm).

ajusta perfectamente a la de la especie de Lea.

Por lo que respecta a los tipos extraamazónicos septentrionales, que presumiblemente deben subordinarse o fueran subordinados a *D. suavidicus*, nos abstenemos de considerarlos aquí ya que poseen una conformación un tanto particular cuyo estudio exige mayor cantidad de materiales del que disponemos o del que hemos podido estudiar hasta el presente.

Diplodon (Rhipidodonta)
hylaesus pazi Hidalgo
(Figs. 4-6)

Unio hylaea Orbigny, 1835

Castalia pazi Hidalgo, 1868

Diplodon hasemani Ortmann, 1921

Diplodon (Diplodon) guaranianus
hasemani Haas, 1931

Ecuadorea bibliana Marshall &
Bowles, 1951

Diplodon hylaesus Orbigny constituye una especie de amplia distribución en el centro del continente sudamericano, presentando una fisionomía inconfundible por el amplio desarrollo de la escultura, su relevancia y gravitación hacia la parte posterior. Aunque no todo parece estar resuelto en torno al conocimiento de esta especie y a los tipos que supuestamente se le atribuyen, creemos que pueden distinguirse dos subespecies: *Diplodon hylaesus hylaesus*, para los ríos del sistema hidrográfico platense, y

D. hylaesus pazi para las aguas de la cuenca amazónica.

La subespecie última, que es la que nos ocupa, viene a caracterizarse por ser en general más redondeada y más regularmente esculturada que la típica. En realidad, el tipo de *U. hylaesus* Orb., correspondiente al Alto Paraguay, se aleja considerablemente de la subespecie amazónica, pero estas diferencias son menos acentuadas en el caso de las formas del Paraguay inferior y Paraná medio, como *U. guaranianus* Orb. y *D. asunsionis* Marshall.

Por lo que hace a los sinónimos consignados, no creo que hagan falta mayores comentarios ni demostraciones para justificar su subordinación. Quizas, no obstante, resulte necesario extenderse un poco respecto a la inclusión de *Ecuadorea bibliana* Marshall & Bowles, forma fósil de la localidad de Biblián, Ecuador, cercana a algunos afluentes del Amazonas. Los depósitos en que la especie fuera encontrada son de edad incierta a estar de los autores, quienes le acreditan una considerable antigüedad en base a que ésta y otras especies de gasterópodos que la acompañan no tendrían representantes actuales. En verdad, no hay nada que separe a *Ecuadorea bibliana* de *Diplodon hylaesus pazi*, siendo los rasgos de la escultura, de marcado tipo convergente, en-

teramente similares. Coincidentes son también el área nodulosa definida hacia la parte posterior y el perfil redondeado de la concha.

Cabe señalar, por último, que esta subespecie parece ser relativamente común en los afluentes del Amazonas próximos a las nacientes del Paraguay, en el Marañón, en el Solimões y el Negro, no existiendo referencias a su presencia en otros puntos de la cuenca.

Tribu: PRISODONTINI

La tribu Prisodontini comprende a un conjunto de especies caracterizadas por la posesión de procesos aliformes a los extremos de la línea dorsal, y el considerable desarrollo del aparato articular de la charnela, con variable tendencia a la formación de denticulos o estrías verticales. El "glochidium" es de tipo parásito, de conformación subtriangular, con dientes divididos distalmente en espinulas agudas.

En un reciente trabajo de OLSON & WURTZ (42) se establecieron bases importantes para la ordenación sistemática del grupo, partiendo de la forma y extensión de los dientes de la charnela respecto a la cicatriz del adductor anterior, y la presencia o ausencia de la escultura. Resumiendo lo expresado por tales autores tendríamos:

- A) Charnela confuertes dientes lamelares anteriores que sobrepasan a la cicatriz del adductor anterior

Género *Paxyodon* Schumacher

(Tipo: *Paxyodon ponderosus* Schumacher, 1817)

- B) Charnela con diente cardinal anterior generalmente no bien definido, a menudo en forma de denticulos, los que alcanzarían pero no sobrepasan a la cicatriz del adductor anterior.

Género *Prisodon* Schumacher

(Tipo: *Prisodon obliquus* Schumacher, 1817)

Este último comprende a los siguientes subgéneros:

- B1) Con superficie de la concha lisa — *Prisodon ss*
 B2) Con superficie de la concha esculturada — *Triplodon* Spix

(Tipo: *Triplodon rugosum* Spix, 1827)

Esta ordenación parece bastante simple y lógica, si bien se estima necesario introducirle algunas enmiendas. Es así que *Prisodon obliquus* Schumacher posee también dientes anteriores que sobrepasan la cicatriz muscular anterior, existiendo 2 en la valva derecha y ge-

neralmente 1 en la izquierda que cumplen tal condición. Esto puede apreciarse claramente en las conchas de ejemplares jóvenes y mediano desarrollo, tendiendo a reducirse en los de mayor tamaño, para ajustarse entonces a la figura de SCHUMACHER. Tal circunstancia y la falta de escultura parece indicar que existen relaciones mucho más estrechas entre *Paxyodon* y *Prisodon*, que entre este último género y *Triplodon* Spix. Además, se considera que este último, por carecer de dientes que sobrepasen la cicatriz del adductor anterior y por la relevancia de la escultura, debe ser elevado a la categoría de género. En consecuencia, el esquema de OLSSON & WURTZ puede ser aceptado provisoriamente con el siguiente reajuste:

A) Charnela con fuertes dientes anteriores que sobrepasan a la cicatriz del adductor anterior. Laterales estriados verticalmente a veces algo divididos. Concha sin escultura.

Género *Paxyodon* Schumacher

(Tipo: *Paxyodon ponderosus* Schumacher, 1817)

B) Charnela con delgados dientes lamelares anteriores que sobrepasan la cicatriz del adductor anterior, los que se reducen sustancialmente con el creci-

miento. Laterales lisos sin estriación vertical. Concha sin escultura.

Género *Prisodon* Schumacher

(Tipo: *Prisodon obliquus* Schumacher, 1817)

C) Charnela fuerte en que los dientes anteriores alcanzan pero no sobrepasan la cicatriz del adductor anterior. Concha fuertemente esculturada.

Género *Triplodon* Spix

(Tipo: *Triplodon rugosum* Spix, 1827 = *Hyria corrugata* Lamarck, 1819)

Los tres géneros así distinguidos serían monotípicos.

Género *PAXYODON* Schumacher

Paxyodon syrmatophorus

(Meuschen)

(Fig. 7)

Mya syrmatophora Meuschen in Gronovius, 1781

Paxyodon ponderosus Schumacher, 1817

Hyria avicularis var. "b" Lamarck, 1819

Unio brownianus Lea, 1838

Hyria complanata Hupé, 1857

Hyria alata Sowerby, 1869

La especie, además de los caracteres de la charnela aludidos, se caracteriza por carecer de escultura, por la existencia de pliegues transversos posteriores en las cercañas del umbón, por poseer pro-

cesos aliformes bien desarrollados y presentar una arista posterior muy marcada. El periostraco es castaño lustroso y el nácar rosáceo dándose localmente un intenso co-

lor asalmonado. El "glochidium" recuerda en su conformación y tamaño al de *Castaliini*, pero los dientes difieren sustancialmente ya que rematan en dos o tres espí-

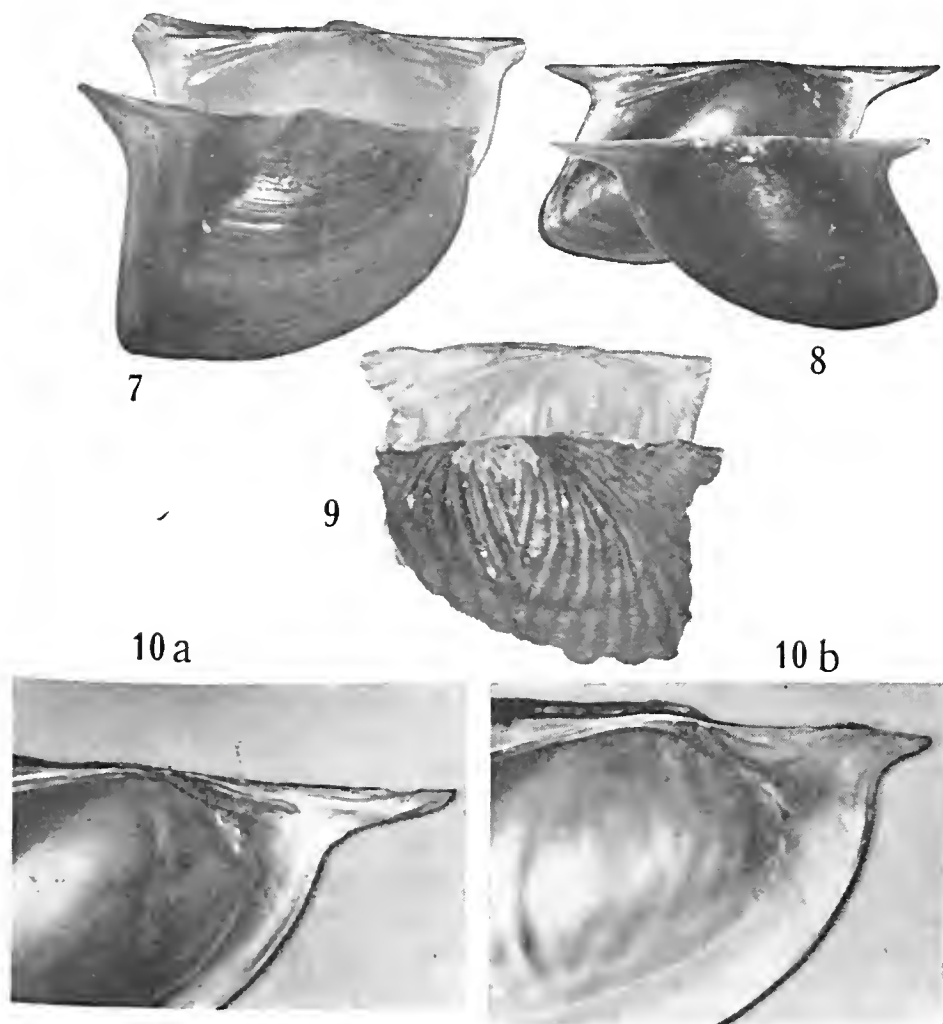


Fig. 7 — Ejemplar joven de *Paxyodon syrmatophorus* Meuschen del río Tocantins; fig. 8 — ejemplar joven de *Prisodon obliquus* Schumacher, del río Iriri; fig. 9 — ejemplar joven de *Triplodon corrugatus* Lamarck, procedente de Santarem, río Amazonas; fig. 10 — extremo anterior de la valva izquierda de *Prisodon obliquus* Schumacher (10a) y de *Triplodon corrugatus* Lamarck (10b), mostrando la posición de los dientes respecto a la cicatriz del adductor anterior.

nulas muy agudas aunque algo más rectas que en caso de *Diplodontini* (4). La marsupia se encuentra claramente desplazada hacia adelante, ocupando los dos tercios anteriores de la branquia.

La especie resulta bastante común en los tramos inferiores del Amazonas y en sus afluentes, existiendo también en las Guayanas.

Género *PRISODON* Schumacher

Prisodon obliquus Schumacher (Fig. 8)

- Prisodon obliquus* Schumacher, 1817
Hyria avicularis Lamarck, 1819
Unio caudatus Wagner, 1827
Diplodon furcatum Spix, 1827
Hyria elongata Swainson, 1841
Unio macropterus Dunker, 1846
Hyria castelnaudi Hupé, 1857
Unio ortonii Lea, 1868
Hyria recta Sowerby, 1869

A los caracteres diferenciales mencionados anteriormente (forma y extensión de los dientes anteriores y la carencia de escultura) que deben considerarse como fundamentales, puede sumarse el marcado alargamiento de la concha, su conformación subtriangular y el color blanco del nácar. Fuera de lo señalado, poco es lo que se puede indicar como rasgo de importancia dado la considerable variabilidad de la especie, como queda trasantado a través de la lista de sinónimos que se acompaña.

Tal lista no requiere mayor justificación. SOWERBY ya estableció

en 1869 la subordinación de *Unio caudatus* Wagner, *Diplodon furcatum* Spix e *Hyria elongata* Swainson respecto a *H. avicularis* Lamarck, concepto que es compartido por SIMPSON. *H. castelnaudi* Hupé e *H. recta* Sowerby son consideradas por SIMPSON como probables sinónimos de *P. obliquus*. *Unio macropterus* Dunker, como señala HAAS (19), se identifica perfectamente con la especie que nos ocupa.

En cambio, *Unio ortonii* Lea plantea mayores dificultades ya que se trata de un tipo basado en un ejemplar grande, desgastado y de crecimiento algo anómalo, en el que los dientes anteriores han conservado en gran parte los rasgos de la concha joven. Se considera, no obstante, que la ubicación acordada es la correcta.

La especie parece ser exclusiva del Amazonas y sus tributarios.

Género *TRIPLODON* Spix

Triplodon corrugatum (Lamarck) (Fig. 9)

- Hyria corrugata* Lamarck, 1819
Triplodon rugosum Spix, 1827
Mya angulata Wood, 1828
Hyria transversa Hupé, 1857
Hyria exasperata Sowerby, 1869
Hyria latialata Sowerby, 1869
Hyria rugosissima Sowerby, 1869
Unio stevensii Lea, 1871
Hyria jamauchinensis F. Baker, 1913
Hyria amazonica Frierson, 1914
Prisodon (Triplodon) rugosissima savillei Olsson & Wurtz, 1951

Los caracteres de la charnela y la escultura hacen que la especie resulte inconfundible, pese que a través del vasto territorio que cubre en su distribución experimentalmente considerables modificaciones, sea en el perfil, el diámetro o en el desarrollo y convergencia de la escultura. Pero tales modificaciones, aunque de aparente relevancia, son de escasa significación, ya que las mismas se relacionan a través de muchas formas de pasaje, lo que indica la inoperancia y falta de validez de los distingos específicos efectuados.

Tal hecho explica, por sí mismo, la lista de sinónimos consignada que, por otra parte, resume y amplía la opinión general de la mayor parte de los autores.

El "glochidium" de la especie es de tipo parásito y resulta muy característico (11). Su contorno responde al de *Diplodon* Spix, a igual que la forma del diente aplicado a cada valva embrionaria. Pero este diente presenta a cada lado una expansión lamelar que se va ensanchando desde el extremo del mismo hasta la base de implantación, para perderse en el reborde del "glochidium". Lo expuesto parecería indicar que el género *Tripodon* — *Hyria* Lamarck, presenta mayor afinidad con el género *Diplodon* que con respecto a *Paxyodon* (el "glochidium" de *Prisodon* resulta aún desconocido), lo que plantea un

problema pleno de interesantes sugerencias.

Esta especie resulta frecuente en la cuenca del Amazonas y sus tributarios, así como también en los ríos de las Guayanas.

Tribu: CASTALIINI

La tribu Castaliini integra un conjunto de especies que poseen caracteres bien definidos entre los que cabe citar la conformación triangular o subcuadrangular de la concha con una variable truncadura posterior, la carencia de procesos aliformes, la arista posterior muy marcada, los umbones prominentes y recurvados, y la charnela de fuerte desarrollo. El "glochidium", de tipo parásito, es subtriangular equilátero o isósceles, con un corto y agudo diente en forma de espina, careciendo de filamento larval.

Género *CASTALIA* Lamarck

Castalia Lamarck, 1819
Tetraplodon Spix, 1827
Castalina Ihering, 1891
Castaliella Simpson, 1900
Chevronais Olsson & Wurtz, 1951

El género *Castalia* Lamarck, de acuerdo a las conclusiones de un ensayo que diéramos a conocer recientemente (10), constituye un conjunto homogéneo cuyos rasgos más característicos están dados por el grosor de la concha, su perfil

subtriangular o subcuadrangular, por los umbones prominentes y variablemente esculturados, la arista posterior bien acusada, una moderada truncadura posterior, y el fuerte desarrollo de las piezas articulares de la charnela. El "glochidium" es de tipo parásito, de forma subtriangular equilátero, con fuertes dientes triangulares.

Dentro de la cuenca amazónica se hacen presente dos especies: *Castalia ambigua ambigua* Lamarck y *Castalia sulcata orbigny* (Hupé & Deville).

***Castalia ambigua ambigua*
Lamarck**

Castalia ambigua Lamarck, 1819
Castalia cuadrilatera Orbigny, 1835
Castalia acuticosta Hupé, 1857
Castalia turgida Hupé, 1857
Castalia retusa Hupé, 1857
Castalia crosseana Hidalgo, 1865
Castalia hanleyana Sowerby, 1869
Castalia latiquadrata Sowerby, 1869
Tetraplodon baro Ihering, 1910
Tetraplodon juruanus Ihering, 1910
Chevronais colombiana Olsson & Wurtz, 1951

Recientemente (10) nos hemos ocupado de esta especie con cierta amplitud, no considerándose necesario insistir sobre el particular. La misma se extiende a toda la cuenca amazónica, y la lista de sinónimos que se acompaña ilustra suficientemente acerca de las modificaciones operadas en las valvas a través de tan extenso territorio.

***Castalia sulcata orbigny* (Hupé
& Deville)**

Castalia sulcata Krauss, 1849
Unio orbigny Hupé & Deville, 1850

Esta especie alcanza un considerable tamaño, diferenciándose de la forma típica de las Guayanas por la falta de surcos concéntricos, la desaparición total de la escultura, la carencia de indicios de estrías verticales en la charnela y el color blanco del nácar.

Género *CALLONAI* Simpson

Callonaia Simpson, 1900

El género *Callonaia* se caracteriza fundamentalmente por su forma triangular, por la arista posterior muy alta, aguda y saliente, que se extiende hasta la base de la concha; por la definida truncadura posterior, el ligamento muy corto y la carencia de escultura. A esto se asocian otros caracteres menos significativos como la relativa delgadez de las paredes de la concha, el considerable diámetro de la misma y el color castaño claro del periostraco, etc. El "glochidium", aunque muy semejante al de *Castalia*, es de mayor tamaño, con evidente predominio de la longitud sobre la altura, poseyendo dientes triangulares más gráciles, con bordes incurvados hacia adentro.

El género comprende una sola especie, propia del Amazonas: *C. duprei* (Recluz).

Callonaia Duprei (Recluz)

Castalia duprei Recluz, 1843
Castalia dolabella Sowerby, 1869

Esta hermosa especie se desarrolla, al parecer, en los tramos inferiores del Amazonas y en los tributarios correspondientes, pudiendo alcanzar un gran tamaño.

CONCLUSIONES

A través del análisis realizado y de los antecedentes expuestos puede expresarse que la fauna de Unionacea del Amazonas viene a caracterizarse fundamentalmente por la presencia de algunos géneros propios, o restringidos a estas aguas y a la de las Guayanas, los que presentan una conformación que se aparta considerablemente de la primitiva que caracteriza al género *Diplodon* Spix, representando así, desde el punto de vista conchológico, las formas más especializadas dentro de los Unionacea neotrópicos.

Estos géneros (*Paxyodon*, *Prisodon*, *Triplodon* y *Callonaia*) son monotípicos, y aun cuando no resultaren correctas las presentes conclusiones sistemáticas, siempre aparecerían con un número muy limitado de especies.

En la cuenca amazónica se encuentran también todos los restantes géneros de Unionacea que se dan los distintos sistemas hidrográficos del continente, incluyendo en esto el género *Diplodon* Spix, con una representación equivalente a la que existe en los grandes ríos del sistema del Plata.

Todo esto induce a pensar que la cuenca del Amazonas constituye actualmente el centro de evolución de mayor importancia para la subfamilia Hyriinae Swainson, que engloba a todos los Unionacea neotrópicos.

Otro aspecto de interés estaría dado por cierta pobreza o limitación en la distribución y numerosidad de las especies del género *Diplodon* Spix, cuyo carácter marcadamente estenoico ya fuera señalado por nosotros en diversos trabajos. Evidentemente, la consideración objetiva del tema exige muchos más elementos de juicio del que disponemos actualmente. Empero, el contraste que presenta con el notable desarrollo, abundancia y amplia distribución de las especies de Prisodontini, es un hecho concreto que indica la necesidad de una adecuada investigación.

Por último, merece señalarse que en las áreas correspondientes a las nacientes del río Paraguay y del Guaporé, parece producirse una zona de engranaje entre las especies propias del Amazonas y las de

los ríos del sistema del Plata (fenómeno que se da también para con diversas especies de Mutelacea), la que se extiende variablemente sobre ambas cuencas. *Diplodon parallelopipedon* Lea, *D. parodizi* Bonetto, entre los Unionacea, y *Anodontites ensiformis* Spix, entre otros Mutelacea, constituyen ejemplos del fenómeno señalado, pareciendo evidente la reciente incorporación de las primeras a las aguas amazónicas, y de la última al río Paraguay y Paraná medio.

RESUMO

Efetua-se uma revisão dos Unionacea da bacia amazônica, analisando o valor dos diferentes gêneros, espécies, subespécies, descritas para a mesma. De tal análise resulta que, ainda que na bacia amazônica existam gêneros próprios, aparte dos que são comuns a outros sistemas hidrográficos de Sul-América, o número de espécies não é muito maior do que o registrado nos grandes rios do sistema do Prata. Assinala-se a relativa escassez e moderado tamanho das espécies de *Diplodon*, o que contrasta com o grande desenvolvimento, abundância, e ampla distribuição alcançada pelas espécies de Prisdontini, estimando-se que o Amazonas constitui atualmente o centro de evolução de maior importância para os Unionacea neotropicais.

SUMMARY

A revision of the Unionacea of the Amazonian Basin is made, analyzing the value of the different genera, species and subspecies described for it. That analysis shows that although there are some genera characteristic of the Amazonian Basin, apart from those that are common to other South American river systems, the number of species is not superior to that registered in the great rivers belonging to the River Plate System. The relative shortage and moderate size of the species of the *Diplodon* genus are noticeable, in contrast with the great development, abundance and distribution of the Prisdontini species. The Amazon is considered as the most important centre of evolution of the neotropical Unionacea at present.

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NOVOS DADOS PARA O CONHECIMENTO DE "PHREATOBIUS CISTERNARUM" GOELDI (Pisces, Pygidiidae, Phreatobiinae)

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(Com uma figura no texto)

Em 25 de março de 1963 recebi do meu amigo R. P. Arlé, naturalista do Museu Nacional a serviço no Museu Emílio Goeldi, Belém do Pará, uns croquis a lápis e a aquarela de um minúsculo bagre, de cor vermelha intensa, encontrado quando cavavam um poço para água potável em terreno de uma rua de Belém. Os croquis estavam acompanhados das notas, que abaixo transcrevemos:

"Aqui segue o croquis de um peixinho achado na escavação de um poço profundo na Angostura. Não tem pigmento melânico e pelo que pude vêr com o bicho vivo, não me parece ter nenhum sinal de olhos. É todo vermelho (pink vivo). Creio que é uma espécie de lençol subterrâneo — larva? adulto? Veja o que pode deduzir pelo croquis e me escreva depressa".

Em baixo dos croquis havia o seguinte:

"Belém — Achado ao cavar um poço na Angostura, com 10-15 metros de profundidade. Todo o corpo vermelho vivo (muito mais vivo que no desenho) as nadadeiras e barbas brancas. De baixo da binocular (animal vivo) não achei olhos, somente um leve tracinho de pigmento transversalmente por cima da boca. O animal encontra-se *vivo* (por enquanto) em aquário meu".

Comuniquei-lhe que pelo que pude apreender dos croquis e notas, tratava-se de *Phreatobius cisternarum* Goeldi, 1904, Pygidiidae muito raro, só conhecido pelos exemplares de GOELDI. Pedi-lhe que procurasse mantê-lo vivo e observasse o seu comportamento em aquário.

Tempos mais tarde, em 1965, recebi do colega Arlé, as seguintes notas:

"O *Phreatobius cisternarum* está fixado após um ano em aquário, resolvi matá-lo para não perdê-lo."

"O espécime foi encontrado ao cavar um poço na travessa Angostura em Belém."

"Foi-me trazido numa garrafa (com farinha) como alimento!! foi transferido para um aquário de 12 litros, altura da água 17 centímetros, fundo de areia com detritos finos, água velha e absolutamente límpida, com algumas plantinhas e algas. O aquário foi colocado em lugar sombrio. À noite costumava acender em cima uma lâmpada fraca para poder observá-lo."

"O peixe era inteiramente *vermelho* com a parte ventral anterior e as barbatanas esbranquiçadas. Conservou a mesma cor viva durante todo o tempo, nadava em plena água com movimentos ondulatórios às vezes descansando sobre pequenas plantas. Percorria sempre com as barbas armadas o fundo do aquário mas não ficava escondido sob folhas ou detritos, parava sempre nos cantos laterais do aquário em *posição vertical* sempre com a cabeça para cima. Nunca aceitou pequenas tubifex mesmo cortadas, nem dafnias, parecia se alimentar somente com coisas extremamente pequenas como algas. Viveu assim em perfeita saúde durante um ano exatamente e teria vivido mais se não o matasse, fixando-o no formol com receio de perdê-lo. Conservou a cor vermelha ainda alguns dias no formol. Ao fixá-lo o tubo digestivo aparecia contendo algas de cor verde."

Decorreram 62 anos desde que GOELDI anunciou o seu achado, sem que aparecesse na literatura espe-

cializada notícia de novos exemplares.

Este ano por interferência do Dr. José Cândido de Melo Carvalho, obtive mais 2 exemplares provenientes de Macapá, Território Federal do Amapá. Foram coligidos em dezembro de 1965, pelo meu velho amigo Reinaldo H. G. Damasceno, quando aprofundavam um poço, durante a estiagem.

A ocorrência da espécie em três pontos distantes, no delta do Amazonas (de Macapá a Belém em linha reta são 320 km) faz-nos supor que a espécie é mais abundante do que parece e que a região do delta está cortada por canais subterrâneos, que das barrancas do rio entram para o interior e a costa da ilha, a uma profundidade de 10 a 20 metros, e provavelmente anastomosando-se.

E' provável também que nos milhares de poços espalhados pela região existam muitos habitados pela espécie, sem que seus proprietários tomem conhecimento da ocorrência. O sucesso dos três achados deve-se à curiosidade e ao interesse pelas Ciências naturais, dos seus coletores.

Infelizmente não pudemos obter a descrição original de GOELDI, tivemos que nos apoiar na monografia de EIGENMANN (1918), que ba-

seou as diagnoses do gênero (monotípico) e espécie na fotografia e no exemplar que lhe fôra cedido por FUHRMANN.

Quanto à côr, EIGENMANN não esclarece nada; diz sòmente "côr uniforme". É provável que nem GOELDI os tenha visto vivos e nem fôsse informado pelo coletor sôbre a côr, em vida, dos exemplares.

P i s c e s

Pygidiidae

Phreatobiinae Myers, 1944

Phreatobius Goeldi, 1904

Tipo por monotipia *Phreatobius cisternarum* Goeldi, 1904

Phreatobius GOELDI, C. R. 6 Congres. intern. Zool. Berne 1904 (1905): 545; FUHRMANN, Verh. Schweiz. Naturf. Gesel. Aarau, 1905 (1906): 50; Arch. Sci. Phys. Nat. Genève, 1905 (1906), 4 (20): 578; EIGENMANN, Rep. Princeton Exped. Patagonia 1896-1899, 1910 3 (4): 387; Mem. Carnegie Mus. 1918, 7 (5): 371; GOSLINE, Bol. Mus. Nac. (n. s.) Zool. 33: 68; MYERS, Calif. Acad. Sci. 4 ser. 1944, 23 (40): 597; FOWLER, Arq. Zool. S. Paulo, 1954, 9: 9.

Phreatobius JORDAN, Stanford Univ. Publ. ser. 43 (Genera of Fishes) 4: 480, 1920, citação e referência er-

radas; Stanford Univ. Publ. Univ. Ser. 3 (2): 151, 1923 (Classification of Fish) citação e referências erradas.

GOELDI (1904) achava que *Phreatobius* deveria ficar entre os *Cetopsidae* e *Trichomycteridae*. FUHRMANN achava-o aliado a *Clariidae* da fauna africana. EIGENMANN (1910) colocou-o na família *Siluridae*, subfamília *Pimelodinae* declarando que não estava seguro quanto à posição do gênero. Em 1918, em sua revisão da família *Pygidiidae*, colocou-o no apêndice daquela monografia. GOSLINE, em 1945, colocou-o entre os *Pygidiidae*, não sabendo porém em que subfamília deveria inclui-lo. MYERS (1944), colocou-o em *Pygidiidae* criando a subfamília *Phreatobiinae*. FOWLER (1954) colocou-o em *Trichomycteridae*, *Phreatobiinae*.

P. cisternarum Goeldi, 1904

Localidade típica — Ilha de Marajó.

P. cisternarum GOELDI, C. R. 6 Congr. intern. Zool. Berne, 1904 (1905): 545; FUHRMANN, Verh. Schweiz. Naturf. Gesell. Aarau 1905 (1906): 50-51; Arch. Sci. Phys. Nat. Genève (4) 20: 578-579, 1905 (1906); EIGENMANN, Rep. Princeton Exped. Patagonia 1896-1899, 1910, 3 (4): 387-388; Mem. Carnegie Mus. 7 (5):

371-373, Fig. 39 pl. 56 fig. 1, 2, 4;
 GOSLINE, Bol. Mus. Nac. (n. s.)
 Zool. 33: 68; MYERS, Proc. Calif.
 Acad. Sci. 1944, Ser. 4, 23 (40):
 594; FOWLER, Arq. Zool., S. Paulo
 1954, 9: 9-10, fig. 596.

Recentemente, um novo peixe
 cego de águas subterrâneas (Família
Characidae), foi descrito por

BRITTAN, M. R. & BOHLKE, J. E., *No-
 tulae Naturae*, n.º 380, outubro de
 1965, publicação da Academia de
 Ciências Naturais de Filadelfia.
 Desta feita, o peixinho, com.....
 23,6 mm de comprimento, foi obti-
 do de uma perfuração de 30 m de
 profundidade, na localidade minei-
 ra de Jaíba.

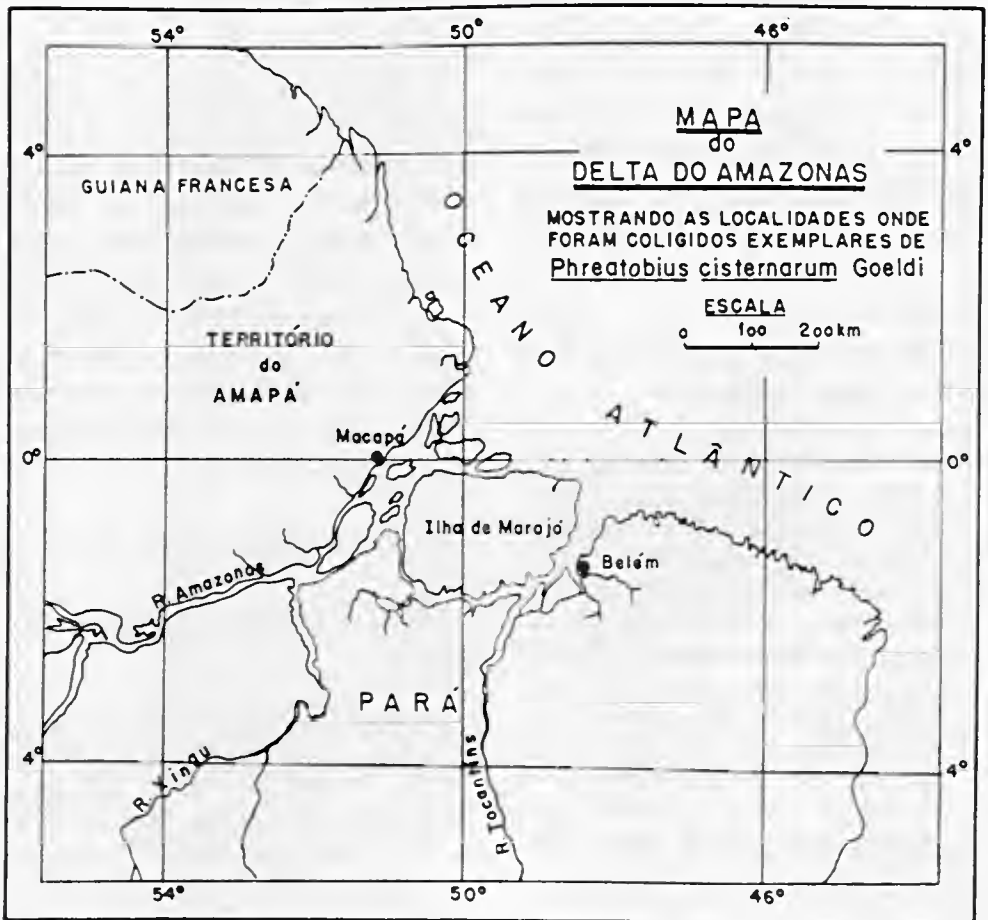


Fig. 1 — Mapa do delta do Amazonas, mostrando as localidades onde foram coligidos exemplares de *Phreatobius cisternarum* Goeldi.

RESUMO

O aparecimento de *Phreatobius cisternarum* em mais duas localidades do delta do Amazonas, decorridos 62 anos da data de sua descrição, em localidades afastadas mais de 300 km entre si, trouxe-nos novos subsídios para o conhecimento da espécie.

Dentre êsses subsídios poderemos enumerar os seguintes:

Um exemplar viveu durante um ano (após o qual foi sacrificado) em um pequeno aquário, instalado em lugar sombrio.

Refugava as tubifex e dafnias que lhe eram oferecidas.

Alimentou-se provavelmente com partículas orgânicas microscópicas e algas verdes.

Percorria o fundo do aquário com os barbilhões armados, como a inspecioná-lo.

Descansava em posição vertical num dos cantos do aquário, sempre com a cabeça para cima, próximo a superfície.

E' de côr vermelha muito intensa, com as nadadeiras, barbilhões e parte infero-anterior do corpo esbranquiçados.

Atingem até 60 mm de comprimento.

Vivem em galerias de águas subterrâneas, na região do delta do

Amazonas, a uma profundidade aproximada de 10 a 20 metros e aparecem nos poços cavados para água potável, quando as galerias são rompidas ao escavarem-se os mesmos.

SUMMARY

The appearance of *Phreatobius cisternarum* in two more localities in the Amazon delta, 62 years after its description and in site 300 km apart, has added new data to our knowledge of the species.

A specimen lived for one year in small, shaded aquarium after which it was killed. It refused the tubifex and daphnia that were offered, and probably ate only green alga and microscopic organic particles.

It swam about the floor of the aquarium with its barbels spread, as though examining the surface. It rest in a vertical position in a corner of the aquarium, always with the head uppermost and near the surface. Its color is a intense red with the fins barbels and anterior ventral surface whitish. The fish reaches 60 mm in length.

They live in the waters of underground galleries in the Amazon delta, at depths of 10 to 20 meters, and may appear in wells when these intersect one of the galleries.

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BASES PARA EL ESTUDIO DE LAS RAYAS DE AGUA DULCE DEL SISTEMA AMAZONICO. NUEVAS SINONIMIAS DE "P. MOTORO" (M.H., 1841)

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(Con 1 figura en el texto)

En nuestro trabajo comunicado al Congreso Latino Americano de Zoología realizado en Santiago de Chile en octubre de 1965 — ampliación de nuestra comunicación con motivo del cincuentenario del Museo Provincial de Ciencias Naturales "Florentino Ameghino" de la ciudad de Santa Fe, en mayo de 1964 — establecimos una revisión de lo realizado hasta la fecha como aporte al conocimiento de la familia de rayas de agua dulce (Potamotrygonidae Garman, 1913).

En el Octavo Congreso Internacional de Medicina Interna en noviembre de 1964 (Buenos Aires) y en el Primer Simposio de Toxinas Animales realizado en Atlantic City (EE.UU.) en abril de 1966 presentamos todos los datos conocidos acerca del aspecto de la toxicidad de este elasmobranquio dulceacuicólo.

Como indicáramos en el trabajo de Chile, los conocimientos que se tienen sobre las rayas de agua dulce

en la cuenca amazónica son muy pobres y hasta confusos, cosa muy diversa por cierto en lo que a la cuenca del Paraná se refiere, en donde gracias al apoyo del Instituto Nacional de Limnología se ha podido iniciar un estudio intenso que está aclarando bastante el panorama.

Para no extendernos demasiado y tomando por base nuestro trabajo presentado a Chile, consideraremos las especies descritas para la cuenca amazónica, las que incluídas en lo que llamamos Región Amazónica — Platense agrupábamnos entonces en la subregión amazónica. Así poníamos las siguientes especies contenidas en dos géneros: *Disceus thayeri* Garman, 1877; *Potamotrygon motoro* (M. H., 1841); *P. hystrix* (M. H., 1841); *P. brachyurus* (Günther, 1880); *P. laticeps* Garman, 1913; *P. circularis* Garman, 1913; *P. Dumerilii* (Castelnau, 1855); *P. humerosus* Gar-

man, 1913; *P. signatus* Garman, 1913; *P. strongylopterus* (Schomburgk, 1843); *P. scobina* Garman, 1913.

En nuestro reciente viaje a los Estados Unidos en donde visitamos el Smithsonian Institute, el American Museum of Natural History y el Museum of Comparative Zoology de Harvard, tuvimos oportunidad de entrar en contacto con la colección Garman, la que hemos revisado cuidadosamente para exponer en la presente comunicación nuestras conclusiones, ya que modifican bastante el cuadro anteriormente expuesto.

De la revisión de los ejemplares de la colección Garman y de la inspección de otro ejemplar gigantesco obtenido del Rio Guaporé y que se halla actualmente en el American Museum (N. York), queda bien claro que *Disceus thayeri* es género válido con especie bien distinguible y exclusiva del interior de la hoya amazónica, hallándosela en toda su extensión.

Con respecto a *P. signatus*, hemos revisado los ejemplares catalogados en Harvard. No habiendo Garman designado tipo, luego de cotejar cuidadosamente los ejemplares con la descripción del autor citado, se ha creído oportuno asignar el tipo al número 304, ejemplar macho. Con respecto a los otros tres ejemplares puede indicarse lo siguiente: El N.º 604 es un

ejemplar de *P. motoro*, siendo aún apreciables las manchas amarillentas del dorso y estando en muy buen estado de conservación sus denticulos dorsales. El N.º 600 es un ejemplar asimilable a *P. motoro*. Finalmente el N.º 560 es un ejemplar de *P. reticulatus* (Günther, 1880).

En lo que respecta a *P. circularis* rotulado bajo el N.º 295 y el *P. scobina* N.º 602, no hemos hallado diferencias apreciables entre ambas y las asimilamos a *P. motoro*.

El N.º 299 rotulado como *P. humerosus*, ejemplar hembra provisto de numerosas y gruesas espinas es también asimilable a *P. motoro* siendo su única característica curiosa el grossor de las espinas que recubren por entero la cola.

Finalmente los ejemplares rotulados como *P. laticeps* divergen en sus aspectos. El N.º 294 es *P. motoro*. El N.º 298 es también asimilable a *P. motoro*. En cuanto al tipo rotulado bajo el número 608 es demasiado joven para ser identificado asimilándose por su morfología en forma indistinta a *P. motoro* o a *P. hystrix*. El N.º 287 es también indudablemente una *P. motoro*.

En un trabajo especial nos proponemos describir cuidadosamente cada ejemplar y fundamentar nuestras aserciones, labor que escapa los fines de la presente comunicación.

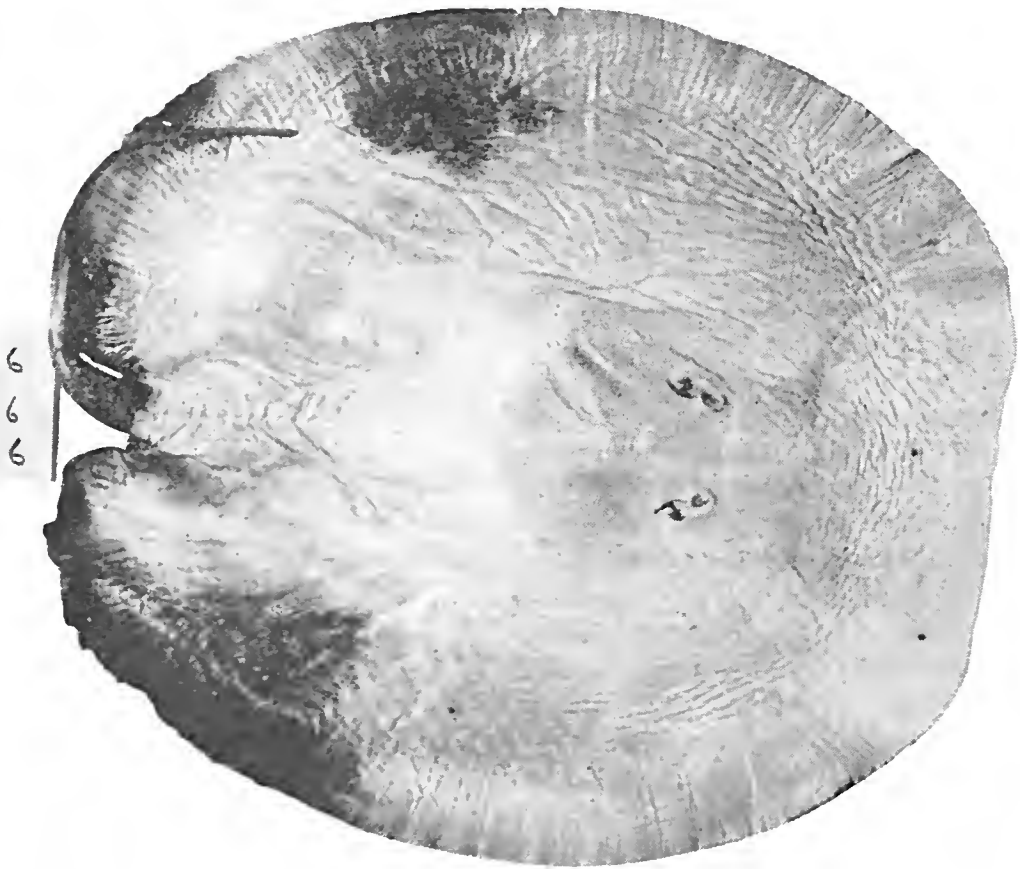


Fig. 1 — *Disceus thayeri*; at. del Museo de Zoología Comparada de Harvard.

No queremos concluir sin indicar que el error de Garman al crear cuatro especies ahora asimilables con *P. motoro* echa raíz en la falta de material, ya que para cuatro especies contó con once ejemplares. Por nuestra parte hemos podido observar en más de cinco mil ejemplares de *P. motoro* observados durante varios años en la cuenca del Río Paraná la variabilidad morfológica de la especie *P. motoro*.

Merecen párrafo especial dos especies que consideramos dudosas: *P. strongylopterus* y *P. dumerilii*. La primera es perfectamente asimilable con *P. signatus*, siendo en ese caso esta última especie sinónima de la primera. En cuanto a *P. dumerilii* cae en las mismas consideraciones que la especie anterior.

Considerados estos antecedentes podemos establecer como base de especies existentes en la hoya ama-

zónica das siguientes: *Disceus thayeri*; *Potamotrygon motoro*; *P. hystrix*; *P. brachyurus*; *P. reticulatus*; e *P. signatus*.

Todas estas especies son comunes con las halladas ya en cuencas nor-amazónicas o ya en cuencas del sur, a no ser *D. thayeri* que es — como dijéramos — exclusiva del Amazonas.

Omitimos las descripciones y las bibliografías pertinentes por considerar que el interesado puede hallarlos en nuestros trabajos anteriores en donde nos hemos referido a ellos en forma exhaustiva.

Queremos señalar como dato de interés que al norte del Amazonas quedan dos especies no hallables en su cuenca. Son ellas *P. magdalenae* propia del sistema colombiano y *P. schroederi* Fernández Yopez, 1958 perteneciente al sistema del Orinoco y que no ha sido aún mencionada para el Amazonas o sus afluentes.

Con respecto al Sistema Paranáplatense hay descritas algunas especies cuya presencia en el sistema amazónico tampoco ha sido señalada. Son ellas *P. labradori* Castex, 1963, *P. pauckei* Castex, 1963, *P. falkneri* Castex, 1963, *P. schuhmacheri* Castex, 1964 y la muy curiosa especie *P. menchacai* Martínez Achenbac., 1966.

Finalmente cabría preguntarse qué posible conexión pudiera tener la especie africana de agua dulce

descrita para el afluente del Rio Niger (*P. garouaensis* Stauch — Blanc, 1962) con las especies amazónicas.

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NEMERTINOS DE ÁGUA DOCE DA REGIÃO AMAZÔNICA

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No rico material de vermes amazônicos, coletado pelo Dr. Harald Sioli, foram verificados quatro espécimes de nemertinos do gênero *Prostoma* Dugès, 1828, coletados no rio Tapajós, em Fordlândia e na desembocadura do rio Cupari, afluente direito do Tapajós.

Três das quatro Ordens de nemertinos são hoje conhecidas para as águas doces da América do Sul e Central: o heteronemertino *Sio-lineus turbidus* du Bois-Reymond Marcus, 1948, do rio Tapajós, duas espécies de hoplonemertinos do gênero *Prostoma*, *P. rubrum* (Leidy, 1850) e *P. eilhardi* (Montgomery, 1895) e o bdelonemertino *Malacobdella auriculae* Blanchard, 1847, do Chile.

Prostoma rubrum, da América do Norte, foi verificado no México (RIOJA, 1941) e na Venezuela (CORDERO, 1943). A distribuição geográfica de *P. eilhardi* ainda não pode ser definitivamente estabelecida devido a dificuldades taxonômicas.

De acordo com a sinonímia de STIASNY WIJNHOF (1938) Berlin, Amsterdam e a Lombardia seriam localidades de *P. eilhardi*. Os achados sul-americanos referiam-se aos Estados brasileiros de São Paulo e Paraná (MARCUS, 1942, 1943). Possivelmente também o material do Uruguai e Argentina pertencem a esta espécie (CORDERO, 1943).

Os principais caracteres do material amazônico são: comprimento cerca de 2,5 a 4,5 mm; largura cerca de 0,3 mm; cor creme; em geral 6 olhos com irregularidade no número e distribuição; cílios ou cerdas táteis ausentes; glândulas cefálicas situadas anteriormente ao cérebro; corpúsculos calcáreos na epiderme e perênquima ausentes; esôfago com epitélio ríncodeal, sem cílios; estômago ciliado, ríncocela longo; ríncódeo sem músculos longitudinais; órgãos sensoriais, frontal e cerebrais, presentes.

Na sua sinopse do gênero *Prostoma*, STIASNY-WIJNHOF (1938) re-

corda 16 nomes diferentes aplicados aos nemertinos de água doce e dá a bibliografia correspondente. Apenas 6 espécies foram reconhecidas como válidas. Afora algumas divergências de opinião considero a lista dêsse autor como correta. Comparei o material amazônico com cada uma delas tendo porém acrescentado a espécie *P. rubrum*, que não foi considerada apesar de ter sido revalidada por CoE (1918), considerando-a idêntica a *P. graecense*.

P. lumbricoideum tem 30 mm de comprimento, é pintada de escuro e possui apenas 4 olhos. *P. rubrum* não possui órgão frontal e os dutos das glândulas cefálicas não são unidos como no material amazônico. *P. grande* tem 35 mm de comprimento, possui manchas verdes, rincocela curto e glândulas cefálicas mais curtas que nos vermes amazônicos. *P. padanum* tem rincocela muito curto e estilete central muito mais longo que o do material amazônico. *P. puteale* é branco, sem olhos.

Esta rápida revisão mostra que os vermes amazônicos não pertencem a nenhuma destas 5 espécies. Restam para comparação mais pormenorizada as espécies *P. graecense* e *P. eilhardi* que foram separadas por STIASNY-WIJNHOF com base nos seguintes caracteres:

1 — sem ou com cílios táteis;

- 2 — sem ou com corpúsculos calcáreos;
- 3 — poros cerebrais laterais ou ventrais;
- 4 — órgão frontal tripartido ou simples;
- 5 — glândulas cefálicas pré-cerebrais ou pós-cerebrais;
- 6 — rincódeo sem ou com músculos longitudinais;
- 7 — base do estilete sem ou com constrição;
- 8 — músculos longitudinais do estômago originados da musculatura cefálica ou do septo;
- 9 — esôfago rincocelal ou ciliado;
- 10 — sem ceco ou com ceco curto;
- 11 — divertículos intestinais ultrapassando o cérebro ou apenas atingindo o cérebro;
- 12 — vaso dorsal projetado no rincocela com um nó ou vaso dorsal normal.

A aplicação de 8 destes caracteres não tem sido satisfatória, nem são eles suportados pelas descrições originais, não podendo assim ser mantidos. Restam apenas 4 dos critérios mencionados dos quais apenas 2 suportam críticas e são usados comumente.

- 1 — Cílios táteis ocorrem em *graecense* e mesmo cerdas táteis na região anal e são ausentes em *eilhardi*. De acordo com a

minha experiência é muito difícil ou impossível detectar cílios ou cerdas táteis em material conservado. Assim não convém determinar todo material fixado, sem cílios táteis, como *P. eilhardi*.

- 2 — Corpúsculos calcáreos são presentes em *graecense* e ausentes em *eilhardi*. Eles são provavelmente restos temporários armazenados que aumentam em vermes mantidos em condições desfavoráveis. Se as condições melhorarem eles são, pelo menos parcialmente, reabsorvidos ou eliminados. Um caráter fisiológico pode certamente servir taxonômicamente tão bem quanto um morfológico, mas seu valor sistemático diminui muito se ele variar de acordo com as condições do ambiente.
- 3 — *P. eilhardi* não possui como *P. graecense* uma espessa camada de músculos longitudinais na parede do rincódeo. Este caráter mencionado por STIASNY-WIJNHOF pode ser aceito sem restrições.
- 4 — O epitélio do esôfago em *eilhardi* é do tipo do epitélio do rincódeo enquanto que o epitélio do esôfago de *graecense* é ciliado. Este caráter, esôfago rincodeal ou não rincodeal,

é considerado também um bom caráter disjuntivo entre as duas espécies.

Como os vermes da região amazônica possuem rincódeo sem camada de músculos longitudinais e esôfago rincodeal, sem cílios, devem ser classificados como *Prostoma eilhardi* (Montgomery, 1895). Acrescento que corpúsculos calcáreos são ausentes.

Tendo tido oportunidade de classificar material a mim enviado, da África do Sul, notei que os vermes podiam, à primeira vista, ser separados em dois lotes. Os cortes vieram confirmar a separação e no material africano encontrei não apenas a espécie amazônica, acima mencionada, mas também *P. graecense* (Böhmig, 1892). Estes possuem rincódeo com camada espessa de músculos longitudinais e esôfago ciliado, não de tipo rincodeal. Esta espécie possui corpúsculos calcáreos no parênquima o que foi utilizado como sinal suplementar (CORRÊA, 1951).

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ON THE ECOLOGY OF AMAZONIAN RAIN-FOREST STREAMS

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(With one text-figure)

The enormous quantities of water which the Amazon is continually carrying to the Ocean have their offspring somewhere and somewhere in hundreds of thousands of springs and streams of its vast tributary area. Before these waters assemble in the main river and change into the homogenous clay - coloured whitewater ("água branca") or Amazon water, they run transparent, occasionally browned by humic acid, for the most part in the shade of virgin forests, and there they represent a particular biotope, the rain-forest stream, which hitherto has hardly been taken notice of. When adding together the surfaces of the innumerable small streams, the result would be many times the multiple of the surface of the Amazon River. And when adding the lengths of these streams, the result would

be a watercourse more than a thousand times longer than the Amazon. From these considerations may be concluded the very important part these streams act in the formation of the Amazonian rain-forest region.

The Amazonian rain - forest stream is fundamentally different in several ecological factors from the streams of other regions and climates. Its water is extraordinarily poor in soluble minerals, direct solar radiation does generally not reach the water surface. The water temperature is extremely constant. Plant life is almost completely missing, the fauna is poor and rather simple. The entire biocoenosis of that extreme biotope depends as for its fundamental alimentation upon allochthonous organic matter conveyed into the stream. The main ecological factor

by which the development of organisms is limited is the scarcity of soluble minerals. This factor, together with the lack of solar radiation, is the reason for the scarceness of plant life and cause, either directly or through the resulting uniform sort of food, the absence of many groups of animals otherwise generally found in streams. The remarkable stability of water temperature, which outside the tropics in inland waters is only found in springs, is considered to be of minor importance.

The typical form of the rain-forest stream is found on the "terra firme" in the central Amazonian region, which has been formed by the sediments of the miocene-pliocene fresh-water lake (compare SIOLI. . .). In the border regions of the Amazonian basin, where the geological formations are different the water chemism is very often not so extreme, so that a partially different composition of the biocoenosis of the streams may result.

On the following pages we will give a description of the rain-forest stream such as it is found in "Central Amazonia". In this context we understand by such a stream a small watercourse that takes its origin from springs. It changes to become a river at a spot where the forest does no longer completely shelter its bed. This occurs, according to the type of forest, at a

width from about 5 to 10 m. In its upper part the stream mostly runs in a narrow valley, deeply cut in soft tertiary sediments; which after joining with other streams most often quickly gets wider and generally soon becomes the wide surface of a river.

From physiographic and ecological points of view three different zones of a stream may be distinguished (Fig. 1): (1) the spring - or erosion-zone, or upper course, (2) the sedimentation-zone, or middle course, (3) the so called Igapó-zone, or lower course. In most of the cases the stream takes its offspring from helocrenes, which in the rain-forest climate more or less continually give water throughout the year. Rheo - or limnocrenes are extremely rare.

In the upper course, i.e. in the spring- or erosion-zone, the stream carrying little water only runs at the bottom of its valley without remarkably meandering. Its drop is relatively strong, but erosion is weak, the small quantities of water being continually dammed by fallen trees and leaves, and regions of running and stagnating water often alternating. Many times the stream in its beginnings gets lost in helocrene-like swamps characterised by quantities of the Buriti palm, *Mauritia flexuosa*.

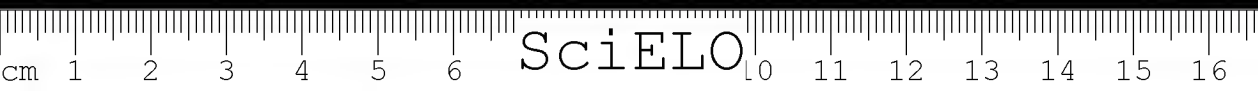
The augmentation of its water volume gives the stream a clean,

sandy bed which is limited by banks fastened by roots. When the valley is becoming wider and the drop is diminishing, the stream starts meandering and changing into its middle course, the sedimentation-zone. After strong downpours the water occasionally flows over the bounds temporarily. The bank is often a little higher than the bottom of the valley. The latter is more or less on the same level as the medium surface of the water of the main river system. Annually during the high water period the stream can therefore be dammed in the region of its middle course and its valley can be more or less flooded. Whilst the water stagnates at the bottom of the valley, it generally goes on running in the proper bed. The middle course is characterised by a sandy bed, mostly devoid of wood, and its strong meanders with a frequent change between flat and deep water. Particularly during the high water period the diminished current causes, at respective spots where both sand and leaves form sedimentations, vast deposits of sand and leaves to be formed.

Very slowly, but also rather abruptly after a cascade formed by soft tertiary arenites, the middle course changes into the lower course, the so called Igapó-zone. The bed of the stream is below the medium high water mark of the main

river system, and according to its low level is annually flooded by the waters of the main river, which fills the wide valley of the stream. In the region of Manaus the water level on an average goes up resp. down for about 13 m. Only during the low water period this part of the river, from an ecological-physiographic point of view represents a stream, whilst during the high water period it represents a section of the main river, the warm water of which covers the cooler water of the stream and its bottom and there to a large extent stagnates. In the Amazonian region the Igapó or flood-wood makes part of the ecologically most extreme biotope, which moreover within the area of the lower part of a stream in the course of the year is subject to a continual change due to rising or falling water and cannot be compared with any other limnic biotope. The following pages will not deal in particular with this dynamical region of waters.

The water of springs resp. streams is, as is indicated in the table, extremely poor in soluble minerals. (Tab. 1) The rain that enters into sour impoverished soils placed on tertiary fresh-water sediments, can in its phase as surface water hardly absorb electrolytes. Of all elements, except silicon, sodium, and potassium, there are only traces available. It



has been impossible by means of hitherto usual methods to trace calcium. The water is, as well as the soils there, very acid, with a pH of about 4.5. The proportion of free CO₂ is about 20 — 30 mg/l. The proportion of oxygen does mostly not reach saturation. On certain edaphic conditions, if there are podsol-soils in the tributary area (compare KLINGE), the surface water gets more or less rich of soluble humic acid, by which it becomes brown to redbrown. The typical biocoenosis of the stream is, however, not influenced by the proportion of humic acid. In the springs the water temperature is on an average 24.5° C. In the stream itself it varies very little. The daily and annual oscillations are about $\pm 1^\circ$ C. As has been initially mentioned, the stream is usually shielded against direct solar radiation. About 1/100th to 1/200th of the mid-day radiation reach its surface.

The stream floor is filled with sand; gravel and stones are missing in this region. Occasionally the water runs over horizontal layers of tertiary arenites, whose ruptures bring about cascades, which, when situated in the middle or lower course, annually remain submerged for a rather long time. The banks are shallow and abrupt and are fastened by thick pads of thin roots. These paddings of fine

roots on the banks represent the most important solid substratum for the rheophile fauna; in addition to these the pieces of fallen trees and fixed leaves and, in sections of weak current, also thick layers of old leaves. In the middle course, but even more in the lower course the roots of epiphytes (Araaceae) hanging down from trees in the water and forming intense ramifications there, constitute a remarkable substratum. Even at a varying water level they are always swimming on the surface and also during an almost complete stagnation during the high-water period they form a suitable substratum for the rheophile fauna. There are to be found in these root-clusters considerable numbers of different species and their individuals.

Aquatic plants are represented, if at all, only by a few forms. Pads formed by Chlorophyceae or Cyanophyceae are completely missing. Lower plants are often represented by clusters of Batrachospermaceae (Rhodophyceae). These algae are obviously refused by animals as food and also as substratum. On the surface level are occasionally found several sorts of Musci and also Hepaticae, and a small fern which tolerates even some months of inundation. The only flowering plant often to be found in the streams is the semi-aquatic *Thurnia sphaerocephala* (Thurniaceae).

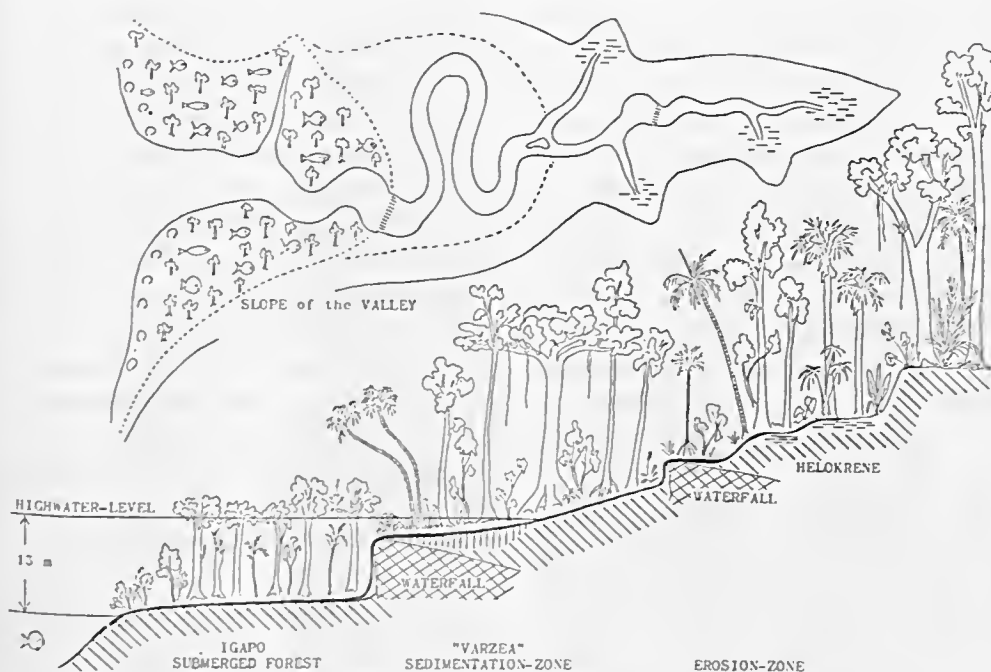


Fig. 1 — Schematic aspect of the different ecological regions of the Central-Amazonian rain-forest stream.

It grows up to the length of a meter or more in deep shade, on muddy banks as well as on the sandy floor in the midst of the current. Only on spots with strong solar radiation it is found submerged and floating in the current. In lenitic sections is occasionally to be found a very small Utriculariaceae. Near cascades the forest is occasionally low owing to the stony surface and does not completely shield off the sunlight. On this sort of spots the likewise semi-aquatic *Tonia fluvialis* (Ericaulaceae) is found rooting in the fissures of rocks, which otherwise are missing in the

stream. On spots where the forest near the streams has been burnt down, so that the sunlight directly reaches the water surface and soluble minerals are conveyed into the stream by rain, grow small quantities of Cyanophyceae and Chlorophyceae, and on the banks Cyperaceae and various kinds of Ericaulaceae.

The composition of the stream fauna is determined as well by the chemism of the water as by the food in offer, the non-existence of the usual autochthonous organic primary production. The complete absence of Amphipods, non-pa-

sitic Isopods, shells, and snails with calcareous cases is probably due to both of these factors likewise. The only molluscs available are small *Ferrissidae* with concholin cases, which biologically do not act a part. The animals living in these streams, as far as they do not lead a predaceous life, feed on the organic substances fallen or conveyed into the water, such as flowers, fruits, pollen, dead organisms, etc., and the products of their decomposition.

Of very little importance for the direct nutrition appear to be the leaves shed by the trees and continually falling into the water. They never show any feeding-traces caused by aquatic organisms. Their organic and mechanic decomposition seems to go on very slowly in the acid water. It will be necessary to elucidate their decomposition and to get to know the active bacteria and fungi in order to understand the nutrition of various animals and the food-chain of these streams. A large number the non-predaceous animals are filtrators, e.g. the larvae of many Trichoptera, Chironomidae, and Simuliidae, which constitute the main part of the invertebrate fauna. One of the most frequent Trichoptera is *Macronema*, which makes protrude its cases in a strong current, on spots where the sand is kept together by a compact

ramification of roots. Its larvae filtrate the water by means of nets whose width of mesh is suitable for catching bacteriae and spores of fungi (compare SATTLER....). Other filtrators, such as the frequent Hydropsychidae (Trichoptera) have less fine nets. The only aquatic animals that are adapted at the highest degree to the very changeable biotope of the lower course, the so-called Igapó-zone, are micro-filtrators, namely sponges of the genus *Parmula*, which are hanging in the trees a good number of meters above the low-water level.

Remarkable is the comparatively high numbers of predaceous insect larvae. Apart from the numerous carnivorous Odonata species are also to be found among the otherwise generally phytophagous Plecoptera, Ephemeroptera, and Lepidoptera. The latter feed in the strong current of cascades on the larvae of Simuliidae.

A general survey on the fauna of these streams shows that in the upper and middle course submersed crustaceous sponges are rare and Bryozoa almost missing; Tubularia are represented by small species from different orders, whilst the greater Tricladida are rare; Tubificidae are always to be found in small numbers; Hirudinae, represented by very small forms, are extremely scarce; Os-

tracoda, represented only by small species, and Copepoda are not frequent; Palaemonidae, represented by a number of species from the genus *Macrobranchium* and related forms can often be found, but Atyidae are missing; Mysidacea, small and transparent animalcules, may be easily overlooked; the biggest invertebrates are represented by the amphibious Potamantidae; the larval stages of the aquatic insects, represented by an extremely large number of species and individuals, constitute the greater part of the invertebrate fauna.

Ephemeroptera are frequent and represented by many specialised forms. Plecoptera are not numerous, represented only by genera of the subfamily Acroneurinae. The larvae of Odonata and Trichoptera are represented by a very big number of species which are well adapted to the various biotopes. Anywhere to be found are Hemiptera; on the surface of the water Gerridae and Veliidae, under the surface some Naucoridae, Corixidae, Belostomatidae, Notonectidae, and *Ranatra*. Apart from the above mentioned carnivorous Lepidoptera there are some rheophile species case-building or even mining in *Thurnia*. Coleoptera are rare; frequent and rich of species are Helminthidae and Gyrinidae; Dytiscidae and Hydrophilidae are

only represented by a few small species. The group that is richest of species are here as well as in other waters Chironomidae. In a small stream may live side by side more than a hundred species. Most of these species are remarkably small. The majority are Chironominae, particularly of the genus *Polypedilum* and of the tribus Tanytarsini. About 15 per cent of the species belong to the predaceous Tanypodinae, particularly to the tribus Pentaneurini and the genus *Coelotanypus*. Ceratopogonidae, Tipulidae, and Stratiomyidae are regularly found in humid or hygropetric substrata.

There are many fishes, most of them are small species. In one and the same stream may be counted upon 30 to 50 different species, the majority of which are Characidae, in addition to these various Siluroidea, Gymnotidae, Cichlidae, and in muddy sections Rivulidae. A big number of these fishes seem to feed on emerging insects or fallen into the water, etc. Outspoken predators are *Hoplia* and the Cichlidae.

To the stream fauna always belong the larvae of frogs or toads, and also various amphibious lizards which by plunging feed on insect larvae. Furthermore can be met small specimens of the crocodile *Jacaretinga trigonus* and occasionally also semi-aquatic sna-

TABLE 1
Average from the analysis of 12 different streams in the central Amazon forests

		y/l		y/l	
μS_{20}	8,52	Na.....	1 296	N.....	297
pH.....	4,5	K.....	1 414	N (NO ₃).....	5,0
Hufa.....	28,5	Ca.....	0	P (total).....	4,8
Alkalinity mval/l..	0,069	Mg.....	21	Si.....	2 480
O ₂ saturation.....	75%	Al.....	112	Cl.....	484
CO ₂ free mg/l.....	30,0	Fe.....	65	SO ₄	26
		Mn.....	18		

kes. There seem to be there no birds which in their mode of life are confined to the stream biotope.

In a rain-forest stream can be distinguished two main biotopes, each with a characteristic fauna determined by the degree of current. Firstly the lenitic region with slowly moving water (below... 20 cm/sec), where a sedimentation of drifting organic stuff takes place, and secondly the lotic region with a rheophile fauna which needs more than 20 cm/sec of current. Whilst in the upper course these two biotopes often change, one after another occurring at small distances, with transitory zones, they find themselves in the meandering middle course often side by side. The lenitic bank is mostly situated opposite the lotic bounce-bank. Within the lenitic area flock together near the bank fine detritus and mudd, which towards deeper water pass over into thick layers of leaves, which final-

ly change into sand. In and on the fine mudd leaves a fauna rich of species that is, however poor of individuals: Turbellaria, Tubificidae, Hydrachnidae, Ostracoda, Copepoda, Ceratopogonidae, a big number of Chironomidae, and Coleoptera of the genera *Laccophilus* and *Anacaena*, small *Corixidae* of the genera *Micronectis* and *Tenagobia*, and the digging larvae of the dragon-fly *Ophiogomphus*. The pure sand is little inhabited, among others by some Chironomidae and *Progomphus*-larvae. On and among the leaves live small Hydroptilidae and the Callamoceratidae *Notiomysis* (Trichoptera), the big digging larvae of *Potamanthus* (Ephemeroptera) and the flattened larvae of *Hagenia* (Odonata), the Naucoridae *Cryphocricos*, and Hydrachnidae. The density of population strongly vacillates and lies between 0.5 and 10 g/m².

In the lotic area are to be found, besides sand, only solid substrata,

such as ramifications of roots, pieces of wood, fixed big leaves, and occasionally bare Arenite stone. The current amounts to 30 cm/sec. on an average, on places where the stream is restricted by pieces of wood and roots and where there is a stronger drop, it may, however, go up to about 60 to 100 cm/sec, and in small cascades even up to 200 cm/sec. The highest density of population of 15 to 20 g/m² will be found in the flowed through systems of roots of the banks of the floor. At these places can be found various Trichoptera of the genera *Psychomyia*, *Potamyia*, *Smicridea*, *Chimarrha*; and of the families Leptoceridae and Hydroptilidae. In addition to these some Ephemeroptera, among others of the genera *Hermanella*, and various Leptophlebiidae, Odonata of the families Libellulidae, Calopterygidae, Agrionidae, Lestidae, and the remarkable *Euphaea*, and furthermore Elminthidae and Plecoptera. On solid wood and stones occur moreover the Trichoptera *Protoptila* (Glossosomatidae), *Marlia* (Odontoceridae), and *Helicopsyche*. At an increased current velocity of more than 40 cm/sec the places of the above mentioned forms are taken by Hydropsychidae, Simuliidae, and various species of the Chironomidae *Rheotanytarsus*. These insect larvae reach the maximum density of population in

the strongest current of the cascades. Among them live as predators the big larvae of *Corydalis*, a Libellulidae well adapted to the ground by its colour, and the above mentioned Lepidoptera species, predatorily feeding on Simuliidae. Where there are some algae on the stones, there are found in strong current moreover the larvae of Baetidae (Ephemeroptera) and *Paragyraactis* (Lepidoptera), on drizzled stones occasionally the Orthoclaidiinae *Cricotopus*.

In the transitory area between water and land lives a Blattidae species that is active at night. Particularly near cascades live on the water level the gleaming larvae of a Lampyridae species and the Trichoptera *Tinodes* which spins long cases.

Wherever in the reverse current or at surface barriers the organic substances drifting on the surface flock together such as fruits, flowers, dead animals, leaves, pollen, etc., there is a rather inconstant biotope constituted by this epineuston, where develops within a short time a characteristic biocoenosis. It can be quickly destroyed by minor water level oscillations. Its surface is always inhabited by Velidae, as a rule found only there. In the aquatic area live some small beetles, Nepidae or Belostomatidae, and the larvae of a Chironomariae, which after the destruction of its



previous biotope fastens itself to the water surface by means of a short thread and hanging on it is drifted to another accumulation of epineuston.

The composition of the above described biocoenosis of the streams changes, when we leave the tertiary central area and get to the adjacent regions, which either belong to archaic, paleozoic, mesozoic formations, or in the foreland of the Andes to young alluvions. According to the geological conditions the water is then more or less rich of nutritive minerals, and pH is getting up to a neutral order. Algae and aquatic flowering plants, shells and snails and phytophagous insect larvae among others are becoming frequent. It is therefore possible to obtain by a biological analysis of stream biocoenoses informations on the water chemism, which admits conclusions on the edaphic and geological conditions of the tributary region of the respective watercourse. These well known relations between the chemism of a water and the one of its tributary area allow by virtue of the inspections carried out on these streams to divide the ecologically apparently homogeneous area of the *Hylea amazonica* into the Central Region which is poor of nutritive substances, and the Border Region which is in any case richer of these substances. The

Border Region, according to its different geological structures can be subdivided into three zones: (1) the zone situated to the North and the South of the Central Region with its predominant archaic formations of the Guyana and Central Brazilian shield, which partially is superimposed by mesozoic layers; (2) to the East the intermediate strictly limited palaeozoic "carbonic stripes", and (3) to the West the foreland of the Andes with its brackish (and marin?) sediments and the young Andine alluvions.

This ecological division of Amazonia which has resulted from the inspection of streams has been corroborated, as far as it has been possible to make use of them, by the biogeographical results of the terrestrial biotopes.

The ecological structure of the Amazonian Region becomes, however, only clear by taking into consideration the fact that this area poor of nutritive substances is cut by many big rivers originating in the border areas and, like the Amazon River itself, partially have dug wide valleys into the soft tertiary sediments and have filled them up with sediments coming from their tributary regions and incessantly renewed from there.

These river valleys with their "Varzea" — landscape have in the Central Region, but for the same climate, ecologically nothing in

common with the adjacent "Terra firme". Their floors correspond to a large extent in their content of nutritive substances to those of the border regions they derive from, they are foreign to their surroundings ("umraumfremd") in Central Amazonia. Those who start thinking from this condition will be able to understand the ecology and biogeography of the Amazon Area.

SUMMARY

The streams of the "Hylea amazonica" represent an extreme biotope. Their water is very poor in dissolved minerals. The trees close over the stream and only a small part of solar radiation touches the ground. The temperature is about 24,5 C° with the daily and annual oscillation of about ± 1 C°. The lack in minerals and light prevents plantlife nearly completely. Except some species of Batrachospermaceae (Rhodophyceae), algae are missing. The only phanerogam is *Thurnia sphaerocephala*, growing semi-aquatically. The basic food of the stream fauna essentially consists of allochthonous organic material, washed or fallen in. Caused by the offered to nutrition and the chemistry of the water, animals, typical elsewhere for the biocoenosis of streams, are missing here completely. For example: mussels and snails — except some *Ferrissia*

without a calcareous shell —, Amphipoda, Isopoda — except parasitic ones —. Turbellaria, Oligochaeta, Hirudinaea and Ostracoda are rare. Larvae of insects, as Ephemeroptera, Odonata, Trichoptera and Chironomidae, are common and numerous.

Generally a stream can be divided into three ecological sectors, the upper course: source- and erosion-zone with relatively strong gradient, where lenitic and lotic areas are changing frequently. The middle course: sedimentation-zone with a lot of meanders and sandy bed.

The lower course: "Igapó"-zone, determined by the immense annual oscillation of the water-level of the main river system. A stream-biocoenosis can develop itself only during a few months of the year. During the other time the water is dammed up, forming a type of waters limnologically not yet defined.

The stream-biocoenosis of the upper and middle-course shows a changing composition, depending on the current velocity. Two main biotopes can be distinguished by a characteristic animal-association: The lenitic biotope — current velocity speed up to 20 cm/sec — with sedimentation of organic material, and the lotic biotope with stronger current velocity speed and a rheophilous fauna. The main

substratum for rheophilous animals is composed of roots and wood, hanging and lying in the water.

Especially in the lower course roots of epiphytes (Araceae) are hanging into the water, being of particular importance, because they are floating on the surface even in the time of stagnation. A very dynamic and isolated biotope with a characteristic fauna is formed by floating epineuston — fruits, pollen, dead animals, skins of emerged insects etc.!

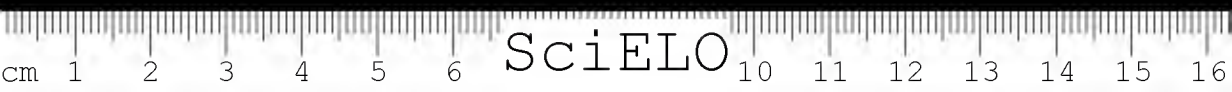
The stream mentioned above is typical for the Central-Amazon region, covered by washed-out deposits of sand and clay, which were accumulated in the tertiary by a large fresh water lake. Its bounding formations are geologically

different and richer in minerals: here molluscs are be found.

By the known close connection among the chemistry of the streams and the geological and edaphic facts we can divide the Amazon region ecologically into the central region, poor in nutrition, and the heterogenous peripheral regions which are richer in it. The central and poor region is cut by the rivers coming from the bordering regions. Their large valleys are filled with alluvions brought from their upper courses, and they are ecologically strange in the central region.

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“EUPERA PRIMEI” SP. N. DE LA REGIÓN DEL RIO UCAYALI, PERU (Mollusca, Pelecypoda)

MIGUEL A. KLAPPENBACH

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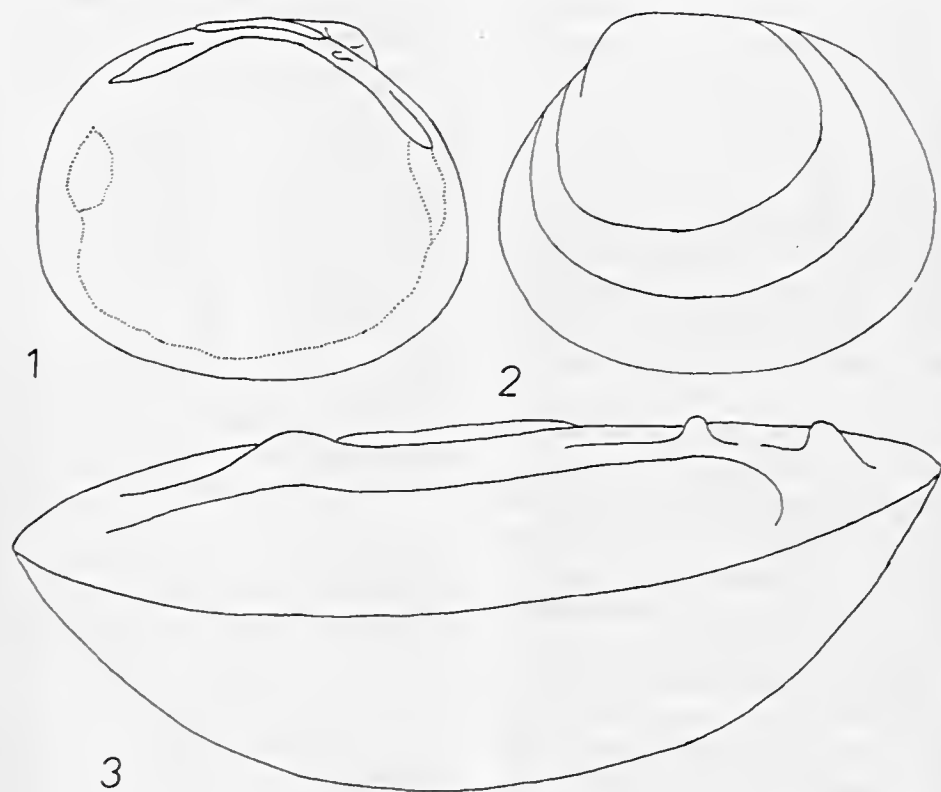
(Con 3 figuras en el texto)

En América, del río de la Plata al sur de los Estados Unidos, se han descrito 26 especies de pequeños bivalvos fluviales pertenecientes a la familia Sphaeriidae, que actualmente son agrupados en el género *Eupera* Bourguignat, 1854. Este género ha sido considerado por numerosos autores como sinónimo del más antiguo *Byssanodonta* D'Orbigny, 1846. No obstante, en un trabajo anterior (KLAPPENBACH, 1960) hemos demostrado que se trata de dos géneros perfectamente diferenciados, debiendo restringirse el uso de *Byssanodonta* exclusivamente para una pequeña almeja del río Paraná, de charnela edéntula. Indudablemente ese número sufrirá modificaciones una vez que se realice la revisión del género y aunque alguna especie posiblemente deba ser sinonimizada, creemos que el mismo irá en aumento a medida que se vaya conociendo mejor

la pequeña fauna malacológica de los grandes ríos sudamericanos. Por ello resulta sumamente curioso el hecho de que las menciones que hemos podido registrar para la enorme cuenca amazónica resulten tan escasas. En una rápida revista de las especies descritas para Sud América, nos encontramos con que la primera lo fué en época relativamente temprana (SPIX, 1827: 32), para el Estado de Bahía, en Brasil, con el nombre de *Cyclas bahiensis*. Luego ANTON (1837: 284) describe dos especies de Sud América, *Cyclas maculata* y *C. modioliforme*. No las figura ni concreta localidades y sus cortas descripciones no permiten la identificación de sus especies. Pocos años después HALDEMAN (1841: 53) describe más brevemente aún su *Pisidium diaphanum* sobre un ejemplar que habría sido encontrado (PRIME, 1863: 33) en el interior

de una gran *Pomacea* procedente de Brasil, sin localidad más precisa. No fué figurado y actualmente (H. B. BAKER, 1930: 53) estaría perdido. Mas tarde BOURGUIGNAT (1854: 663) describe y figura aceptablemente *Pisidium moquinianum*, del centro de América Meridional, sin establecer localidad más definida. Transcurren varios años hasta que CLESSIN (1879:246/47) describe su *Limosina tumida*, también de Bahía y cuya ilustración deja bastante que desear. Diez años después JOUSSEAUME (1889: 257/58) nos hace conocer una nueva especie de Caracas, Venezuela, con el nombre de *Limosina simoni*. Descripción e ilustración son buenas. F. BAKER (1913: 663/64) describe y figura, sin nominar, una especie de *Eupera* del lago Papary, en el Estado de Rio Grande do Norte, Brasil. Posteriormente DOELLO-JURADO (1921: 73/75) describe *Eupera platensis* de Rio Santiago, Provincia de Buenos Aires, Argentina, sobre el rio de la Plata. Luego H. B. BAKER (1930: 56/57) aumenta la lista con *Eupera gravis*, de Venezuela. Nos correspondió cerrarla (KLAPPENBACH, 1962: 102) con *Eupera doellojuradoi* de Puerto Platero, Colonia, Uruguay. Esta es, cronológicamente, la última especie del género descripta para Sud América. No entrando a considerar las especies del sur, cuenca del rio de la Plata,

E. platensis y *E. doellojuradoi* y prescindiendo de las especies de ANTON y HALDEMAN, insuficientemente descriptas, no figuradas, totalmente imposibles de identificar y sin localidades típicas concretas, tenemos para el norte de Sud América cinco especies de *Eupera*: *E. bahiensis*, *E. moquiniana*, *E. tumida*, *E. simoni* y *E. gravis*; ninguna de ellas concretamente dentro del área amazónica. Constituyen excepción tres citas de HAAS (1949a: 153; 1949b: 307; 1952: 111), las únicas que hemos podido hallar en la literatura malacológica, basada todas ellas en material colectado por el Dr. Harald Sioli en localidades de los Estados de Pará y Amazonas. Estas citas de HAAS son referidas en su totalidad a *Eupera bahiensis* (Spix, 1827). Por nuestra parte al revisar el material de *Eupera* existente en la colección del American Museum of Natural History, de Nueva York, encontramos un numeroso lote no identificado procedente de la zona del rio Ucayali, en Perú, que estimamos pertenece a una especie nueva, cuya descripción damos a continuación, dejando expresa constancia de nuestro particular agradecimiento al Dr. William K. Emerson, Chairman y Associate Curator y Sr. William E. Old Jr., Museum Specialist, por su hospitalidad y generosa



Eupera primei sp. n., holotipo N.º 1220 Col. Mal. Mus. Nac. Hist. Nat. Montevideo, largo 7 mm — Fig. 1: Valva izquierda, vista interna; fig. 2: idem, vista exterior; fig. 3: idem, vista inferior, mostrando la ubicación de los dientes.

cesión de ejemplares. La especie es nominada en homenaje a Temple Prime, uno de los primeros especialistas en estos diminutos bivalvos.

Eupera primei sp. n.

Diagnósis: Concha diminuta aunque más bien grande dentro del género (7.00 X 6.00 mm). Se caracteriza por su forma oval muy corta y eje vertical elevado, resultando proporcionalmente muy

alta. Umbones pequeños y charnela relativamente débil. Perióstraco marrón muy claro, con estrías lamelosas bajas y poco conspicuas.

Holotipo: N.º 1.220 Col Malac. Mus. Nac. Hist. Nat. Montevideo. Colector: H. Bassler, fecha: Noviembre de 1923.

Localidad Típica: Pequino, próximo al río Ucayali, Perú.

Medidas (en milímetros): largo, 7.00; alto, 6.00.

Descripción: Concha equivalva, cerrada, inequilateral. Valvas ovales, con el eje mayor orientado en sentido antero-posterior, delgadas pero de textura bastante sólida para el tamaño. Borde dorsal corto, sub-recto; anterior fuerte y regularmente curvado, se une al inferior en una suave línea descendente. Borde inferior largo, de curva amplia y abierta, se continúa con el posterior, más corto pero también ofreciendo una curva muy regular. Umbones pequeños, prosogiros, algo desplazados en dirección anterior. Dientes cardinales simples en ambas valvas, pequeños, más bien bajos, colocados inmediatamente por debajo del umbón; el izquierdo más grueso y compacto, el derecho más comprimido formando una pequeña lámina curva que presenta en su cara inferior una zona levemente excavada donde juega el cardinal izquierdo. Este, a su vez, presenta en la base de la cara superior una foseta estrecha y alargada, para alojamiento del cardinal derecho. Los dientes laterales, dobles en la valva derecha, son simples en la izquierda. En ésta última el lateral anterior se presenta más corto, grueso y elevado, en forma de triángulo sub-equilátero. El lateral posterior es más alargado, fino y bastante más bajo. En la valva derecha los anteriores son cortos, gruesos, bajos; el superior más débil, separados por una

fosa alargada, relativamente profunda, para alojamiento del lateral anterior de la valva izquierda. A su vez los posteriores de la valva derecha son un poco más alargados y la fosa que los separa no es tan profunda, siendo el lateral inferior más grueso que el superior. Ligamento algo corto, fino, comienza a la altura de los laterales posteriores y se extiende hasta llegar frente a los cardinales. Superficie exterior aparentemente lisa, con dos fuertes estadios de crecimiento bien marcados. Bajo fuerte aumento es posible observar las estrías lamelosas y concéntricas que forma el fino perióstraco de color marrón claro y que por transparencia deja ver las manchas pardo violáceas ya conocidas de otras especies del género. Superficie interna amarillenta, deslucida y áspera por dentro de la línea paleal. Por fuera de esta línea se torna pulida y brillante, formando una banda sobre el borde inferior interno, que se extiende desde la impresión muscular posterior a la anterior. Las inclusiones pigmentarias ya mencionadas, adquieren en la superficie interna de las valvas un aspecto grumoso, arracimado, en relieve. Impresión paleal entera, visible. Impresiones musculares también visibles, bastante grandes.

Paratipos: Lote N.º 1.309 Col. Malac. Mus. Nac. Hist. Nat. Montevideo. 13 ejemplares, igual proce-

dencia, colector y fecha que el Holotipo. Se dan las medidas de cinco ejemplares: (en milímetros).

<i>largo</i>	<i>alto</i>
7.00	5.50
6.00	5.00
6.00	4.75
5.75	4.75
5.50	4.50

Lote N.º 89.158 Col. Malac. American Museum Natural History New York. Numerosos ejemplares, igual procedencia, colector y fecha que el Holotipo.

Observaciones sobre Paratipos:

La totalidad de los ejemplares presentan gran uniformidad en forma, coloración y aspecto general. Aún los ejemplares pequeños no ofrecen diferencias o variaciones apreciables. Vistos en norma superior, los dientes laterales de la valva derecha no alcanzan a pasar el borde superior de ésta, resultando invisibles para el observador. En cambio, los de la valva izquierda sobrepasan dicho borde, siendo perfectamente visibles para el observador. En cuanto a los umbones, estos no exceden la línea del borde superior cuando son vistos en norma lateral.

Distribución: Conocida únicamente de la localidad típica.

Discusión: De las cinco especies que hemos seleccionado más arriba como posibles de ser encontradas en la cuenca amazónica, pres-

cindiremos de *E. tumida*, pequeña especie que como su nombre lo indica, presenta un exagerado desarrollo en sentido lateral, al punto de resultar casi cilíndrica. No considerando a *E. simoni* y *E. gravis*, la primera de borde posterior truncado y la segunda de contorno casi circular y umbones fuertes y altos, podemos comparar nuestra especie con *E. bahiensis* y *E. moquiniana*. *E. primei* difiere de la especie de SPIX, entre otros caracteres, por sus umbones, que en ésta última son prominentes mientras que en aquella resultan pequeños y poco conspicuos. A su vez la especie que estamos describiendo es bastante comprimida lateralmente, resultando su ancho comparativamente mucho menor que en *E. bahiensis*, de la que se puede decir que es evidentemente abultada. En cuanto a *E. moquiniana*, presenta un borde posterior con un notorio trunco oblicuo, recto, resultando sub-angulosa la unión con el borde inferior, mientras que en *E. primei* ese borde es regularmente curvado. La primera a su vez también es de fuerte desarrollo lateral, frente a nuestra especie, que como quedó dicho, es francamente deprimida. Finalmente *E. primei* presenta los pequeños umbones que no exceden la línea del borde superior, mientras que *E. moquiniana* muestra los umbones sobrepasando dicha línea.

SUMARIO

Se efectúa una breve revisión de las especies de *Eupera* descritas para America del Sur, destacando las escasas menciones para la cuenca amazónica. Se describe *Eupera primei* sp. n., de Pequino, próximo al rio Ucayali, Perú. Caracterizada por su forma oval muy corta, eje vertical elevado, umbones pequeños y charnela débil, resultando facilmente separable de *E. bahiensis* y *E. moquiniana*, especies estas últimas con las que es comparada.

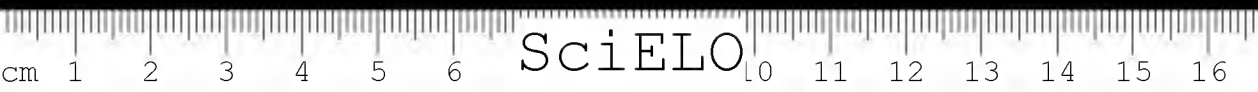
SUMMARY

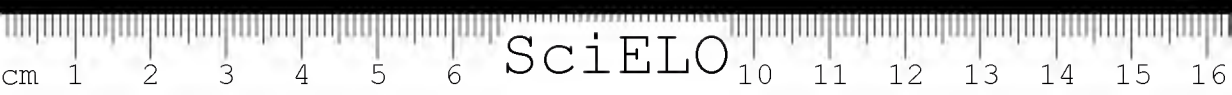
The above presents a brief revision of the *Eupera* species described for South America, emphasizing the scarce references registered for the large Amazonian basin. *Eupera primei* sp. n. from Pequino, near Ucayali river in Peru is described. Characterized by its very short oval outline, small umbos and weak hinge, it is easily separable from *E. bahiensis* and *E. moquiniana*, with which species it is compared.

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SciELO

PODZOL SOILS: A SOURCE OF BLACKWATER RIVERS IN AMAZONIA

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Acidic freshwater of brownish colour which is due to dissolved or suspended organic matter of allochthonous origin, is commonly referred to as 'blackwater' (SCHNEIDER, 1961).

Blackwater rivers are a typical feature of the humid tropical belt. They occur also in non-tropical regions. It is a well known fact that blackwater rivers flow from both peat and swamp soils. But relatively little is known about podzol soils commonly associated with blackwater rivers, in the tropics. The reason why tropical podzols have been neglected so far is no doubt the low agricultural potential of these soils.

PODZOLS

The Russian word podzol is meaning 'soil under ash' and is applied to acid raw humus soils the essential process of which is term-

ed podzolization, i.e. destruction of both primary and clay minerals, and translocation of sesquioxides and/ or humus from the topsoil into the subsoil (ANON., 1964; MUIR, 1961).

The topsoil of podzols consists of an organic matter layer over a bleached quartz sand layer. In the subsoil, organic matter, sesquioxides, or both are accumulated.

Tropical podzols being often identical with 'white sandy soils' or 'bleached sands' are soils which show a bleached layer of white quartz sand which may attain a thickness of several meters, below the surface humus layer. The raw humus at the soil surface may be absent, due to its destruction by erosion or agricultural and other practises of man. The white sand layer which gave the name to the above white sandy soils is due to bleaching and is followed by the

accumulation zone. This accumulation horizon may be endured and is referred to as *ortstein*, *pan*, or *coffee rock*, the latter expression being mainly used by Australian authors.

If in the formation of podzols groundwater fluctuations are involved the soils are referred to as groundwater podzols, hydromorphic podzols, gley podzols, or aquods; groundwater podzols of the tropics are *thermaquods*; podzols without groundwater influence are normal or well drained podzols (ANON., 1960).

Commonly, 'lowland tropical podzols' — a term proposed by RICHARDS (1941) to distinguish tropical podzols of low elevation from tropical mountain podzols and non-tropical podzols as well have developed from quartz sandy modern deposits accumulated by marine or river actions.

The vegetation of lowland tropical podzols differs characteristically from the normal tropical rain forest (RICHARDS 1957) and is considered to be an edaphic climax of the latter. Heath forest, *kerangas*, and *padang* as well of Australasia, *wallaba* forest and *muri* bush of northern tropical America, *caatinga* forest of the Rio Negro, *campina* forest, and certain *campos* of the Lower Amazon are plant communities which growing on lowland tropical podzols are charac-

terized by the tendency of one or some plant species towards dominance (RICHARDS, 1945).

BAKKER (without year) gives some reasons of extreme bleaching of soils, under tropical environmental conditions. One of them is the extreme acidity of leaf extract and litter of certain tropical plant species.

DISTRIBUTION OF TROPICAL PODZOLS

The distribution of lowland tropical podzols shows a remarkable geographic pattern (KLINGE, 1965a). After D'HOORE (1964) they are rare in Africa where they occur in small patches. They have developed from both coastal sandy sediments along the east and west coast of this continent, and from river sediments, and at few places in the Congo basin; they are also known to exist on the islands of Mafia and Madagascar. Most African blackwater rivers, however, flow from moor and swamp land.

In Australasia (DUDAL & MOORMANN, 1964) where lowland tropical podzols are often associated with swamps and peat formation, they partially occupy extent areas. These podzols are known to occur in the Mekong basin, eastern Malay Peninsula, upon Borneo, New Guinea, and some other Indonesian islands as well, in tropical and

subtropical Australia, and upon the North Island of New Zealand. Seepage of podzol areas is of the blackwater type (DUDAL & MOORMANN, 1964; VAN STEENIS, 1957).

Lowland tropical podzols of America are reported from Florida and the Guianas as well where they occur in areas of relatively large extent. Podzols have been described from some of the Antilles and eastern Central America. In the Amazon basin where lowland tropical podzols are widespread they occupy small isolated patches. Lowland tropical podzols are always associated with blackwater rivers, but these rivers flow also from peats and swamp soils, mainly in Florida and the Guianas.

Podzols of mountains within the tropical belt have been reported from all continents and are bound to acid rocks, or impeded drainage, and to cool humid climatic conditions as well.

UNESCO, within its Humid Tropics Research Programme, is actually preparing a symposium on tropical podzols, their vegetation, and blackwater rivers associated with these soils.

PODZOLS OF TROPICAL SOUTH AMERICA

In tropical South America podzols are known to exist in both lowlands and uplands.

Podzols occur at some places of the coastal regions of Colombia and Brazil as well.

There is no literature on podzols of the Orinoco basin. Rather detailed informations, however, are available on lowland tropical podzols of the coastal plains in Suriname, British and French Guiana as well.

There are only few informations on podzols in western Amazonia including the eastern parts of Colombia, Ecuador, Peru, and Bolivia. ELLENBERG (1959; 1964) reported shortly on these soils which were observed in the surroundings of Iquitos, Peru, and WRIGHT (1964) described a mature soil trending towards a tropical gley podzol, from eastern Bolivia. GRUBB. *et al.* (1963) referred briefly to soils which show similarities with podzols of temperate regions, in Ecuadorean Amazonia.

Podzols of Brazilian Amazonia are dealt with in the subsequent chapter.

Mountain podzols have been reported from the Andes and the Guiana Highlands as well.

LOWLAND TROPICAL PODZOLS OF BRAZILIAN AMAZONIA

The relationship between blackwater rivers and podzols of Amazonia is not touched in the pre-war literature. BUT SIOLI (1954; 1956),

in papers on blackwater rivers of the Upper Rio Negro, pointed out that these rivers flow from sandy wet soils (not studied by the author) covered with caatinga forest (HUECK, 1966; RODRIGUES, 1961; TAKEUCHI, 1962). The fact that these blackwaters contained free aluminum which never before were found in any other Amazonian river water, induced the conclusion that the aluminum content of the blackwater is due to the breakdown of aluminum silicates in the sandy soils from which the blackwater flows and that podzolation is going on in these soils.

The association of blackwater rivers and white sandy soils has been already observed by SPRUCE (1908) and others.

The pedologist who first studied Amazonian podzols appears to be DAY (1961). He described both very sandy groundwater podzols developed on Quaternary sediments under poor to imperfect drainage conditions, and well drained Pará podzols which are more of academic interest than of any agricultural value. Some data on both types of podzols are tabulated below.

TABLE 1

Groundwater podzols and Pará podzols of Amazonia (After Day, 1961)

	Groundwater podzols	Pará podzols
Relief	Level to gently sloping, low lying terraces.	Flat to gently sloping or undulating.
Drainage	High water table. Natural drainage is poor. Run-off of surface water is slow.	Excessive.
Vegetation Use	Poor to very poor forest. Essentially non agricultural soils of very low fertility.	Brushes and low trees. Extremely low fertility and water-holding capacity limit the agricultural usefulness of these soils.
Distribution	In small drainage-ways. Probably widespread throughout the Lower Amazon. Of very limited extent in any individual unit and total area is relatively small.	Observed in two localities in the Lower Amazon (near Belém, Pará, and north of Macapá, Territory of Amapá).

In 1962, several authors have reported on Amazonian podzols. KLINGE published data on carbon and nitrogen contents of Amazo-

nian soils, including some podzols under caatinga and campina forests, and wet campos as well. SIO-LI & KLINGE discussed relations be-

tween podzols, blackwater rivers and podzols vegetation, especially of the Rio Negro. VIEIRA & SANTOS described a groundwater podzol of the surroundings of Breves, Pará, giving also some analytical data on this soil. VIEIRA & FILHO discussed results of soil investigations performed in caatingas of Uaupés, the soils being described as podzolic regosol, on brown soils of granitic origin, and regosol, both developed from sandy river sediments.

FALESI (1964) described podzols of the Zona Bragantina, Pará, and KLINGER & OHLE (1964) reported on chemical properties of both soils and waters, in Amazonia.

Recently, ALTEMÜLLER & KLINGE (1964), and KLINGE (1965 b) described catenary soil sequences in which giant podzols occur, from the Manaus area. The catenas were found on slopes of small valleys drained by blackwater rivers. The giant podzols occupying the lowest sites of the catenas are characterized by a few meters deep bleached sand layer and a remarkable thin humic cemented ortstein as well. The thin ortstein is suggested to be related to lateral percolation of rain water which carries away the organic matter migrating through the podzol profile. The mobil organic matter, subsequently, passes into the creeks and so doing deter-

mines the characteristics of the blackwater.

Blackwater rivers have been related to lateral percolation on podzols, in other tropical countries too (DAMES, 1962; DOST, 1964).

RELATIONS BETWEEN TROPICAL PODZOLS AND BLACKWATER

Since von HUMBOLDT (1860) reported on blackwater rivers of equatorial South America, and MUNTZ & MARCANO (1888) discussed the origin of blackwater colour, literature on blackwater in South America has grown much, and many theories about blackwater rivers and the colouring substances as well have been forwarded.

KOCH-GRÜNBERG (1909) reported on Indian talks in which the colour of blackwater rivers is explained by extracts of the salsaparilla plant. (*Smilax*).

After BEEBE (1927) the colour is mainly caused by stains derived from the leaves of the Wallaba tree (*Eperua falcata* Aubl.) The same explanation was given by DAVIES & RICHARDS (1933).

De CIVRIEUX & LICHY (1950), in a brief historical summary of opinions about blackwater and its colour, referred to von HUMBOLDT who reported on thick grass mats and roots of salsaparilla (*Smilax*),

as sources of the staines; von HUMBOLDT gave notice too on Upper Orinoco Indians who believed that the staines are extracts of the moriche-to palm. DE CIVRIEUX & LICHY themselves supposed that the key to solve the problem is in the swamp forests from which blackwater rivers flow.

By other authors (HUBER, 1906, SIOLI, 1956) the opinion was expressed that blackwater rivers originate in the so-called igapó forests which accompany many Amazonian blackwater rivers.

In tropical and non-tropical regions as well, blackwater rivers are known to flow from peat soils. In these cases the colour of the water is due to organic matter derived from the peat.

There are, however, tropical blackwater rivers flowing from podzol soils. The following facts speak in favour of a genetic relationship between both podzols and blackwater:

I) Blackwater rivers may be intimately associated with podzols growing specific forest types, in Amazonia and other tropical South America as well, mainly the Guianas (BLEACKLEY & KHAN, 1963), and others). This association has been observed too by geographers, botanists and limnologists as well, in the tropical

belt (cf. Proc. Unesco Symposium held at Abidjan, Tjiaw and Kuching).

- II) The blackwater character of groundwater in podzols soils points on a genetic relationship between both the soils and the water, in the tropics (VAN STEENIS, 1935 a; 1935 b; 1957).
- III) The observation that the colour of blackwater becomes more intensive when it rains after a period of droughtiness, is supposed to be related to the outflow of dark coloured groundwater which subsequently is diluted by further rain.
- IV) Podzol ortsteins the thickness of which does not correspond to that of the bleached sand horizons, are found at sites where drainage is mostly lateral, and have been described from Amazonia (KLINGE, . . . 1965 a), and the Guianas (BLEACKLEY & KHAN, 1963; DOST, 1964) as well.

This communication based more on literature studies than on field or laboratory work may be concluded with a reference to RICHARDS (1957) who wrote:

"Blackwater" streams are also found flowing from Tropical moor forest (peat swamp), but where no

extensive swamps are known to exist 'blackwater' is a trustworthy guide to the presence of bleached sands." As said above, these bleached sands are often to be classified as podzols, from the pedological point of view.

SUMMARY

The intention of this literature review is to point on the very striking association of blackwater rivers and podzols under specific plant communities which is known since the first naturalists traveled through the humid tropical belt.

After defining the pedological terms podzol, tropical podzol, and lowland tropical podzol as well, the distribution of lowland tropical podzols and their association with blackwater rivers in Africa, America, and Australasia are regarded.

Special reference is made to Amazonia and its Brazilian portion from where podzols have been reported in recent years. These podzols are found under both caatinga and campina forests, and wet campos as well, and are always associated with blackwater rivers.

It is well understood that blackwater rivers flow from peat and swamps, in tropical and non-tropical countries as well. There is no doubt, however, that blackwater rivers originate in podzol areas, in

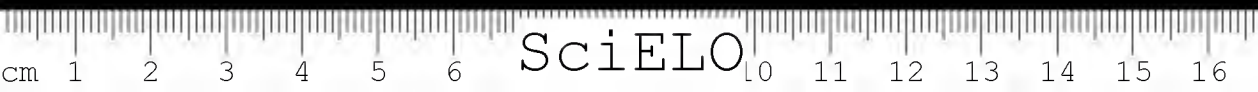
the humid tropics. Some facts which point on a genetic relation between both blackwater rivers and podzols are tabulated.

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THE ARTIFICIAL BROKOPONDO LAKE OF THE SURINAME RIVER. ITS BIOLOGICAL IMPLICATIONS

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(With 6 text-figures, 1 map and 3 graphs)

On February 1, 1964, the dam across the Suriname River at Afo-baka (Surinam) was closed and the artificial Brokopondo Lake began to fill. The lake will ultimately cover an area of 1.500 km² tropical forest and the water is being used for hydroelectric purposes. At the end of 1963 a team of four biologists were enabled by the Netherlands Foundation for the Advancement of Research in Surinam and the Netherlands Antilles (WOSUNA) to study the alterations in plant and animal life in the lake region. The work is being carried out under the auspices of the Netherlands Foundation for Scientific Research in Surinam and the Netherlands Antilles ("studiekring"). Hydrobiological research was started some months before the closure of the dam by P. LEENTVAAR and continued at pre-

sent by J. V. D. HEIDE. The botanist, Dr. J. VAN DONSELAAR carries out botanical inventarisations. Ichthyological inventarisations are being carried out by various investigators. Few biological data were known from the river before the closure and the available time until the dam was closed was short; consequently our knowledge of plant and animal life before the changing of the environment is scarce. A few trips on the river and regular sampling at Pokigron in the upper course, yielded an impression of the undisturbed river.

The description of the river is of interest for comparison with tributaries of the lower Amazon basin which rise also in the Guiana highlands. The Suriname River and its tributaries Pikien Rio and

RIVON communication nr 234.

Gran Rio rise in the highlands of Guiana just north of the Brazilian border. The river flows northward through tropical rainforest. The riverbed is rocky. Trees border the river, but neither swampy vegetation nor areas with stagnant water occur along the banks. The water flows swiftly where rapids and falls are present. Between these obstacles the river flows, sluggishly. The river carries little silt and there is practically no mud at the bottom. Sand flats are visible at dry times. The water is poor in minerals, as is shown by the low electric conductivity of about $20\mu\text{S}$. The pH is about 6.5 and the water is almost saturated with oxy-

gen. The temperature varies between 28 and 30°C . The transparency, measured with the Secchi-disc, is about 1.5 meters. The colour of the water is greyish-brown; it originates from brown particles suspended in the water and not from dissolved humic substances. There is a high amount of silica and some iron. In small, shallow tributaries, such as the Sarakreek (map), the turbidity of the water is higher and more iron is present; the electric conductivity is higher, the oxygen content is lower and the temperature is also lower due to shadow by trees. The colour of the water is turbid-brown. For the Amazon basin SIOLI (1964) distin-



Fig. 1 — *The barrage in the Suriname River at Ajobaka, with dead trees in the lake (June 1964).*

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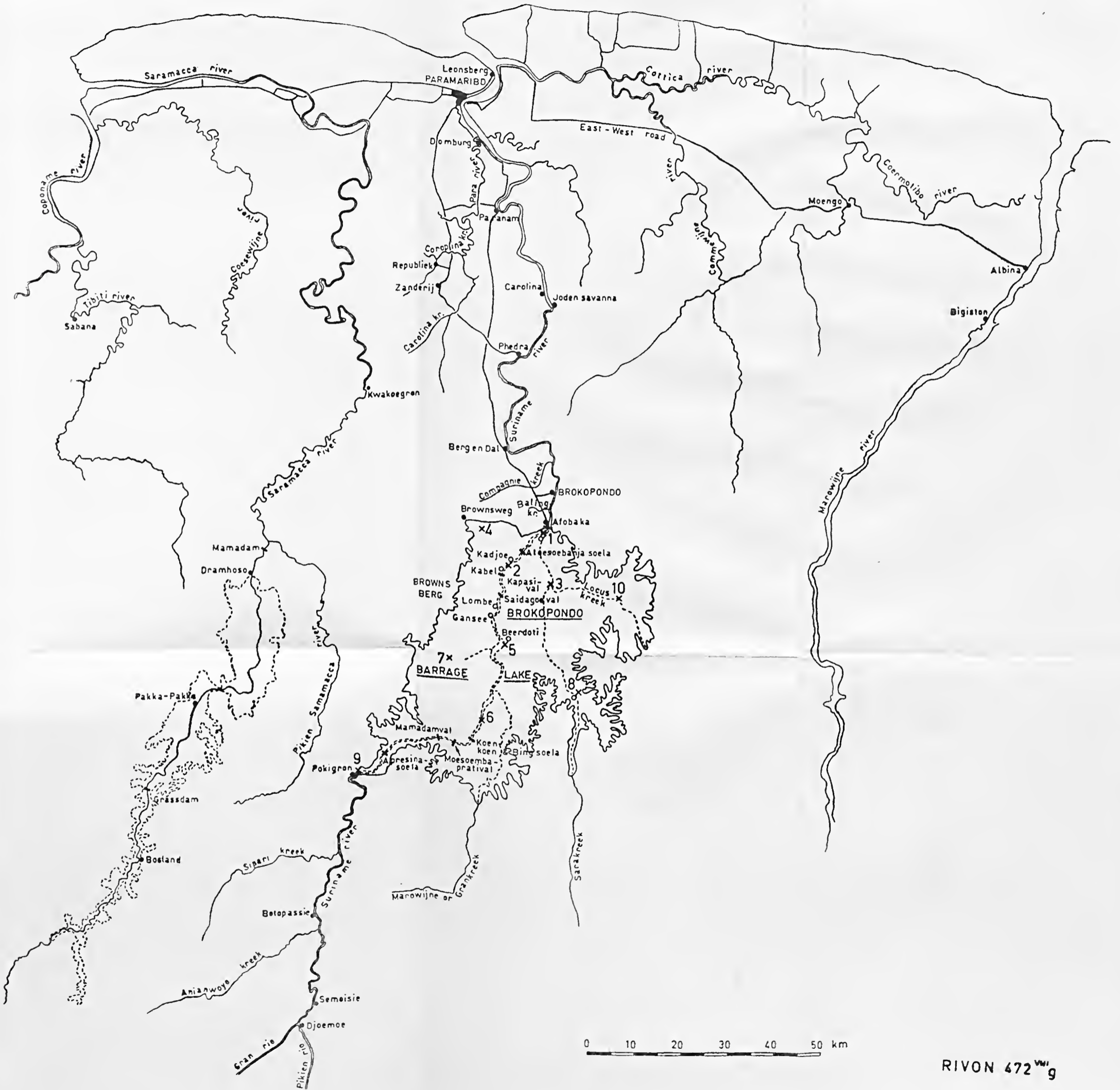


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The total mass of organisms and also of plankton is low. Therefore it is surprising, that the river is comparatively rich in fish. The food chain of the fish is not clear; probably some of the fish feed on the relatively numerous shrimps, but several species prey on other fish.

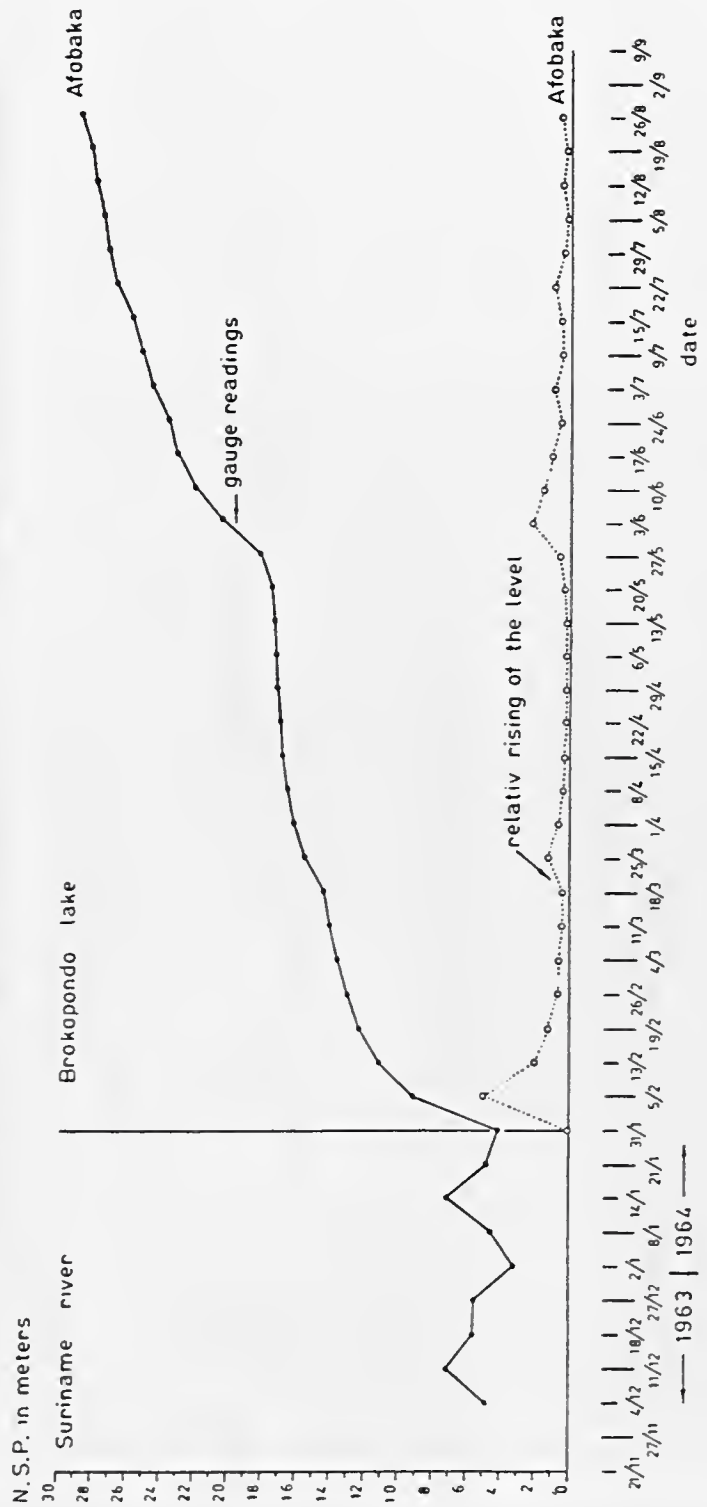
River conditions vary in the dry period and the rainy period. According to weekly observations at Pokigron in the upper course of the river, the water level is fairly stable from December until March. In the last week of May, the main

rainy season starts and the water level rises about 2 meters for a period of two months. In the dry season plankton is developing but soon after the beginning of the rains, this plankton is washed downstream. Plankton catches are composed now of species, which occur in tributaries; when the rains last long practically no more plankton is found. Therefore, during the months of July and August, pure water flows down the river. At this time the pH and electric conductivity of the water are lowest. This seasonal fluctuation



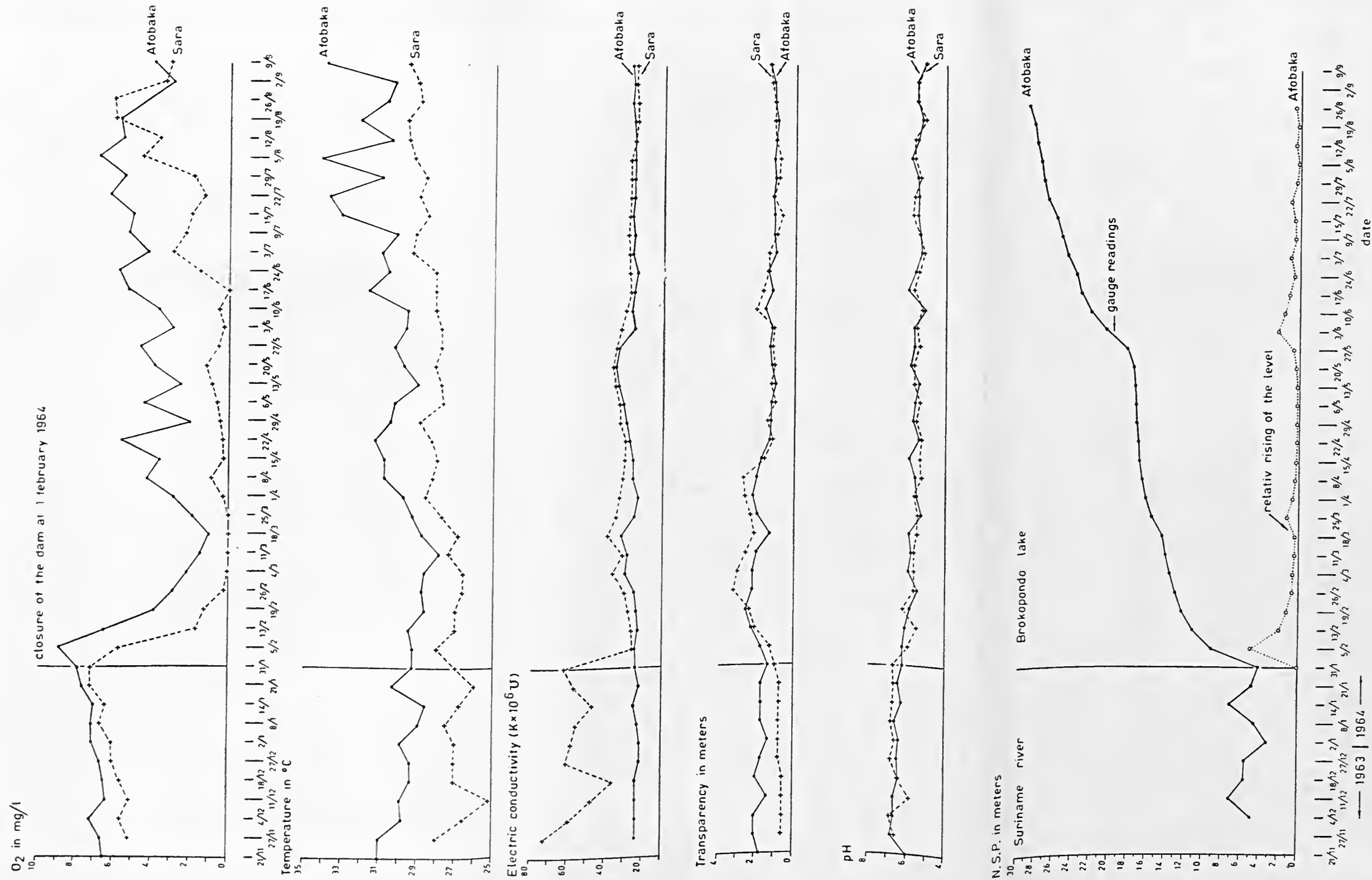
Fig. 3 — Growth of filamentous algae in quiet parts of the lake, between inundated trees, near the village Koffiekamp (July 1964).

CHEMICAL ANALYSES AND WATER LEVEL OF THE SURINAME RIVER AND THE BROKOPONDO LAKE IN 1963 AND 1964



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CHEMICAL ANALYSES AND WATER LEVEL OF THE SURINAME RIVER AND THE BROKOPONDO LAKE IN 1963 AND 1964



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Fig. 4 — Suriname River near the village Koffiekamp in the dry season (January 1964).

in plankton and mineral content in the flowing river affected conditions in the expanding lake, when the water entered this lake.

After the closure of the dam observations were started at 2 of the future 10 sampling stations. The following data concern only these two stations, (until September 1964) located at Afobaka near the dam in the midst of the river and in the Sarakreek inside the forest.

As is shown in graph 2, the water level rose quickly. The gauges are given in NSP = New Surinam Level. During the short rain in March and in the long rainy period following the end of May the

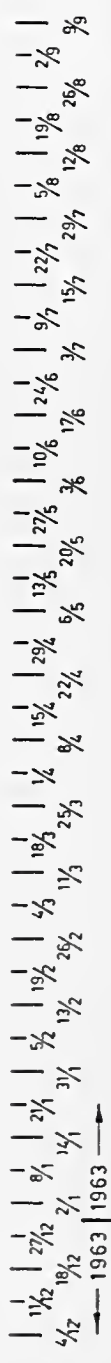
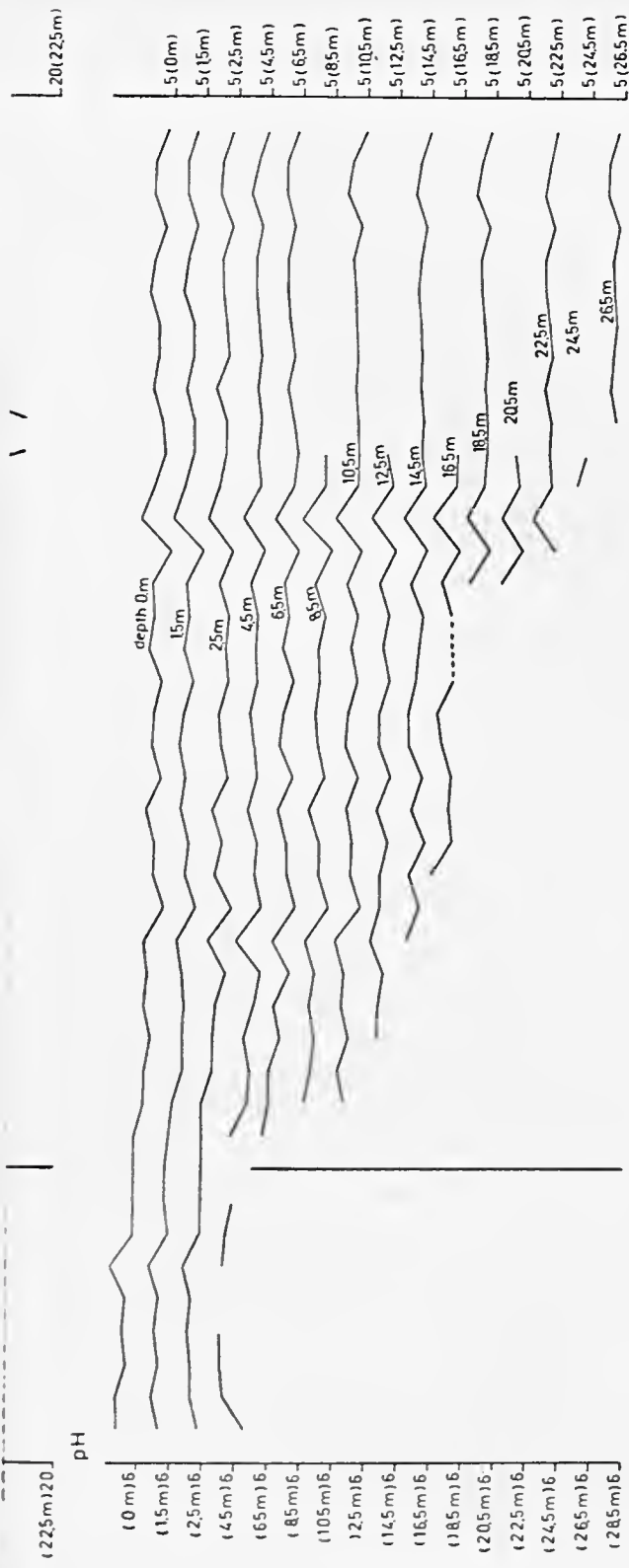
rise in level was accelerated. In the same graph the surface values are given of oxygen, temperature, pH, electric conductivity and transparency measured with the Secchi-disc. The differences between Suriname River and Sarakreek before the closure are easily detected in the graph. Soon after the closure the water stagnated at both stations and a sharp drop in oxygen content occurred. At Sara the exhaustion was greater as more decaying organic matter was present and stagnation was enhanced by lack of wind between the trees. In Sara station for several weeks no oxygen was found from top to bot-

tom. After 18 March 1964 the oxygen content increased again, but only in the upper 3 to 4 meters. Two periods of increasing oxygen content are obvious, especially in the curve of Sara. The first increase occurred during the dry time of April and May; the second during the prolonged rain period after June. In September both stations obviously became equal in oxygen content. At this time more open space appeared between the trees by the rising water level at Sara, even more, by the total inundation of trees. As a consequence the improved illumination of the

water surface favoured oxygen production by the plankton. Also the temperature increased, but the temperature at Sara — more shadowy by trees — remained about two degrees lower than at Afobaka. Higher temperatures were found at the surface of the stagnant water than in the flowing stretches. At Afobaka the maximum temperature recorded was about 35° C. Temperature and oxygen were fluctuating strongly during the day in the stagnant water (graphs 3 and 4). The transparency of the water at Sara increased more than at Afobaka, de-



Fig. 5 — *Growth of waterhyacinth in the lake (August 1964).*



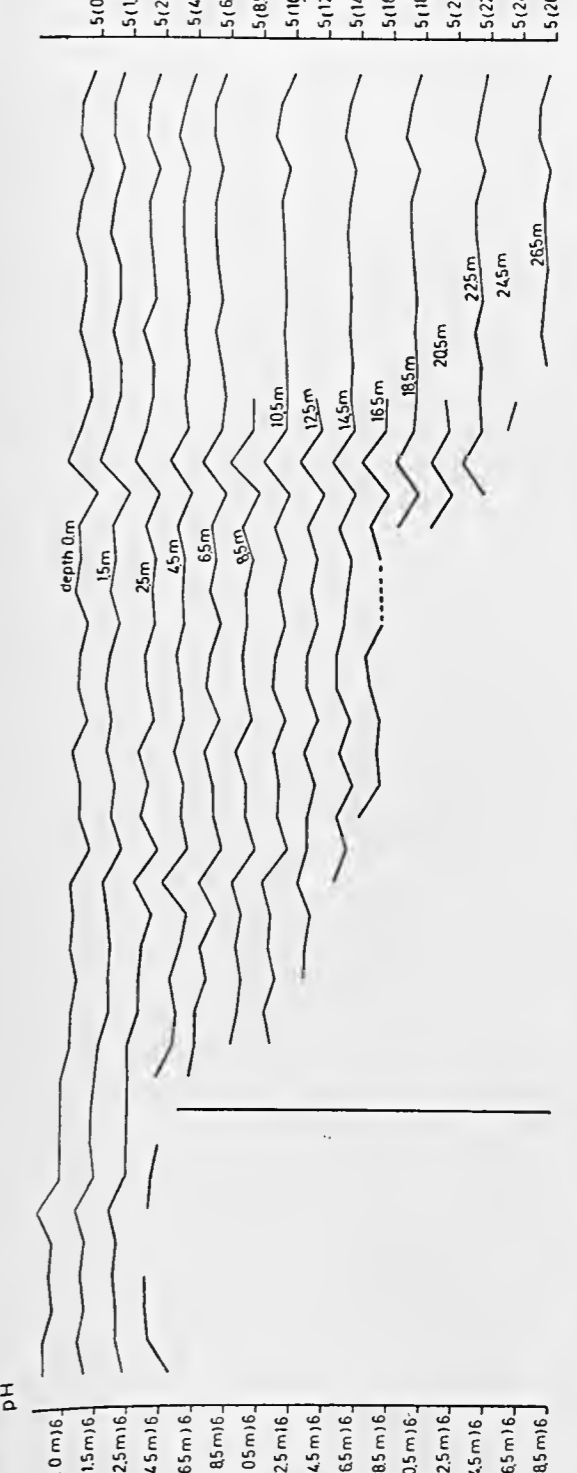
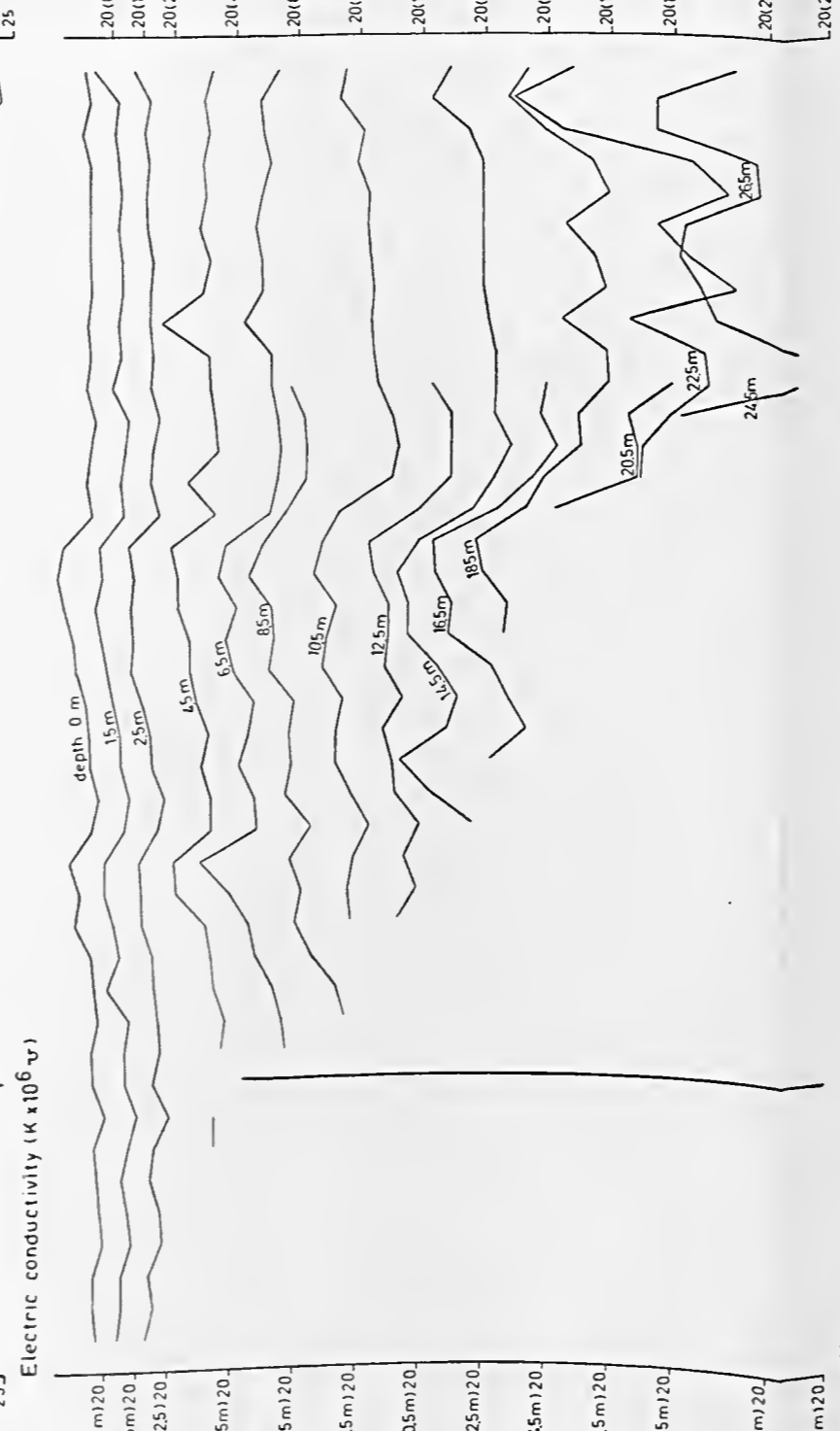
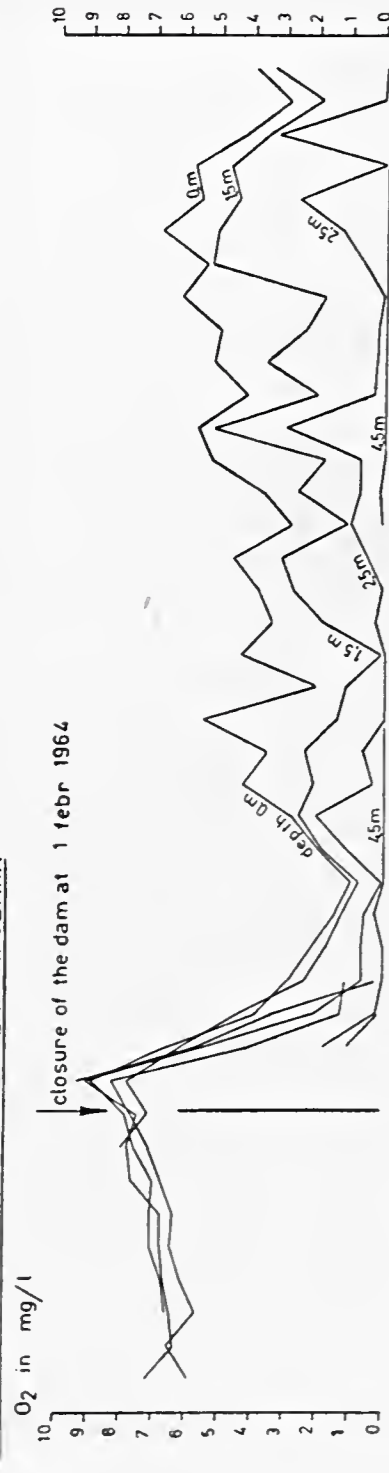
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BROKOPONDO BARRAGE LAKE NEAR AFOBAKA

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closure of the dam at 1 febr 1964



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Fig. 6 — *The dry riverbed below Afobaka, after the closure of the dam (February 1964).*

monstrating the greater stagnation in the water between the totally drowned trees. During the rain time the transparency increases and the electric conductivity decreases by dilution. In dry times the electric conductivity increased gradually. In deeper water layers an increasing amount of minerals was found, as is shown in graph 3 in which curves are plotted for each depth. The fluctuations in the deeper water are greater. After stagnation the pH dropped to about 5.5 at both stations; in graph 3 it is clearly visible, that a fluctuation of short duration occurred at the beginning of each

rain time, in all water layers. The lower pH found after stagnation may be caused by the larger amount of CO_2 derived from decaying material and also from dissolved humic substances, which now made their appearance in the water. The colour of the water turned to light brown. Iron was precipitated and could be found suspended near the anaerobic zone at 3 or 4 meters. In the anaerobic deeper water the amount of dissolved iron increased and the same was true with regard to phosphate. Also H_2S was formed.

The said physical and chemical alterations in this aquatic environ-

ment strongly affected plant and animal life. It is hardly possible to indicate which of the factors had the strongest influence on the biocommunity. The absence of flow caused a chain of alterations of which the change in oxygen content is the most important. This is illustrated by the general observation, that in the flowing river the oxygen content was higher at night than at daytime and that in the stagnant water of the lake the oxygen content at night was considerably lower than at daytime. The oxygen metabolism in the river is abiogenic. Differences in temperature rule the oxygen content in the diurnal cycle since plant and animal life is scarce in the river. Oxygen production and consumption in dark and light bottles could hardly be measured by the paucity of plankton. In the lake oxygen was found in an upper layer where the light penetrated; the present larger amount and other species of plankton produces sufficient oxygen at daytime. At night the oxygen content dropped sharply by respiration activity and by the presence of large amounts of reducible substances (see graph 4).

The differences in temperature in the diurnal cycle cause conversions in the upper layers only. The

effect of insolation is restricted to the upper 2.5 meters of water (see further LEENTVAAR, 1966). BRAUN (1952) found instable thermoclines at 2-3 meters in shallow lakes in the Amazon region.

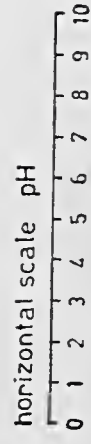
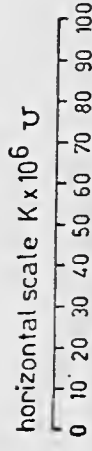
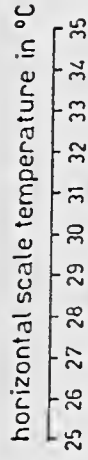
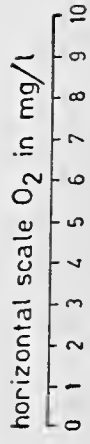
As mentioned above, the river plankton was composed mainly of diatoms and desmids. The most frequent diatom was *Eunotia asterionelloides*; other species were *Melosira* sp., *Rhizosolenia* spp. and *Surirella* spp. After closure the river plankton could not exist any longer; it became succeeded by a transitional plankton and eventually by a more stable "lake plankton". In the transitional period, when the oxygen decreased in all layers, the diatom *Eunotia* disappeared and also other species from the river plankton. Other elements such as *Eudorina elegans* developed in great numbers and the water got a green colour. Thus the transitional zone (period) could be detected by its colour; as the lake area expanded southward a green "wave" of the transitional zone also moved southward. Other elements in this plankton were *Cyclops*, *Diaphanosoma* and rotifers. In special cases and temporarily the organisms of the transitional zone also developed strongly in the flowing river, i.e. during disturbances, occurring at the beginning and at the end of a rainy period. It is an example of selfpu-





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rification of the river under natural circumstances. The permanent disturbance caused by the dam interrupted the normal cycle and the community was succeeded by plankton, composed of many unicellular flagellates (*Trachelomonas*, *Strombomonas*) and numerous crustaceans and rotifers, occurring only in the oxygenated 3 or 4 meters below the surface. This community was composed of many species typical of stagnant water. No detailed description is given here of the final "lake plankton"; it may be said however, that at the end of my observation period (September 1964) large colonies of green algae, such as *Dictyosphaerium*, and many crustaceans and rotifers seemed to be the more permanent components of the plankton.

It is interesting to note, that near the anaerobic zone of the lake numerous specimens of the rotifer *Sinantharina spinosa* appeared and also numerous wiftly moving turbellarian worms (*Catenuella lemnae*). The above picture of various plankton stages is based on observations in open water. In forest areas with drowned trees, oxygen was limited to a thin top layer and, as a result, the vertical distribution of plankton was more restricted. Also other organisms typical of shallow stagnant water were found. Since the trees acted

as a windscreen extensive fields of *Lemnaceae* developed temporarily, as well as large masses of floating filamentous algae (*Spirogyra*, *Mougeotia*). The algae produced large amounts of oxygen, often leading to supersaturation, but outside the algal mats oxygen was absent. Many organisms were found in the threads of algae, such as bottom living Cladocerans (*Euryalona occidentalis*, *Ilicryptus*, *Chydorus*) and many specimens of the big Conchostracod *Cyclestheria hislopi*. These organisms occurred also in open water, transported by wind action. Also other organisms could be found in the algal mats, such as ephemerids, odonata, hemiptera, and locally the gastropods *Drepanotrema anatinum*, *Aplexa marmorata*, *Gundlachia*, *Taphius khünianus* and *Acroloxus*. They did not occur in the former flowing water and must have come from shallow, stagnant parts. The dead leaves of the drowned trees soon became covered with green masses of filamentous algae. When the water level rose these algae died by lack of light but reappeared at a higher level. On the dead leaves also many tubes could be found of oligochaetae (*Dero*, *Aulophorus*, *Pristina*, *Aeolcsoma*).

Most of the organisms which lived on the former riverbed died on

account of lack of oxygen at the bottom. Some however were found living at floating substrate such as sponges, ephemerids and odonata. Fish only occurred as surface dwellers in the oxygenated layer. The bottom dwelling fish of the former river died or escaped the anaerobic water. At Afobaka the first dead fish were seen on 28 February. The number of dying fish, however, was only a small fraction of the former population in the normal river. Most fishes probably fled upstream and for this reason, after the longer stagnation in August and September, many fish was seen in the upper courses of the Suriname River.

The first fish found dead were the stingray and a *Plecostomus* sp. The latter lives in the turbulent water of the rapids and soon after stagnation this species could be found floating dead on the water above former rapids. The amount of fish which remained in the oxygenated layer after stagnation was not great. Catfish (*Siluridae*, *Callichthyidae*) disappeared; species such as *Leporinus*, *Characidae* and a few *Serrasalmus* remained. *Gymnotus* sp. was found living between the roots of water-hyacinth.

The records of the organisms present before and after the closure are given in a table at the end of this communication.

The greatest depth of the lake will be 50 meters near the dam. Large areas of the shallower parts will become swampy. Fishing with nets and navigation will be difficult. The submerged trees of the forest will decay very slowly in the acid anaerobic water; it was impossible to clear the area of the future lake before filling. The tree tops remaining above water will serve as centres of floating vegetation. The waterhyacinth (*Eichhornia crassipes*), which was scarce in the river, developed into great numbers after stagnation because of favourable conditions: the illumination of the water surface increased as the dead leaves lost their leaves and also the mineral content of the water increased. The control of this "million-dollar-weed" was started by spraying, but the result is not quite satisfactory. Perhaps it is worth to make an experiment of biological control by introducing manatees into the lake (BERTRAM, 1963). The introduction of the manatee into the lake would be, at the same time, a contribution to the protection of this threatened animal.

Finally we would point out the possibility of explosions of mosquitoes and malaria on account of the developing and expanding waterhyacinth, and perhaps of the waterfern *Ceratopteris pteroides*.

Presence of various organisms before and after the closure
1 February 1964 until September 1964

SURINAME RIVER

Fishes: Many species and specimens

Potamotrygon hystrix

Siluridae, *Callichthyidae*

Plecostomus sp.

Electrophorus electricus

Gymnotus sp. (in creeks)

Hoplias sp.

Serrasalmus sp.

Characidae

Belone sp. (in creeks) etc.

Other organisms:

Diatoms and Desmids are the most important plankters.

Freshwater shrimps (*Macrobrachium*) and crabs (*Potamocarcinus* sp) are common.

Hemiptera: *Gerridae*, *Velidae* and *Belostomidae* are scarce.

Ephemeroptera on bottom and in rapids.

Trichoptera on rocks and in rapids.

Libellulidae, many species.

Megaloptera and *Cataclysta* lived in rapids.

Simuliidae and other midge larvae recorded.

Sponges on rocks.

Bryozoa recorded.

Mollusca: *Pomacea* spp. and *Doryssa* spp. lived on rocks.

Diplodon voltzi and *Castaliella* lived on sand.

Oligochaetae: earthworm species occurred in the sand.

Podostemaceae in rapids. Few *Eichhornia crassipes*. Few *Ceratopteris pteridoides*.

Filaments of blue algae on rocks in rapids.

BROKOPONDO LAKE

Few species and specimens. Dead fish appeared shortly after stagnation. Most fish escaped anaerobic water. Some hide in floating water-hyacinth. Surface dwellers like *Leporinus* remained in the oxygenated layer at the surface.

Other species of phytoplankton developed. Cladocera, Copepods and Rotifers appeared in great numbers, but only in the oxygenated top layers. New elements typical of stagnant water appear: *Cladocerans*: *Euryalona occidentalis*, *Iliocryptus*; *Conchostraca*: *Cyclestera hislopi*; Rotifers: *Sinantherina* spp., *Octotrocha*, *Lacinularia flosculosa*. Bottom living organisms died or appeared on floating substrate.

Many *Microvelia* sp. Also *Belostomidae* in floating material.

Only *Asthenopus* and *Callibaetes* were recorded.

Trichoptera disappeared.

Libellulidae are still present. Both disappeared.

Larvae of *Simuliidae* disappeared; other forms were recorded. Sponges disappeared except those on floating substrate.

Bryozoa not recorded.

All species disappeared, some were found dead. New elements typical of stagnant water are recorded:

Drepanotrema anatinum, *Aplexa marmorata*, *Gundlachia*, *Acroloxus*, *Taphius*.

Not recorded. Many small species like *Dero*, *Aulophorus* and *Pristina* appear on decaying substrate.

No *Podostemaceae*.

Strong development of *Eichhornia* and *Ceratopteris*.

Filaments of blue algae on roots of waterhyacinth and floating substrate. Temporary growth of filamentous green algae (*Spirogyra*, *Mougeotia*) floating at the surface. Growth of *Lemnaceae*.

SUMMARY

The construction of big dam across the Suriname River, which was completed at February 1, 1964, caused a radical change of the environment in which so far a tropical rainforest dominated. The impounded Suriname River soon flooded large areas of forest: the artificial lake will ultimately cover an area of about 1.500 km². About 5.000 inhabitants of negro villages along the river were transmigrated to new settlements. Wild animals such as deer, pig, opossum, baboon, tree porcupine, tree anteater and sloth tried to escape the rising water. Many of them were rescued by the action of the American Society for the Protection of Animals. Game hunting is forbidden for some years in the lake region.

The drowned forest trees died after a few months but their stems remained below the water level, some parts also above it. No attempts could be made to clear the future lake region before actual filling occurred. The dead trees are a nuisance for navigation and fishing with nets. They also prevent water circulation, resulting in great stagnation and oxygen exhaustion. Open spaces of water remain only in the former riverbed and in those of the tributaries. As the water

of the lake will be used only for generating electric power little attention is being paid to the said drawbacks.

The waterhyacinth *Eichhornia crassipes* was a rare plant in the former Suriname River but developed rapidly as soon as the water stagnated. Large fields of floating plants formed along the borders. Attempts were made to control it by chemical sprays, without much result. At the midst of 1965 the plant covered an area of 18000 ha. which is about 1/8 of the total area of the lake. Also the waterfern *Ceratopteris thalictroides* spreads rapidly; it used to be limited to the smaller tributaries of the Suriname River.

As the lake will remain shallow for the greater part (the greatest depth does not exceed 50 meters, near the dam), large areas will be covered by a swampy vegetation. This vegetation will cause an increase of the evaporation, which will be much higher than that of open water. (The rate of evaporation of open water in the lake has only been measured incidentally). The lake did not reach its final level at the expected date. In fact the water level lowered slightly when two of the turbines were started.

An invertebrate fauna — formerly scarcely noticed — developed in the stagnant water among the floating vegetation of waterhyacinth. It may be that malaria mosquitos will become numerous after prolonged impoundment. Snails, a potential vector in bilharzia disease, were not recorded; as a matter of fact they were absent in the Suriname River because of the acidity of the water and the absence of a suitable environment. Other species of snails occurred however.

After stagnation of the water occurred, the river fish of the running water disappeared. Exhaustion of oxygen caused some dying of fish. Oxygen started decreasing some weeks after the stagnation and then only few specimen were found at the surface. Below a depth of 2 to 3 meters no oxygen was found. H_2S developed by decaying of organic material.

The plankton community of the running river was mainly composed of desmids and diatoms. It soon changed and became limited to an upper layer of 2-3 meters. Cladocera, Copepoda, Rotifer and unicellular Flagellates (*Strombomonas*, *Trachelomonas*) developed, sometimes in large numbers. Bottom organisms of the former riverbed

died or were found living on floating material. Plant species belonging to the family of *Podostemaceae*, typical of the rapids, died also.

The chemical composition of the water changed too. The water of the Suriname River was poor in minerals, slightly coloured by iron and silica and had a pH of about 6.5. It resembles the "Clear water type" as characterized by Sioli in the Amazon. The tributaries are brownish and turbid on account of iron. The Suriname River system originally has turbid-brown water and differs from the so-called "Brown waters", where colour is due to dissolved humic substances.

After impoundment the water colour changed into light brown, due to dissolved humic substances, the pH dropped to about 5.5. The mineral content increased. The amounts of mg pro liter of PO_4 , NO_3 and SO_4 increased already after 6 months of stagnation.

Very little was known of the water, plants and animals in the Suriname River region. Some months before the closure of the dam a team of four biologists began its investigations. The project is being financed by the Netherlands Foun-

dation for the Advancement of Tropical Research (Wotro) and the National Museum of Natural History, Leyden.

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EL GÉNERO "PALEOSUCHUS" EN AMAZONIA

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(Con 1 mapa)

El género *Paleosuchus* consiste en dos especies, *P. trigonatus* y *P. palpebrosus*. Representa indudablemente un grupo muy antiguo, quizás, el más primitivo de la familia *Alligatoridae* y difiere de los géneros *Caiman* y *Melanosuchus* por una serie de caracteres morfológicos externos y anatómicos craneales. Se desconocen todavía datos paleontológicos exactos sobre el origen de este género. LANGSTON (1965: 151) anotó que "La ascendencia del caimán se rastrea hasta el principio del Eoceno, en cuya época el *Eocaiman cavernensis* parece haber sido un adecuado antecesor estructural de formas semejantes al caimán, con la posible excepción del *Paleosuchus*".

El autor de la presente contribución hizo observaciones y estudios desde 1950 en las hoyas del Amazonas y Orinoco, coleccionando

principalmente de noche con arpon y desde una canoa para evitar la destrucción del cráneo, si se recolectaran mediante armas de fuego. Durante estas cacerías se hicieron numerosas observaciones sobre la ecología y las costumbres en el ambiente natural de ambos *Paleosuchus*, comunmente denominados como "Cachirre" y "Jacaré coroa" por los nativos de las diferentes regiones.

Los datos aquí presentados no pretenden ser completos; constituyen más bien base para estudios futuros más profundos. A pesar de que ambas especies se conocen desde la época de CUVIER (1807), existen solamente unos pocos datos aislados y generalizados sobre su ecología. La nomenclatura también permaneció en estado bastante confuso debido a las numerosas alteraciones que ha sufrido la sinonimia.

Debido al espacio limitado, presentamos únicamente la sinonimia principal, evitando así meras reiteraciones, y nos referimos para una nomenclatura más completa a MEDEM (1958 a: 228-230). Igualmente nos limitamos a presentar los datos más esenciales acerca de las características morfológicas externas y de anatomía craneal, ya que han sido descritos anteriormente por varios autores, entre ellos KÁLIN (1933), MERTENS (1943) y MEDEM (1952, 1953, 1958 a). En cambio, nos referimos en forma más detallada a las observaciones sobre la ecología y comportamiento por razón de que representen posiblemente informaciones útiles para otros profesionales en su trabajo en el campo.

Se usan las siguientes abreviaciones: CNHM — Chicago Natural History Museum; MVZ — Museum of Vertebrate Zoology, University of California, Berkeley; MNHNP — Museum National d'histoire Natural de París; ICN — Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá; FM, Pp, Pt — Federico Medem, colección particular, *P. trigonatus* y *P. palpebrosus*. El material está depositado en el CNHM, MVZ, ICN y en la colección particular.

Nomenclatura

Orden *Crocodylia*
Familia *Alligatoridae*

Género *Paleosuchus* Gray, 1862, Ann. Mag. Nat. Hist., (3), 10: 330; propuesto como subgénero de *Caiman*. Tipo: *Crocodylus trigonatus* Schneider.

Paleosuchus trigonatus (Schneider)

Crocodylus trigonatus Schneider, 1801, Hist. Amph., p. 161, pls. 1-2. Tipo: actualmente perdido. Localidad típica: desconocida.

Caiman trigonatus Boulenger, 1889, Catal. Chelon...: 296.

Jacaretinga trigonatus Vaillant, 1898, Nouv. Arch. Mus. Hist. Nat. Paris, (3), 10: 171 etc., fig. 1.

Paleosuchus trigonatus K. P. Schmidt, 1928, Field Mus. Nat. Hist. (Zool. Ser.), 12: 209, fig. 1.

Crocodylus palpebrosus, var. 2, Cuvier, 1807, Ann. Mus. Hist. Nat. Paris, 10: 38 pl. 2, fig. 1.

Tipo: MNHNP No. 7.525, ejemplar de 80 cm., Gautier don. Localidad típica: Cayenne — *vide* Vaillant, 1898: 174, fig. 1.

Alligator palpebrosus, var. B, Duméril & Bibron, 1836, Erp. Gén., 3: 72. Tipo: MNHNP No. 7527, ejemplar de 1.17 metros, localidad desconocida *vide* Vaillant (*op. et loc. cit.*).

Jacaretinga moschifer Spix, 1825, Animalia nova... lacertarum, p.] Tab. I. Tipo: Originalmente en München, actualmente perdido.

Localidad típica: lago en la ciudad Bahía, Brasil.

VAILLANT (*op. cit.*: 173-174, nota al pié) anotó que *moschifer* es una composición de ambas especies. Según la descripción se trata de *palpebrosus*, mientras la ilustración

muestre indubablemente un *trigonatus* de tamaño mediano. Sería lo más indicado, incluir a *moschifer* definitivamente en la sinonimia de *trigonatus* ya que no solamente la Tabla I de SPix comprende una ilustración en colores bien elaborada de *trigonatus*, sino también en el texto se notan algunas discrepancias: mientras la descripción del color corresponde a *palpebrosus*, la de la cabeza reza "*caput acutum*" (p.1), lo que es característico de *trigonatus*.

Paleosuchus palpebrosus
(Cuvier)

Crocodylus palpebrosus, var. 1, Cuvier, 1807, Ann. Mus. Hist. Nat. Paris, 10: 28; pl. 1, figs. 6, 17; pl. 2, fig. 2. Tipo: MNHN No. 7530, ejemplar de 1.29 metros, Gautier don, Localidad típica: Cayenne, fide Vaillant (op. et loc. cit.).

Alligator palpebrosus, var. A. Duméril & Bibron, Erp. Gén., 3: 67. Tipo: MNHN No. 7530, fide Vaillant (op. et loc. cit.).

Caiman (Aromosuchus) palpebrosus Gray, 1862, Ann. Mag. Nat. Hist., (3), 10: 330.

Paleosuchus palpebrosus Müller, 1924, Zeitschr. Morph. Okol. Tiere, 2: 441, pl. 5, fig. 31.

Champsia gibbiceps Natterer, 1841, Ann. Wien. Mus., 2: 324, pl. 28. Tipo: Originalmente en Viena, evidentemente perdido.

Localidad típica: Ribeirão do Guacurizal, un caño en las montañas alrededor de Jacobina, 3 millas al oriente de Villa María, río Paraguai, Mato Grosso, Brasil.

Coloración — El color de los ejemplares vivos ya ha sido descrito anteriormente (MEDEM, 1952 1953); por esta razón anotamos solamente las diferencias principales correspondientes a los adultos y juveniles.

En *P. trigonatus* la tabla craneal es parda oscura y una faja ancha negra se extiende desde el borde posterior de espacio interorbital hacia adelante a lo largo de los nasales hasta los dientes maxilares Nos. 5-6. En cambio, en *P. palpebrosus* la tabla craneal es de color rojizo de herrumbre intenso y la cabeza carece de la faja negra.

Las mandíbulas presentan zonas anchas amarillas, interrumpidas por unas 5-6 fajas transversales pardas oscuras en *trigonatus*, mientras las de *palpebrosus* muestran un color rojizo, salpicado por unas 4-5 manchas pardas oscuras de tamaño y configuración irregulares.

La parte dorsal del cuerpo y de la cola de *trigonatus* es básicamente parda oscura; existe, sin embargo, el fenómeno en que virtualmente todos los juveniles desde unos 600 mm para arriba y los adultos tienen el lado dorsal cubierto por una densa capa de algas verdes la cual es aún más espesa en ejemplares viejos; por esta razón un *trigonatus* de tamaño mayor parece, en realidad, verdusco mohoso.

El lado dorsal de *palpebrosus* es más oscuro y en ejemplares viejos

negruzco. Nunca se ha observado la presencia de algas verdes en *palpebrosus* en su ambiente natural, sino únicamente en un solo ejemplar (No. 370), que vivió dos años en cautividad.

Ventralmente el color del tegumento es gris ratón con varias zonas más oscuras en *trigonatus*, mientras en *palpebrosus* es negro brillante con algunas zonas grises claras o de color de cuerno.

Los juveniles de ambas especies tienen una coloración más clara y intensa que los adultos. Ejemplares muy pequeños se distinguen fácilmente en que la tabla craneal en los de *trigonatus* es carmelita clara, mientras en los *palpebrosus* es amarilla yema brillante. Este color cambia después de unos ocho meses; así por ejemplo, de tres ejemplares capturados en diciembre 1, 1950, uno (MVZ No. 2018) de ellos sobrevivió hasta septiembre 5, 1951; según HENDRICKSON (*in litt.*, octubre 11, 1951) el color permaneció amarillo hasta julio 1951 y luego cambió a rojizo caoba (MEDEM, 1953: 417). El iris de los ojos de ambas especies es carmelito claro.

Escamado — Desde la época de CUVIER (1807) se consideró la disposición de las escamas postoccipitales como uno de los factores diagnósticos específicos, es decir, se postuló que *trigonatus* invariablemente tenía una sola hilera y, en contraste, *palpebrosus* dos de ellas.

En realidad, 28 de los 37 ejemplares de *trigonatus* estudiados en 1954, tenían las escamas postoccipitales en dos hileras claramente discernibles, independientes de la edad y procedencia; en cambio, de unos 50 *palpebrosus*, todos poseían dos hileras.

Existen también diferencias claramente discernibles entre ambas especies respecto al escamado cervical, dorsal, ventral y caudal (MEDEM, 1958 a: 236). Finalmente, nos referimos a las diferencias más esenciales y fácilmente discernibles tanto del escamado como de la anatomía craneal de ambas especies que sirven como factores diagnósticos para su clasificación.

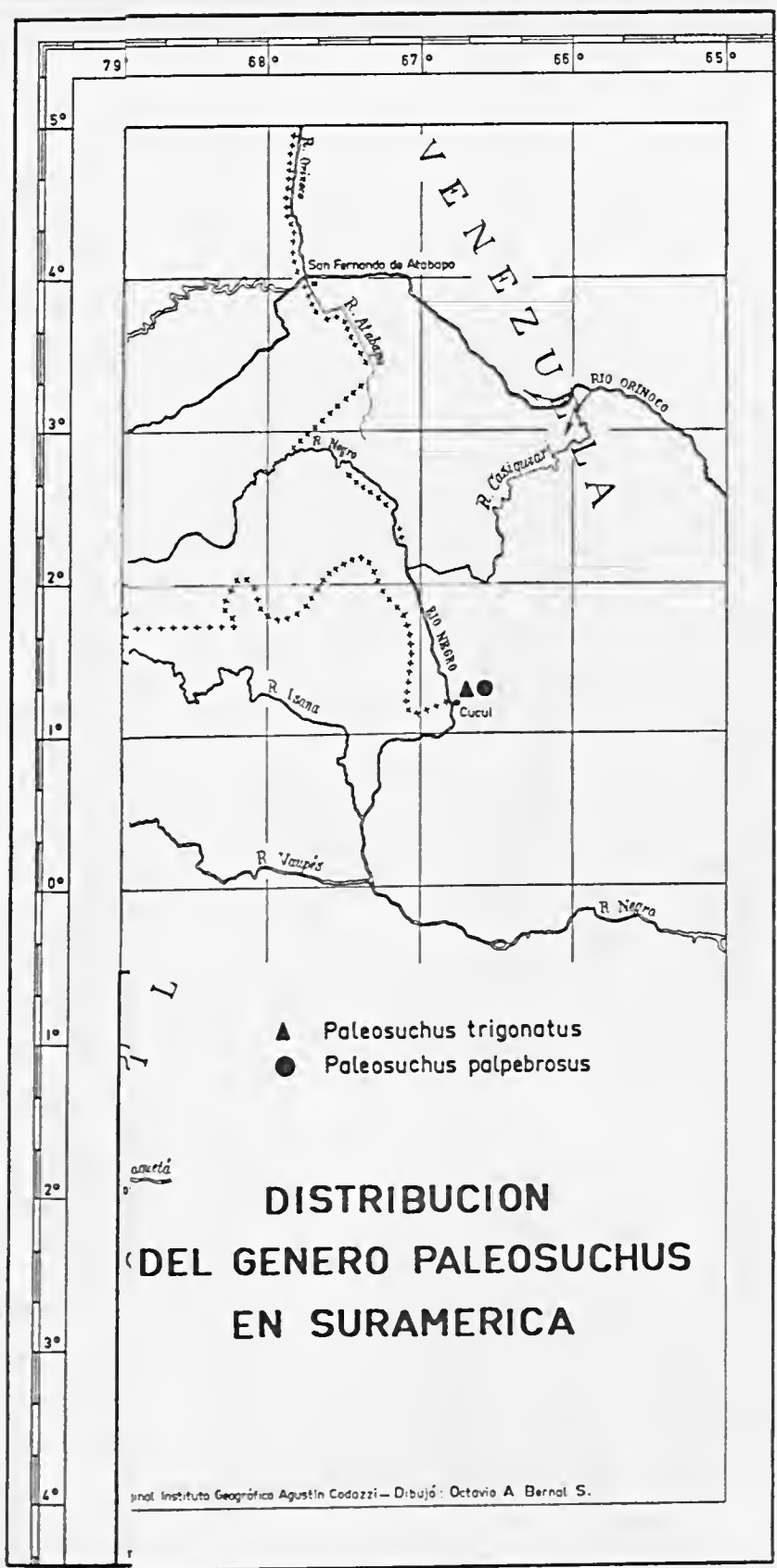
ESCAMADO

Paleosuchus trigonatus

- 1) Escamas postoccipitales en una o dos hileras; las de la segunda siempre más pequeñas.
- 2) Hileras pre-lumbares de 2-3-4 placas; las centrales o lisas o con cresta vestigial; existe gran variedad individual.
- 3) Hileras lumbares igualmente de 2-3-4 placas; las centrales o lisas o con cresta vestigial.

Paleosuchus palpebrosus

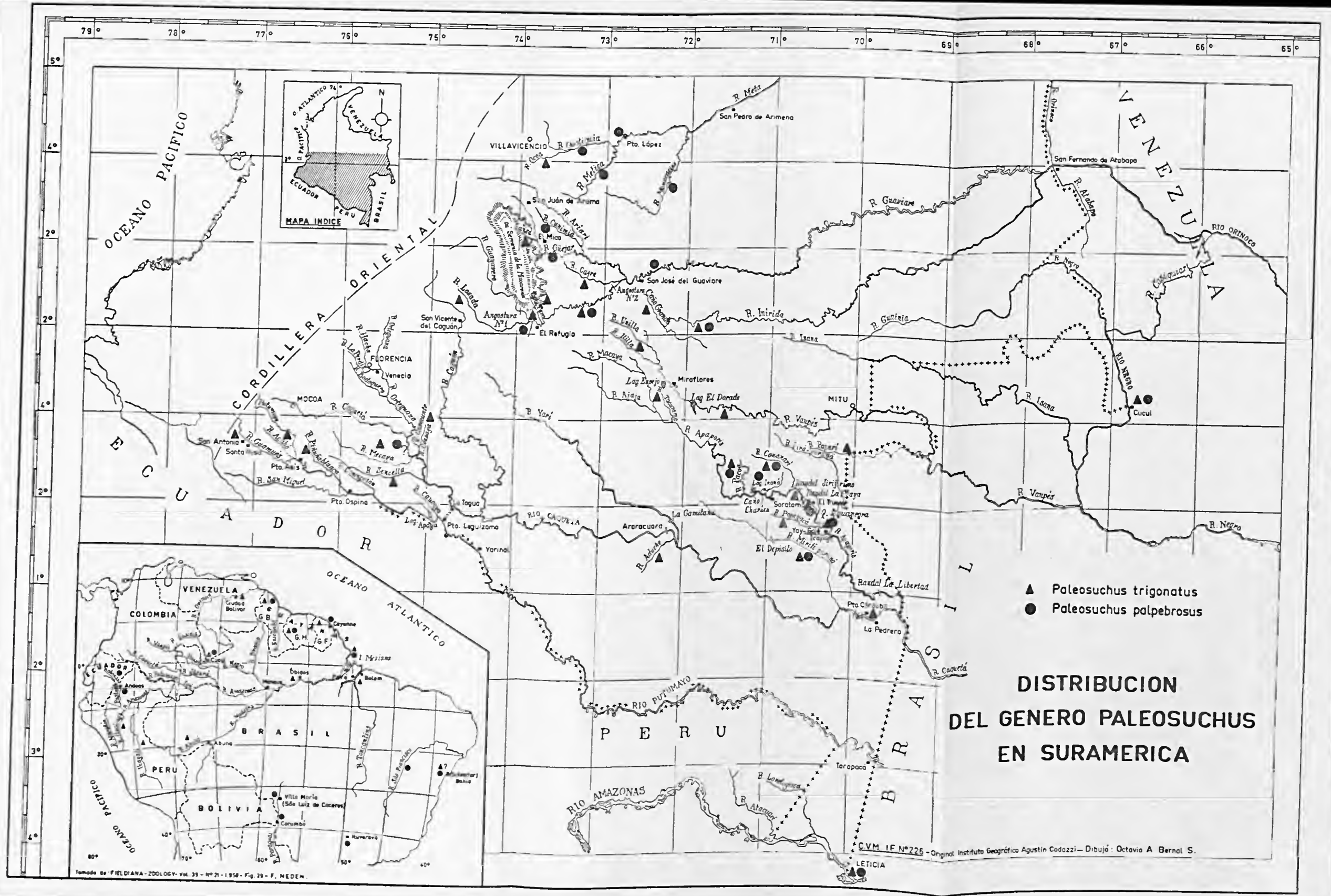
- 1) Escamas postoccipitales siempre en dos hileras; las de la segunda ligeramente más pequeñas; solamente en los ♂♂ viejos de tamaño igual.

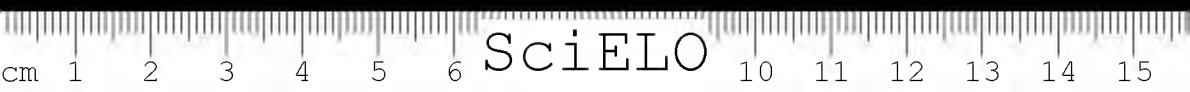


▲ *Paleosuchus trigonatus*
 ● *Paleosuchus palpebrosus*

**DISTRIBUCION
 DEL GENERO PALEOSUCHUS
 EN SURAMERICA**

Inst. Instituto Geográfico Agustín Codazzi—Dibujó: Octavio A. Bernal S.





- 2) Hileras pre-lumbares casi siempre de 4 placas encrestadas; pocas excepciones en ejemplares juveniles.
- 3) Hileras lumbares usualmente de 4 placas aquilladas; pocas excepciones en juveniles.
- 5) *Foramen mandibulares externum* pequeño y angosto; los bordes son siempre mellados o dentados.
- 6) *Fenestrae supratemporales* totalmente obliteradas en adultos y juveniles.

C R Á N E O

Paleosuchus trigonatus

- 1) Hocico alargado; punta angosta; no volteada hacia arriba.
- 2) Proyección anterior de los nasales larga y puntiaguda.
- 3) *Canthus rostralis* falta; lacrimales prominentes y muy elevados.
- 4) Declive lateral de los maxilares no pronunciado.
- 5) *Foramen mandibulare externum* grande y ancho; los bordes son siempre lisos.
- 6) *Fenestrae supratemporales* abiertas en juveniles, cerradas en adultos, pero usualmente con una brecha bien discernible.

Paleosuchus palpebrosus

- 1) Hocico comprimido; punta ancha y volteada hacia arriba.
- 2) Proyección anterior de los nasales corta y ancha.
- 3) *Canthus rostralis* prominente entre los lacrimales y los dientes maxilares Nos. 4.
- 4) Declive lateral de los maxilares muy pronunciado.

MEDEM & MARX (1955: 1) señalaron la presencia de las *Fenestrae supratemporales* muy pequeñas en juveniles de ambas especies; esto fue un error y no corresponde a los *P. palpebrosus*.

Tamaño — Como en todos los *Crocodylia*, los ♂♂ alcanzan un tamaño mayor que las ♀♀. En *trigonatus* las longitudes mayores conocidas hasta la fecha son de 2256 mm para los ♂♂ (CNHM No. 81980) y 1330 mm para las ♀♀ (Pt. 15).

El tamaño mayor señalado en la literatura para *palpebrosus* es 1720 mm (LUEDERWALDT, 1926); hasta la fecha no se ha coleccionado un ejemplar de semejantes dimensiones en Colombia; el mayor tamaño comprende 1545 mm para los ♂♂ (CNHM No. 69871) y 1230 mm para las ♀♀ (CNHM No. 69868). Datos sobre la madurez sexual en relación con el tamaño no existen, pero un *palpebrosus*, ♂, (Pp 3) de 854 mm era ya adulto, según el estado de desarrollo del pene y testículos.

Ecología y comportamiento — En lo concerniente a la ecología

y las costumbres nuestro conocimiento es todavía insuficiente. Con toda la razón SCHMIDT (1928: 210); LEITÃO DE CARVALHO (1951: 134-135) y DUNN (1945: 333) ya han expresado que virtualmente no se sabe nada al respecto.

NATTERER (1841: 318) señaló por primera vez la localidad exacta y el habitat para *P. trigonatus* como: "Río Negro, alrededor del Cerro Cocuí, en caños y lagos dentro la selva"; mencionó, además, que *P. palpebrosus* se encuentra en el Río Branco, donde se excavó un ejemplar de una cueva de una brazza (1.67 metros) de profundidad, situada en un pantano seco de una llanura.

MÜLLER (1912: 39; 1924: 455) encontró ambas especies juntas en la Isla Mexiana y apuntó que viven en los igarapés dentro la selva y se retiran a las cuevas situadas en la orilla de las aguas durante el día.

Habitat y nicho ecológico — Ambos *Paleosuchus* son coexistentes con *Caiman sclerops* y *Melanosuchus niger* pero se encuentran en un ambiente preferido diferente y bien definido el cual se puede denominar como: aguas correntosas dentro la selva tropical. Así por ejemplo, en el río Pacoa los *Paleosuchus* se encontraron con certeza siempre en tales partes donde el agua corría sobre un fondo rocoso, alrededor de chorreras, cachoeiras,

saltos y remolinos, mientras los *Caiman sclerops apaporiensis* vivían en las vueltas y grandes charcos donde las aguas eran mansas y algo estancadas.

En las lagunas Inaná, *P. palpebrosus* se encontró solamente en el caño que conecta la segunda y tercera laguna y a unos 50 metros de distancia de su desembocadura en la segunda laguna (MEDEM, 1953, mapa 2).

En los ríos grandes ambas especies se encuentran siempre alrededor de raudales, angosturas, remolinos y chorreras.

En regiones donde no existe la selva tropical propiamente dicha, como por ejemplo, en las mesetas semi-áridas del Vaupés entre los ríos Querarí y Guaracú, y en los Llanos Orientales, los *Paleosuchus* están presentes en los pequeños afluentes, pero únicamente en tales partes donde la orilla está cubierta por un monte espeso; en cambio, evitan las partes del mismo caño donde consiste en llanuras. Esto no quiere decir, sin embargo, que los *Paleosuchus* nunca entren a aguas estancadas, sino únicamente que nunca han sido observados en tal nicho ecológico, con la sola excepción de un *P. trigonatus* (Pt 29) en las aguas mansas de un monte inundado por el invierno.

Abundancia — Ambos *Paleosuchus* son mucho menos abundantes que, por ejemplo, *C. sclerops* y,

en tiempos pasados, *M. niger*; son, sin embargo, no tan escasos como siempre se ha pensado.

Así por ejemplo, en el Alto Inírida y su afluente el Caño Grande se observaron durante el día de Enero 23 a febrero 9, 1957, 18 *trigonatus*, 2 *palpebrosus* y 102 *C. sclerops*; en agosto 8, 1957 en el caño Icapuyá 6 *trigonatus* y un solo *palpebrosus* de las 7:00 — 11:00 p.m. y en noviembre 19, 1958 de las 9:00 — 11:00 p.m. 5 *trigonatus* y 10 *sclerops*. El señor Carlos Alberto Velásquez observó en diciembre 1958 en el caño Pachaquirito (Meta) de noche en un área de unos 130 metros aproximadamente 16 *palpebrosus*, entre ellos 2 grandes.

Alimentación — Es muy variada y no se observó un grupo de animales como alimento preferido. Los juveniles se alimentan principalmente de moluscos, crustáceos e insectos acuáticos y terrestres (*Pomacea* sp; camarones, cangrejos, *Coleoptera*, *Orthoptera*, *Odonata*); en los adultos se encuentran también invertebrados con frecuencia; además peces hasta unos 300 milímetros; ranas (*Lepidodactylidae*, *Hylidae*); serpientes; escamas de *C. sclerops*; uñas de ejemplares juveniles y adultos de *Caiman* o *Paleosuchus*; plumas de diferentes aves pequeñas; uñas de garzas (*Ardeidae*); mamíferos (*Marsupialia*, *Rodentia*). El conte-

nido de un *palpebrosus* de 854 mm (Pp 3) consistió en 3 larvas de moscas (*Diptera*), una araña acuática (*Arachnidae*), 3 cangrejos (*Crustacea*), un camarón (*Crustacea*) y desperdicios de nuestra comida botada al caño (costillas y carnes de un Tayassú, pedazos de bananas).

En casi todos los ejemplares adultos y juveniles de ambas especies se encontraron una cantidad considerable de pedrezuelas (guijarros) hasta un diámetro de 2 a 4 centímetros. Así por ejemplo, un *trigonatus* de 2256 mm (CNHM No. 81890) tenía 94, un *palpebrosus* de 1530 mm (CNHM No. 69867) 69 guijarros. Solamente un pequeño *trigonatus* (380 mm; CNHM No. 69888) no tuvo ningún objeto sólido en su estómago; en cambio en un *palpebrosus* de 257 mm (mvz No. 2016) se encontraron unos 32 diminutas pedrezuelas, según las fotografías tomadas con rayos X de ambos ejemplares. La cantidad de guijarros evidentemente no aumenta con el tamaño individual en todos los ejemplares, ya que varios grandes capturados en aguas de fondo rocoso tenían solamente entre 2 y 5 pedrezuelas en el estómago, mientras otros del mismo sitio las tenían en cantidades; quizás, las eliminan por vía natural; en el *colon* nunca se encontraron guijarros sino únicamente barro.

Como ectoparásitos se encontraron sanguijuelas (*Hirudinae*) en la boca y entre las escamas laterales de *trigonatus*; además se observó en todos los ejemplares de esta especie un tábano (*Diptera, Tabanidae*) que succiona principalmente la zona negra entre el espacio interorbital y la punta del hocico la cual es blanda y muy irrigada por la sangre (MEDEM, 1958 b: fig. 10); nunca se observó este tábano en *palpebrosus* el cual carece de esta zona.

Un solo *trigonatus* y 4 *palpebrosus* tenían como endoparásitos entre uno y tres nemátodos en los estómagos; se encontró un tremátodo en el *Ductus nasalis* de un *palpebrosus*; úlceras estomacales se observaron en un solo ejemplar de cada especie, posiblemente causadas por las espinas de peces.

Reproducción — Hemos encontrado un solo dato al respecto en la literatura, BATES (1864: 119-120) apunto: "Jacaré curua; female; not more than 2 feet long; according to the Indians it was full grown. Captured near its nest containing eggs. Eggs larger than a hen's, regularly oval. Nest near water edge. The Jacaré curua lives only in shallow creeks. Never seen again."

Faltan los datos exactos sobre la especie, localidad y fecha, pero según el diario ésta comprende entre septiembre 27-30. Igualmente no hemos encontrado huevos de

ambos *Paleosuchus* en todas las colecciones estudiadas hasta la fecha.

Ni GOELDI (1898) ni HAGMANN (1902; 1906-1907; 1909-1910) que hicieron tantas contribuciones al conocimiento sobre la ecología de los *Alligatoridae* del Amazonas, suministraron datos respecto a los *Paleosuchus*. Faltan todas las observaciones personales respecto a la anidación, etc.; solamente hemos observado en enero 5, 1957 en el río Gafre una ♀ de *trigonatus* (1330 mm; Pt. 15) perseguida por dos ♂♂ (1602 mm, Pt 14), todos evidentemente en celo y tan ocupados que se logró capturar a uno de los ♂ y la ♀; los ovarios bien desarrollados no contenían óvulos. Además, presentamos algunos datos obtenidos por los indios y cauqueros, personas que conocen bien a ambos *Paleosuchus*:

- 1) El señor Alirio Mejía encontró entre octubre 20-23, 1956, cerca del campamento "El Trueño" a cinco horas arriba del Pirá-Paraná, en el río Apaporis un nido de *palpebrosus* cerca de la orilla de un caño; contenía unos 22 huevos de cáscara blanca, lo que indica que eran recién puestos; eran de tamaño de los de *C. sclerops* aproximadamente pero su diámetro era algo menor. La ♀ no defendió el nido sino escapó al agua.

- 2) El indígena Perimaté de la tribú de los Tanimúca, oriundo de la misma región y compañero en las cacerías nocturnas, aseguró que ambos "Jacaré coroa" nunca ponen en el verano (diciembre-marzo) sino entre agosto y noviembre; los huevos son tan grandes como los del "Jacaré tinga" pero más alargados y delgados, algo como de las culebras; los nidos son hechos de hojarasca amontonada; la 2 acumula las hojas con la cabeza y la cola y luego hace el cúmulo con movimientos laterales de la cola.
- 3) En la región del río Guayabero-Guaviare ponen en febrero-marzo y la cría sale en abril-mayo. Posible se trata de *trigonatus*, la especie predominante entre San José del Guaviare y la Angostura No. 2.
- 4) El señor Castro Losada encontró a mediados de diciembre de 1949 un nido de un "Cachirre negro" (evidentemente *palpebrosus*) en un caño cerca del río Guatiquía, región de Villavicencio, de un metro de altura por 80 centímetros de ancho aproximadamente el cual contenía unos 18 huevos; la ♀ no escapó sino atacó furiosamente hasta que la mataron.

Enemigos — Los *Paleosuchus* de tamaño mayor devoran ocasional-

mente a los más pequeños; el "Güio negro" (*Eunectes murinus gigas*) muy posiblemente se alimenta también de ellos, ya que se han encontrado repetidas veces ejemplares de *C. sclerops* hasta unos 2050 milímetros en los estómagos de estas serpientes. Tanto el "Jacaré assú" (*M. niger*) como el "Tigre" (*Felis onca*) y el "Tigrillo" (*Felis ozelot*) son otros enemigos potenciales; hemos observado el último capturando y luego comiendo *C. sclerops* de unos 600 milímetros e Iguanas. Sin embargo, el enemigo principal es indudablemente el indígena; los indios distinguen dos formas del "Jacaré coroa" y las prefieren por su carne superior a la del "Jacaré tinga" (*C. sclerops*); consecuentemente, en regiones habitadas por indígenas los *Paleosuchus* son escasos y muy ariscos. A pesar de que hemos usado con frecuencia como alimento a los adultos de ambos géneros, no hemos encontrado ninguna diferencia acerca del sabor.

Hábitos y costumbres — Son principalmente nocturnos; salen entre las 7:00 — 7:30 p.m. y cazan generalmente hasta las 10:30 p.m.; en los grandes ríos se encuentran generalmente escondidos dentro las palizadas; en aguas profundas su posición es algo diferente de la de *C. sclerops*; mientras el cuerpo del último se queda por lo general a poca profundidad bajo la superficie y es visible, en los *Paleosuchus*

se encuentra "colgado" casi verticalmente hacia el fondo, no es visible y bastante difícil para apuntar con el arpón. En regiones donde nadie los molesta salen también de día para asolearse; los *trigonatus* permanecen con frecuencia bajo rastrojo al borde de las aguas y evitan las orillas que carecen de vegetación; los *palpebrosus* se asolean en general en aguas poco profundas o en las rocas y árboles gruesos dentro de las chorreras con la cabeza pronunciadamente erguida. Sorprendidos en lo seco y especialmente en las orillas elevadas, saltan con gran rapidez al agua y no corren en cuatro patas, como lo hacen *C. sclerops*; repetidas veces saltaron así sobre la canoa y desaparecieron en el agua a una distancia de unos 2-3 metros. Viven en cuevas en las orillas bajo la superficie del agua; ejemplares recién salidos mostraron muchas veces rastros de barro en sus cabezas; cuando el nivel de las aguas se baja durante el verano, se observaron las entradas de estas cuevas cuya profundidad varía entre 1.50 — 2.50 metros aproximadamente.

En relación con su nicho ecológico de aguas correntosas sus movimientos son muy ágiles; nadan con gran velocidad aún contra la corriente fuerte y cambian rápidamente la dirección. Su modo de cazar peces es muy efectivo; en tres ejemplares amarrados en un caño

con un guaral de unos diez metros de largo se observó durante tres semanas que el adulto permaneció inmóvil hasta que una manada de peces se acercó a cierta distancia y luego súbitamente formó casi un círculo mediante los movimientos de la cola y la cabeza, empujando así los peces hacia la boca, nunca falló; en cambio, los dos juveniles raras veces cogieron algo.

Nunca se encontró a ambas especies en agrupaciones, como es común en *C. sclerops*, sino casi siempre solitarias. Por lo general, en los caños se ve un solo *Paleosuchus* durante cada hora; los adultos ocupan aparentemente un nicho individual extenso y lo defienden contra otros individuos invasores. Cada vez cuando un ejemplar había sido capturado y el nicho se quedó vacío, en pocos días otro ocupó este terreno. Aún los juveniles recién nacidos se separan evidentemente pronto y nunca se observó una nidada entera en el agua; al contrario, los *palpebrosus* (MVZ 2016; FM Nos. 763-766) fueron capturados en las partes de aguas movidas de pequeños riachuelos, donde permanecieron con la cabeza erguida contra la corriente, y nunca se observaron más de dos juntos. La coloración tiene indudablemente un valor selectivo en el sentido de que por una parte protege al individuo en su ambiente natural contra sus enemigos y por



otra facilita capturar animales para su alimento. Así por ejemplo, en *trigonatus* la zona negra a lo largo del hocico "disuelve" la forma de la cabeza totalmente; y junto con la capa espesa de algas en el cuerpo hace que un ejemplar que permanece inmóvil en el fondo de las aguas poco profundas sea virtualmente invisible aún a distancia corta; ejemplares adultos se parecen a un tronco podrido y únicamente la cresta caudal sencilla, debido a sus escamas aserradas y sobresalientes, indica su presencia. El efecto "disruptivo" es aún más conspicuo en los *palpegrosus*; el contraste entre el color de herrumbre de la cabeza, aún más intenso en el agua, y el negro del cuerpo es tan pronunciado que un individuo adulto en un caño sobre un fondo de hojas podridas y de piedras de múltiples colores desaparece por completo. Andando en pequeños caños de unos 50 centímetros de profundidad contra la corriente para mejor visibilidad, hemos pasado ejemplares grandes a un metro de distancia sin darnos cuenta de su presencia hasta que súbitamente se movieron con gran velocidad; trataron casi siempre de escapar; solamente en un caso el animal nos atacó.

KÄLIN (*op. cit.*: 705) opinó que las especializaciones morfológicas en los *Paleosuchus* indiquen una tendencia hacia la vida terrestre;

evidentemente no los conoció en su habitat. Nunca hemos observado que en su ambiente natural ambas especies muestren una pronunciada preferencia por alejarse de las aguas. Al contrario, son aparentemente más acuáticos que *C. sclerops*; aún en cautividad permanecieron más en un tanque que *sclerops*, pero lo abandonaron enseguida cuando el agua estancada se volvió sucia y verde. Se mueven, sin embargo, con gran velocidad en tierra a cortas distancias; igualmente, andan a veces muy lentamente en las cuatro patas levantadas y sin arrastrar el cuerpo, semejando los movimientos de un gato cuando se acerca a una presa; posiblemente cogen de esta manera animales en tierra. Nunca hemos observado un caso de estivación en ambas especies, como lo mencionó NATTERER (*op. et loc. cit.*) para *palpebrosus*. Un *palpebrosus* (FM No. 370) mostró una resistencia extraordinaria a las temperaturas bajas a gran altura: Traído a Bogotá (2.650 metros) permaneció primero en el Instituto de Ciencias Naturales sin calefacción artificial; escapó y fue encontrado después de nueve días en el pasto al lado de un pozo cerca del laboratorio, completamente sano, agresivo y bien alimentado; evidentemente comió durante esta época ranas (*Hyla labialis*) abundantes en este sitio; la temperatura bajó

de noche a 6°C. y un *C. sclerops* adulto murió en tres días. Luego vivió en mi casa en un tanque con calefacción por más de un año, pero muchas veces salió y permaneció escondido por días en el seco, donde la temperatura fluctuaba entre 19° — 13°C.; finalmente vivió otro año en un clima tropical donde murió por accidente, entrando a un tanque de agua marina.

Distribución geográfica — Indudablemente el centro de la distribución está situado en el sistema hidrográfico del Amazonas, tomado en un sentido amplio, e incluyendo el Orinoco el cual está en conexión con el Amazonas propiamente dicho por el brazo Casiquiare del río Negro. Aparentemente la evolución del género *Paleosuchus* tuvo lugar a principios del Terciario en esta área, un habitat que virtualmente no ha cambiado, sino todavía persiste; su migración y presencia actual en otras regiones extensas está en estrecha relación con su adaptación a un nicho ecológico definido. Muy posiblemente, hoy en día falta en muchas áreas donde antes existía, debido a la alteración del ambiente por actividades humanas (tala de bosques, etc). Así por ejemplo, la presencia de *palpebrosus* y, posiblemente, *trigonatus* en Bahía siempre fue considerada como negativa, pero evidentemente existieron allá en la época de Spix (ME-

DEM, 1958 a: 244-245). Este autor (*cp. et loc. cit.*) describió *J. moschifer* de dicha localidad y, según VAILLANT (*op. cit.*: 174, tabla), en 1843 LEMELLE — DEVILLE coleccionó 2 *palpebrosus* en Bahía (MNHN No. 7526, 920 mm y MNHN No. 7528, 1100 mm). Además SPIX & MARTIUS (1828: 636) se refieren a la localidad exacta, como sigue (traducido): "...El [foso] corre a lo largo del extremo oriental del suburbio Barril. En este foso viven muchos caimanes pequeños que poseen un hocico largo (*Jacaretinga moschifer*) y que despiden un olor de almizcle muy fuerte..." No obstante, el término "hocico largo" corresponde más bien a *trigonatus* y, quizás, ambos coexistieron en esta localidad; es altamente dudoso, sin embargo, que un *Paleosuchus* actualmente existe en un suburbio de esta ciudad. Por lo general se presume, que existe un "círculo interno" donde se encuentran ambas especies y otro "externo" a donde se extendió únicamente *palpebrosus*. Según los pocos datos exactos sobre localidades encontradas en la literatura, parece que fuera así; no obstante, esta opinión tradicional es muy posiblemente errónea, ya que en realidad hay muy pocos estudios detallados al respecto. Por lo menos no es el caso en el territorio colombiano, donde la vertiente de la Cordillera Oriental for-



ma el límite de extensión hacia el norte para ambos *Paleosuchus*. En cambio, existen los siguientes fenómenos, inexplicables todavía.

- 1) Cuando coexisten ambas especies, una de ellas siempre es predominante, como por ejemplo, *palpebrosus* en el Alto y *trigonatus* en el Bajo Apaporis hasta el raudal "La Playa" y en el Alto Vaupés.
- 2) Hay vastas regiones donde se observaron exclusivamente una u otra especie. Así por ejemplo, en el Alto Putumayo existe evidentemente *trigonatus* sólo y en el Alto Caquetá se observó también únicamente esta especie, aunque los nativos informaron que *palpebrosus* se encuentra muy escasamente; en cambio, coexisten en el Bajo Caquetá. Igualmente, se encontró *trigonatus* sólo en el río Catre, parte sur de la Sierra de la Macarena, mientras ambos coexisten en el Guayabero-Guaviare. En contraste, tanto en la parte norte de La Macarena como en los Llanos Orientales *palpebrosus* es tan predominante que se puede considerarlo como el único representante del género en estas regiones; ya que entre 1951 — 1960 se coleccionaron dos *trigonatus* solos de los ríos Sansa y Ocoa respectivamente y no se observó ningún otro ejemplar más. Indudable-

mente existen uno o varios factores ecológicos que forman la causa para esta separación y, posiblemente, se trata también de una competencia biológica; de todos modos será una de las tareas más llamativas para un ecólogo tratar de esclarecer estos fenómenos.

CONCLUSIÓN

Entre los *Alligatoridae* de la América del Sur, el género *Paleosuchus* ocupa una posición especial; por un lado representa un estado muy primitivo de esta familia desde el punto de vista de la evolución orgánica, y por otra parte no está condenado a la extinción, como pasa con muchas formas primitivas, sino es altamente adaptado a la vida en un nicho ecológico definido y, sobretodo, muy capaz de competir efectivamente con representantes de los géneros más avanzados. De las dos especies, *P. trigonatus* representa indudablemente la forma "básica", mientras *P. palpebrosus* la más avanzada y especializada, debido al grado mayor de la osificación del cráneo y del escamado como también a otras características morfológicas.

Estos caracteres externos están estrechamente relacionados con el nicho ecológico de los *Paleosuchus*: el alto grado de osificación de la cabeza, incluyendo los párpados en

los adultos, las placas óseas gruesas del escamado, especialmente en las postoccipitales y cervicales constituyen evidentemente una adaptación protectora en relación con la vida entre las rocas de las aguas corrientosas; los dientes pronunciadamente puntiagudos y encorvados hacia atrás son igualmente bien adaptados para agarrar presas ágiles y resbaladizas en aguas caudalosas. El contraste entre los colores de las diferentes partes del cuerpo y de la cabeza tiene efecto mimetizante y protector, tanto en el agua como en tierra. Movimientos muy ágiles y agresividad caracterizan ambas especies, factores que también tienen un valor selectivo.

Los conocimientos sobre las interrelaciones ecológicas son todavía demasiado insuficientes para explicar satisfactoriamente ciertos problemas acerca la coexistencia y migración.

Existe un paralelismo sorprendente entre las dos especies del género suramericano *Paleosuchus* y las dos del género africano *Osteolaemus* (*Crocodylidae*), *osborni* y *tetraspis*, procedentes del Congo y del Africa occidental respectivamente. Este paralelismo se extiende hasta detalles como el color, ciertas características morfológicas externas, osificación de los palpebrales, número de los dientes premaxilares, etc. y es discutido por

KÄLIN (*op. cit.*: 707); MERTENS (*op. cit.*: 260) y INGER (1948: 18). Se trata indudablemente de un caso típico de la convergencia adaptativa, *sensu* MAYR (1963: 609) y representaría un problema de mayor importancia para estudios ecológicos comparativos en el futuro.

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A n e x o.

Las Tablas presentadas comprenden, como sigue:

- 1) Localidades exactas de *P. trigonatus* en Colombia.

- 2) Localidades exactas de *P. palpebrosus* en Colombia.
- 3) Dimensiones de 35 ejemplares de *P. trigonatus*
- 4) Dimensiones de 28 ejemplares de *P. palpebrosus*.

La dimensión "cuerpo" significa la longitud desde la punta del hocico hasta el borde posterior del orificio anal, y el término "(reg.)" que la cola no está completa sino regenerada y había sido mutilada a mordiscos durante la lucha intraespecífica lo que es muy común en los *Paleosuchus*.

El mapa representa las localidades de *Paleosuchus* en Colombia, con la excepción de los ríos Vichada, Casanare y Arauca en los cuales no se hizo ningún estudio, y, además, los límites de distribución en la América del Sur conocidos hasta la fecha.

SUMARIO

El género *Paleosuchus* consiste en dos especies, *P. trigonatus* (Schneider), 1801, y *P. palpebrosus* (Cuvier), 1807. Ambos se distinguen respecto a sus características morfológicas externas (escamado y color) y en la anatomía craneal. *P. trigonatus* es el más generalizado, mientras *palpebrosus* posee caracteres más constantes y, consecuentemente, es más especializado. La tendencia hacia la osi-

ficación tanto de los huesos craneales como de las placas dermales óseas es más marcada en *palpebrosus* que en *trigonatus*. Debido al menor grado de osificación, en *trigonatus* la forma del cráneo es alargada y la punta del hocico recta y angosta; en cambio, en *palpebrosus* es comprimida, todos los huesos individuales son más anchos y cortos y la punta del hocico es ancha y volteada hacia arriba, tanto en ejemplares adultos como en pequeños juveniles. El color de la tabla craneal es pardo oscuro en adultos de *trigonatus* y de color de herrumbre en *palpebrosus*; castaño claro en juveniles de *trigonatus* y amarillo yema en *palpebrosus*. La parte dorsal de los adultos es pardo oscuro en *trigonatus* y virtualmente negro en *palpebrosus*. El contraste entre los colores de la cabeza y del cuerpo tiene un efecto mimetizante en su habitat natural. El tamaño mayor en los ♂♂ es de 2256 mm y 1330 mm para las ♀♀ de *trigonatus*, 1720 mm y 1230 mm respectivamente en los ♂♂ y las ♀♀ de *palpebrosus*.

El habitat comprende la Selva Tropical Pluvial para ambas especies y el nicho ecológico es bien definido. Consiste principalmente en aguas caudalosas sobre un fondo rocoso; muy probablemente el alto grado de osificación tanto del escamado como del cráneo y, además, la gran agilidad de los movi-

mientos tanto en el agua como en tierra constituyen una adaptación a este medio ambiente. A pesar de que no se ha observado ninguna diferencia marcada acerca del nicho ecológico de ambas formas, posiblemente existe. Así por ejemplo, en *trigonatus* la parte dorsal de todos los ejemplares adultos y subadultos está siempre cubierta por una densa capa de algas verdes, lo que indica la posible permanencia en aguas mansas y expuestas al sol por temporadas; en cambio, nunca se ha observado el mismo fenómeno en *palpebrosus* en su ambiente natural, sino solamente en cautividad.

La alimentación es muy variada; los juveniles se alimentan principalmente de moluscos acuáticos, crustáceos e insectos, los adultos de invertebrados y vertebrados (peces, ranas y sapos, serpientes, pequeños ejemplares del mismo género y de *Caiman sclerops*, aves y mamíferos); además se encuentran guijarros en abundancia en todos los ejemplares mayores de 250 mm. Parásitos, como nemátodos y sanguijuelas (*Hirudinae*), poco frecuentes; es muy común en *trigonatus* un tábano que succiona especialmente la zona entre el espacio interorbital y la punta del hocico, la cual es blanda y muy irrigada.

Respecto a la reproducción faltan datos exactos sobre las dimen-

siones de los huevos; la ♀ construye el nido cerca de las orillas de los caños y bajo del rastrojo; nidos de *palpebrosus* que se encontraron en Noviembre y Diciembre, contenían 18 y 22 huevos respectivamente; juveniles de *palpebrosus* recién nacidos fueron capturados en Diciembre 1, 1950; en Enero 6, 1957, se observaron 2 ♂♂ y una ♀ en celos; la disección demostró la carencia de óvulos en los ovarios.

Ninguna de estas especies fueron vistas en grupos sino solitarias; son principalmente nocturnas; viven en cuevas excavadas en la orilla bajo de la superficie de las aguas; de movimientos rápidos y ágiles, nadan con gran velocidad contra la corriente y cambian súbitamente la dirección; ejemplares arponeados saltaron frecuentemente dentro de las canoas; cuando reposan en la orilla, saltan al agua y no se arrastran como es habitual en *C. sclerops*. No son escasos pero nunca tan abundantes como *C. sclerops*.

Dentro de la hoya del Amazonas propiamente dicha, ambos *Paleosuchus* tienen una amplia extensión; *trigonatus* ha sido registrado en varias localidades situadas en el Brasil, Bolivia y Perú y *palpebrosus* del Brasil, Ecuador y Perú. En Colombia, se extienden virtualmente hasta la vertiente de la Cordillera Oriental; *trigonatus* ha sido registrado por primera vez

en el río Apaporis, afluente del Caquetá (Yapurá) en 1952; ambos se encuentran en los ríos Vaupé (Cayari), Apaporis, Caquetá y Putumayo (Iça) y sus respectivos tributarios. Existe, sin embargo, un fenómeno inexplicable hasta la fecha. En varios de estos ríos ambos son co-existentes, mientras en otros se encuentran solamente ó *trigonatus* ó *palpebrosus*; en este caso de la co-existencia, una de las especies es siempre la más abundante.

El género *Paleosuchus*, es, quizás, el más primitivo de la Familia *Alligatoridae* y evidentemente su evolución se ha efectuado en épocas geológicas pasadas dentro del Habitat de la Selva Tropical del sistema hidrográfico del Amazonas, medio ambiente que virtualmente no ha cambiado, sino que todavía persiste; su migración y presencia en otras áreas extensas está en estrecha relación con su adaptación a un nicho ecológico definido.

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TABLA 1

Especie: *Paleosuchus trigonatus*

No.	Sexo	Localidad y Fecha
CNHM 81980	♂	Río Cafre, afluente del río Guayabero (Meta), Febrero 19, 1957, F. Medem, Modesto Guevara
Pt 17	♂	Misma localidad y fecha
Pt 20	♂	Misma localidad, Febrero 20, 1957, mismos colectores
Pt 11	♂	Misma localidad, Enero 4, 1957, mismos colectores
Pt 1	♂	Alto río Guayabero, vertiente sur de la Sierra de La Macarena, Enero 22, 1959, F. Medem
Pt 14	♂	Río Cafre (Meta), Enero 5, 1957, F. Medem & M. Guevara
Pt 12	♂	Misma localidad, Enero 4, 1957, mismos colectores
Pt 28	♂	Caño Itilla, cabeceras del río Vaupés (Vaupés), Febrero 26, 1958, F. Medem
CNHM 69882	♂	Soratama, río Apaporis (Vaupés-Amazonas), Abril 2, 1952, F. Medem
CNHM 69879	♂	Misma localidad, Abril 11, 1952, F. Medem
Pt 29	♂	Caño Casaeunte, afluente del río Consaya, Alto Caquetá (Caquetá), Noviembre 28, Hugo Arévalo
Pt 3	♂	Caño Losada, afluente del Alto Guayabero (Meta), frente a La Macarena, Marzo 10, 1959, George Dahl
Pt 46	♂	Caño Acahé, afluente del río Putumayo, arriba de Pto. Asís (Putumayo), Octubre 23, 1958, F. Medem
Pt 15	♀	Río Cafre, Enero 6, 1957, F. Medem & M. Guevara
Pt 25	♂	Caño Tacunema (Vaupés), afluente del Alto Apaporis, campamento "Grito", Diciembre 30, 1957, F. Medem
Pt 30	♀	Caño Aguas Negras, afluente del Apaporis, abajo del raudal "La Playa" (Amazonas), Agosto 7, 1957, F. Medem
Pt 27	♂	Río Vaupés, abajo del lago "El Dorado" (Vaupés), Enero 7, 1958, F. Medem
Pt 24	♂	Caño Tacunema (Vaupés), campamento "Grito", Diciembre 30, 1957, F. Medem
CNHM 69881	♂	Soratama, río Apaporis, Marzo 30, 1952, F. Medem
CNHM 69876	♂	Misma localidad, Enero 28, 1952, F. Medem
Pt 26	♂	Caño Tacunema, Diciembre 30, 1957, F. Medem
Pt 31	♂	Caño Icapuyá, afluente del Apaporis, región de Yay-Gojé (Amazonas), 3 horas abajo del Pirá-Paraná, Agosto 8, 1937, F. Medem, Perimaté Tanimúca
Pt 13	♂	Río Cafre, Enero 4, 1957, F. Medem & M. Guevara
Pt 9	♂	Río Apaporis, arriba de Yay-Gojé (Amazonas), Junio 16, 1952, Isidoro Cabrera
Pt 45	♀	Caño Piñuña Blanco (Piyuyá), afluente del Alto Putumayo, abajo de Pto. Asís, Octubre 27, 1958, F. Medem
Pt 16	♂	Río Cafre, Febrero 19, F. Medem & M. Guevara
CNHM 69877	♀	Río Apaporis, arriba del campamento cauchero "Soratama", Abril 16, 1952
Pt 19	♂	Río Cafre, Febrero 20, 1957, F. Medem & M. Guevara
CNHM 69878	♂	Río Apaporis, Soratama, Abril 16, 1952, F. Medem
Pt 21	♂	Río Cafre, Febrero 20, 1957, F. Medem & M. Guevara
CNHM 69883	♂	Caño Churúcu, afluente del río Apaporis (Vaupés-Amazonas), Enero 26, 1952, F. Medem
CNHM 69873	♂	Río Pacoa, afluente del río Apaporis, arriba de las lagunas Inaná (Uinaná), Febrero 6, 1952, F. Medem, Jaime Gómez
Pt 2	♂	Sierra de Macarena (sur), caño No. 2, afluente del río Guayabero, alrededor del campamento No. 1, Febrero 24, 1959, Carlos Alberto Velásquez
CNHM 69870	♂	Río Apaporis, arriba de Soratama, Diciembre 12, 1952, Carlos Balcázar
CNHM 69888	♂, juv.	Puerto Córdoba, río Caquetá, arriba de la Pedrera (Amazonas), Octubre 8, 1952, Isidoro Cabrera

TABLA 2

Especie: *Paleosuchus palpebrosus*

No.	Sexo	Localidad y Fecha
CNHM 69871	♂	Soratama, río Apaporis (Vaupés-Amazonas), Octubre 21, 1951, Isidoro Cabrera
CNHM 69867	♂	Río Cunimá, Sabana de San Juan de Arama (Meta), Marzo 14, 1951, mismo colector
Pp 11	♂	Caño Cajuy, hacienda San Antonio, 26 km de Villavicencio (Meta) hacia Pto. López, Diciembre 30, 1951, Federico Medem & Carlos Alberto Velásquez
Pp 5	♂	Caño Aguascalaras, finca Graciela, 3 km al sur de Villavicencio (Meta), Julio 23, 1956, mismos colectores
Pp 15	♂	Caño Churúcu, región de Soratama, río Apaporis, Enero 26, 1952, F. Medem
CNHM 69868	♀	Caño Manacacas, Sabana de San Juan de Arama (Meta), Marzo 24, 1951, I. Cabrera
Pp 6	♀	Caño Cajuy, hacienda San Antonio, Mayo 19, 1957, F. Medem & C. A. Velásquez
Pp 7	♀	Misma localidad y fecha
CNHM 69872	♂	Soratama, río Apaporis, Marzo 30, 1952, F. Medem
CNHM 69874	♀	Laguna Inaná (Uinaná), río Apaporis, caño entre la segunda y tercera laguna, Febrero 21, 1952, F. Medem
CNHM 69875	♂	Misma localidad y fecha
Pp 22	♂	Río Manacacas, afluente del río Meta (Meta), hacienda La Venturosa, Diciembre 29, 1960, F. Medem
Pp 30	♂	Caño Aguabonita, afluente del río Guejar, frente a la Sierra de La Macarena (norte) (Meta), Abril 9, 1951, F. Medem
Pp 9	♂	Caño Cajuy, hacienda San Antonio, Abril 6, 1958, C. A. Velásquez & F. Medem
Pp 1	♂	Río Guayabero (Meta), en un pequeño afluente en la sabana frente a La Macarena (sur), Enero 19, 1959, F. Medem
Pp 2	♂	Puerto López, río Meta, Agosto 28, 1958, C. A. Velásquez
Pp 8	♂	Río Guaviare, remolino "Playa Alta", arriba de San José del Guaviare (Vaupés), Diciembre 31, 1955, F. Medem
FM 370	♀	Región de Pto. López (Meta), Noviembre 23, C. A. Velásquez
MVZ 2017	juv.	Caño Cboriari, vecindad de la finca El Mico (Meta), frente a La Macarena (norte) Diciembre 1, 1950, Robert C. Stebbins, John Hendrickson & Carlos Balcázar
CNHM 42701	♂ juv.	Misma localidad y fecha
MVZ 2018	juv.	Misma localidad y fecha
CNHM 42702	♂ juv.	Misma localidad y fecha
FM 762	juv.	Caño Pacbaquiarito, región de Pto. López (Meta), Diciembre 4, 1962, C. A. Velásquez
MVZ 2016	juv.	Caño Cboriari, Diciembre 1, 1950, R. C. Stebbins, J. Hendrickson & C. Balcázar
FM 764	juv.	Caño Pachaquiarito (Meta), Diciembre 4, 1962, C. A. Velásquez
FM 766	juv.	Misma localidad y fecha
FM 765	juv.	Misma localidad y fecha

TABLA 3

Crocodylia *Paleosuchus trigonatus*

No.	Sexo	Total mm	Cola mm	Cuerpo mm	Extremidad anterior derecha mm	Extremidad anterior izquierda mm	Extremidad posterior derecha mm	Extremidad posterior izquierda mm
CNHM 81980	♂	2256	896 (reg.)	1360	320	314	482	467
Pt 17	♂	2145	959 (reg.)	1282	300	290	478	445
Pt 20	♂	2100	840 (reg.)	1260	272	275	442	421
Pt 11	♂	1984	778 (reg.)	1206	281	282	435	440
Pt 1	♂	1775	702 (reg.)	1050	235	243	356	351
Pt 14	♂	1602	612 (reg.)	990	233	235	340	351
Pt 12	♂	1537	602 (reg.)	935	240	242	350	347
Pt 28	♂	1470	653	817	195	190	300	300
CNHM 69882	♂	1365	605	760	201	200	285	289
CNHM 69879	♂	1365	585 (reg.)	780	175	180	264	270
Pt 29	♂	1356	603	753	192	198	275	283
Pt 3	♂	1338	533 (reg.)	805	195	205	310	305
Pt 46	♂	1335	460 (faltan 150)	865	210	108 (falta la mano total)	340	336
Pt 15	♀	1330	468 (reg.)	862	323	220	335	332
Pt 25	♂	1303	59	712	175	174	278	270
Pt 30	♀	1110	455	605	177	174	247	240
Pt 27	♂	1073	483	590	150	156	226	228
Pt 24	♂	1056	444	592	172	172	242	250
CNHM 69881	♂	1035	473	562	152	153	222	230
CNHM 69876	♂	986	391 (reg.)	795				
Pt 26	♂	935	422	513	133	135	203	205
Pt 31	♂	883	486	497	131	138	190	185
Pt 13	♂	875	386	489	125	127	188	187
Pt 9	♂	817	397	420	/	/	/	/
Pt 45	♀	806	364	442	115	116 mm	175	175
Pt 16	♂	795	368	427	117	120	170	168
CNHM 69877	♀	750	313 (reg.)	437	124	119	174	172
Pt 19	♂	742	353	407	112	108	164	165
CNHM 69878	♂	715	330	385	107	109	152	158
Pt 21	♂	682	307	375	102	102	150	152
CNHM 69883	♂	677	296	381	/	/	/	/
CNHM 69873	♂	660	292	368	/	/	/	/
Pt 2	♂	584	315	269	79 mm	82	120	122
CNHM 69870	♂	570	235 (reg.)	335	90	89	131	130
CNHM 69888	♂ juv.	380	214	166	/	/	/	/

TABLA 4

Crocodylia *Paleosuchus palpebrosus*

No.	Sexo	Total mm	Cola mm	Cuerpo mm	Extremidad anterior derecha mm	Extremidad anterior izquierda mm	Extremidad posterior derecha mm	Extremidad posterior izquierda mm
CNHM 69871	♂	1545	648 (reg.)	897	/	/	/	/
CNHM 69867	♂	1530	662 (reg.)	868	/	/	/	/
Pp 11	♂	1419	576 (reg.)	843	/	/	/	/
Pp 5	♂	1365	540 (reg.)	825	193	189	302	308
Pp 15	♂	1261	598	663	/	/	/	/
CNHM 69868	♀	1230	550	680	190	191	290	294
Pp 6	♀	1216	540	690	172	176	280	278
PP 7	♀	1116	546	570	155	148	242	238
CNHM 69872	♂	1101	510	591	157	159	224	223
CNHM 69874	♀	1063	491	672	/	/	/	/
CNHM 69875	♂	942	462	480	/	/	/	/
Pp 22	♂	917	448	469	120	125	194	195
Pp 30	♂	854	408	450	/	/	/	/
Pp 9	♂	847	404	443	110	115	170	170
Pp 1	♂	805	390	390	110	115	166	163
Pp 2	♂	760	367	376	110	112	153	153
Pp 8	♂	760	336	370	95	98	151	152
FM 370	♀	740	345	395	107	110	164	163
MVZ 2017	juv.	565	275	290	67	68	105	105
CNHM 42701	♂ juv.	556	270	286	/	/	/	/
MVZ 2018	juv.	521	252	269	66	67	98	98
CNHM 42702	♂ juv.	520	246	274	/	/	/	/
FM 762	juv.	516	248	267	68	70	102	102
MVZ 2016	juv.	257	130	127	40	41	53	55
FM 763	juv.	255	129	126	38	37	51	55
FM 764	juv.	254	127	130	36	35	53	55
FM 766	juv.	249	124	125	36	38	52	53
FM 765	juv.	248	126	124	38	37	56	57

RECONNAISSANCE INVESTIGATIONS OF THE DISCHARGE AND WATER QUALITY OF THE AMAZON

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(With 8 text-figures)

When the International Association for Scientific Hydrology (IASH) in 1957 began a program for assessment of river-borne dissolved solids from all sources carried to the oceans, the investigators found little published information on the Amazon River. The information on the water discharge of the Amazon, because of the wide range in published values, did not provide a reliable estimate of average annual discharge upon which a computation of the annual dissolved solids load of the river could be made. On the basis of the scanty information available to the investigators, the Amazon appeared to supply about 10 percent of the total continental water discharge into the world's oceans. However, if the estimated Amazon discharge was in error by as great a percentage as appeared probable,

the calculated annual salt discharge to the oceans could be seriously affected.

This situation led, in May 1961, to a joint proposal by Luna B. Leopold, then Chief Hydrologist of the Geological Survey, Walter B. Langbein, Staff Scientist of the Geological Survey, and Professor H. O'R. Sternberg, then Diretor, Centro de Pesquisas de Geografia do Brasil, Universidade do Brasil, for measuring the flow, solute load, and sediment concentration of the Amazon. Professor Sternberg gained the backing of Vice Admiral Helio Garnier Sampaio, Diretoria de Hidrografia e Navegação, Ministério da Marinha, for logistic support. The Marinha do Brazil would supply the necessary gaging vessel

Cooperative investigations by Ministério da Marinha do Brazil, University of Brazil and U.S. Geological Survey.

and the Geological Survey would provide the gaging manpower and equipment. Arrangements for the first of three reconnaissance expeditions to the lower Amazon were completed in the spring of 1963. Space does not permit acknowledgment of the assistance of the many other individuals and organizations that helped in carrying out the reconnaissance work.

Four engineers of the Geological Survey — Frank C. Ames, Luther C. Davis, George R. Staeffler, and the writer — composed the gaging team, which was most ably assisted by several Brazilian naval officers. Professor Sternberg assisted the team during much of the second expedition.

It is the purpose of this paper to present a few of the notable results and conclusions obtained by the joint expedition for the Obidos location and other pertinent sites on the lower Amazon. A final report, in preparation, will provide information on all the work done, including that in the Manaus vicinity.

ESTIMATES OF AMAZON DISCHARGE

Scientists conducting a literature search for information on the discharge of the lower Amazon may become confused by the many different estimates of discharge published by investigators of South American or world river discharge.

Table 1 contains a list, from 14 sources, of selected published estimates of some aspect of the Amazon discharge, such as stream geometry, mean velocity, and total discharge made at the general location of Obidos or the mouth. The earliest estimate in the list is that of SPIX & MARTIUS published in 1831. The latest estimate in the list is that of the eminent hydrologist Maurice Pardé published in 1955. One may note the wide range of listed values for the average annual discharge at mouth — a range from 68,000 (Alexander Siemens) to 204,000 (Military Engineer).

Upon inspection of the source documents one finds such perplexing circumstances as the following:

The published estimate for discharge at mouth in the *Military Engineer* (1958, 50 (337): 386) is credited to Dr. H. P. Guppy. Upon examination of Dr. Guppy's tabulation of discharge of large rivers of the world found in *Nature*, one finds that he credited his value for Amazon discharge (at mouth) to Elisée Reclus. Thus, the real source of the estimate published in the *Military Engineer* is RECLUS. However, during the compilation of estimates by GUPPY and those in *Military Engineer*, the original RECLUS estimate of 100,000 cm (cubic meters per second) for the aver-



TABLE I

Selected published estimates of flow of the lower Amazon River

Source	Date	Location	Data of estimate				Remarks	
			Date or season	Cross-section area (m ²)	Width (m)	Mean velocity m/sec		Discharge (m ³ /sec)
Spix and Martius	1831	Obidos	Low water	—	—	0.7	14,000	
Wallace	1853	Obidos	Low water	—	—	1.62	—	Velocity estimate attributed to Wallace by F. Katzer
Lallemont	1860	Obidos	High water	—	—	—	319,476	
Guppy	1880	Moutb	Annual	—	—	—	70,000	Estimate attributed to Reclus by H. P. Guppy
Smith	1880	Obidos	Annual	22,500	1,892 (from Penna)	1.0 1.0	21,500 21,500	Based on data reported by Penna, Wallace, and Martins
Selfridge	1882	Parintins	Aug. 3, 1880	—	—	—	110,404	—
Reclus	1895	Obidos	June	116,000 to 140,000	1,520 to 1,830	2.04	(100,000) 237,000— 286,000	Figure in parenthesis is published but is apparently in error.
Siemens	1896	Mouth	Annual	—	—	—	68,000	Basis of estimate unknown.
Katzer	1898	Obidos	Early July 1896	100,000	1,890	1.2	120,000	From article: "Die Stromenge des Amazonas bei Obidos."
Le Cointe	1922	Obidos	End of May 1918	—	—	3.15	—	Float observation at crest of flood.
			Low water	105,000	1,890	0.6	63,000	Area based on soundings of others.
			High water	117,500	1,890	1.25	146,775	
Carvalho	1942	Moutb	Low water	—	—	—	60,000	
			High water	—	—	—	140,000	
Jarvis	1945	Obidos	Annual	—	—	—	85,000	Computed on basis of rainfall-runoff relation.
Parde	1955	Obidos	Annual	—	—	—	90,000 100,000	Based mainly on Le Cointe's data.
Military Engineer	1958	Moutb	Annual	—	—	—	204,000	How Guppy's published 70,000 cm became 204,000 is unknown

* See list of references at end of report.

age annual discharge for Obidos became 70,000 cm at mouth of river in Guppy's table, and 204,000 cm at mouth in the table in *Military Engineer*. Furthermore, upon examination of RECLUS' work one finds the width at the Obidos narrows quoted as 1,520 to 1,830 meters and mean depth quoted as

about 76 meters, which would provide a cross-sectional area of 116,000 to 140,00 square meters. Using RECLUS' value of velocity of 8,000 yards an hour equivalent to 2.04 meters per second, one would compute an average discharge at Obidos of 237,000 to 286,000cm. Thus, the whole chain of published

estimates (RECLUS, GUPPY, and *Military Engineer*) is a compounding of errors.

If one accepts the estimates published by scientists who actually visited Obidos and vicinity and made personal observations of channel geometry and stream velocity as reliable estimates, the data would be narrowed down to that of KATZER, SELFRIDGE, SPIX & MARTIUS, WALLACE, SMITH, LECOINTE, and LALLEMONT (note: CARVALHO's estimate may also be valid). These valid estimates apply to differing river stages; for example, KATZER's observation was made in early July 1896; SELFRIDGE's (at Parintins) in early August 1880. LECOINTE appears to be the most helpful. He provides for Obidos a measured width at the narrows of 1,890 meters (obtained by triangulation), low water cross section of 105,000 square meters, high-water cross section of 117,000 square meters, and discharges ranging from 63,000 cm (low water) to 146,775 cm (high water). PARDE, in his study, based his estimate of the average annual discharge at Obidos largely on LECOINTE's data and reported it as from 90,000 to 100,000 cm.

One may wonder why estimates only, instead of measurements, of the Amazon discharge at Obidos are available. The techniques for gaging large rivers were well de-

veloped during the 19th century. REVY reported application of completely satisfactory methods in measurements of the Paraná at Rosário made in 1871. Although the maximum depth of the Rosário cross section was only 22 meters — shallow in comparison with the 61-meter maximum depth found in the discharge measurement at Obidos on July 16, 1963 — the same procedures used for holding the measuring vessel in place at Rosário would have worked at Obidos, and the current-meter suspension for measurement of velocities at Rosário would have been satisfactory at Obidos. After establishment of the river gage at Obidos in 1928 by the Brazilian Government and the commencement of daily river-stage readings, the attraction to measure the flow and develop a stage-discharge relation for Obidos was stronger, for then the annual flow regime could be completely charted. The task of determining the geometry of a selected cross section on the Amazon at Obidos was relatively simple. Although complete information is not available on the techniques used by the scientists who have reported measured cross-sectional area, it is probable that the method fully described by REVY as used on the Paraná work for obtaining measured depths was used on the Amazon. Depth measurements of a selected



cross section are made, following Revy's method, by sounding with a weighted line from a ship drifting with the current. In this way, the sounding line remains nearly vertical because there is only minor current drag on it near the bed. As the ship drifts across the desired measuring section, the sounded depth is observed and the location of ship on the cross section (distance from either bank) is determined by standard surveying methods (sextant readings on flags located on the ends of a measured base line established on shore, or theodolite readings taken to the ship from a shore-based instrument). With great care and repetition, a very reliable cross section could be so measured. The measurement of stream velocities could have been obtained by anchoring the gaging vessel to permit observations of subsurface velocities with standard current meters or by using subsurface floats. If a few such measurements, referenced to the Obidos gage, had been made to cover the range of discharge from low to high water and an approximate stage-discharge relation established for the Obidos location, a much better estimate of the average annual discharge at Obidos could have been computed.

Although Jarvis' discharge for the Amazon at Obidos is the only

one tabulated known specifically to be based on rainfall-runoff relationships, the map of world runoff published by L'Vovich, also based on hydrologic calculations, permits an estimate of the discharge at mouth to be measured. Jarvis using data then available to him, computed the average annual precipitation for the drainage area tributary to Obidos as 1,570 mm. He based his average annual runoff estimate on a ratio of runoff to precipitation of 34 percent. The estimate one may derive from L'Vovich's map is equivalent to about 110,000 cm for either the Obidos or at-mouth location. Precipitation data in the Amazon Basin are presently much more adequate for assessment of basin average annual rainfall than was the case for Jarvis or L'Vovich. Using Thornthwaite's potential evapotranspiration approach and the presently available climatic data, the writer has calculated average annual runoff for area above mouth of 800 mm, equivalent to average annual discharge of 150 000 cm.

RESULTS OF RECONNAISSANCE WORK

As discussed in Geological Survey Circular 486, "Amazon River Investigations — Reconnaissance Measurements of July 1963," the lack of data for discharge and dissolved solids of the Amazon ham-



pered work on the project of the International Association of Scientific Hydrology (IASH) for calculation of the salt balance of the oceans. The Amazon River was known to be the world's largest in terms of discharge, but the degree of uncertainty in the available estimates of the discharge led to the investigations jointly sponsored by the Brazilian Navy, the University of Brazil, and the U. S. Geological Survey. The results collected during the first measurements (July

1963) reported in Circular 486 have been supplemented by results obtained in October-November 1963 and August 1964 and will be discussed in detail in a final report (in preparation). The results of the measurements of flow at Obidos are discussed in this section; the measurements of water quality and sediment are discussed in a later section.

The major features of the three measurements of discharge at Obidos are presented in Table 2.

TABLE 2
Discharge measurements at Obidos

Date	Stage (m)	Width (m)	Area (m ²)	Mean Depth (m)	Mean Velocity (m/sec)	Discharge (m ³ /sec)
7/16/63....	5.8	2,290	110,000	48.0	1.97	216,000
11/20-21/63	— 0.5	2,260	92,400	41.0	0.79	72,500
8/ 9/64....	4.76	2,280	106,000	46.5	1.55	165,000

The methods used in collecting the data for the measurements have been discussed in Circular 486. All three discharge measurements were made at the same cross section. The August 1964 measurement used subsurface velocities after loss of a 136-kg sounding weight and current meter on an under-water obstruction led the gaging party to conclude it would be prudent to conserve the

remaining equipment. However, the depths for the measurement were taken with a sonic sounder and the results should be nearly as reliable as are those of the first two measurements. The width of section, ranging from 2,260 to 2,290 meters is different from that measured by LeCointe (1,890 meters) because the cross section selected for the 1963-64 work was



about 2 km downstream from Le-Cointe's section.

The datum of the gage used at Obidos in 1928-46 and destroyed (according to local information) during the great flood of 1953 was recovered by reference to a photograph (courtesy of Departamento Nacional de Produção Mineral, Divisão de Águas) of the location of the original high-water staff-gage

section. Fortunately, the Obidos municipal warehouse against which the original staff section had been photographed existed during the 1963-64 visits, and by careful measurements the datum was recovered within a possible error range of 10 cm. Fortunately, also, overlapping records of river stage are available at Manaus and Taperinha.

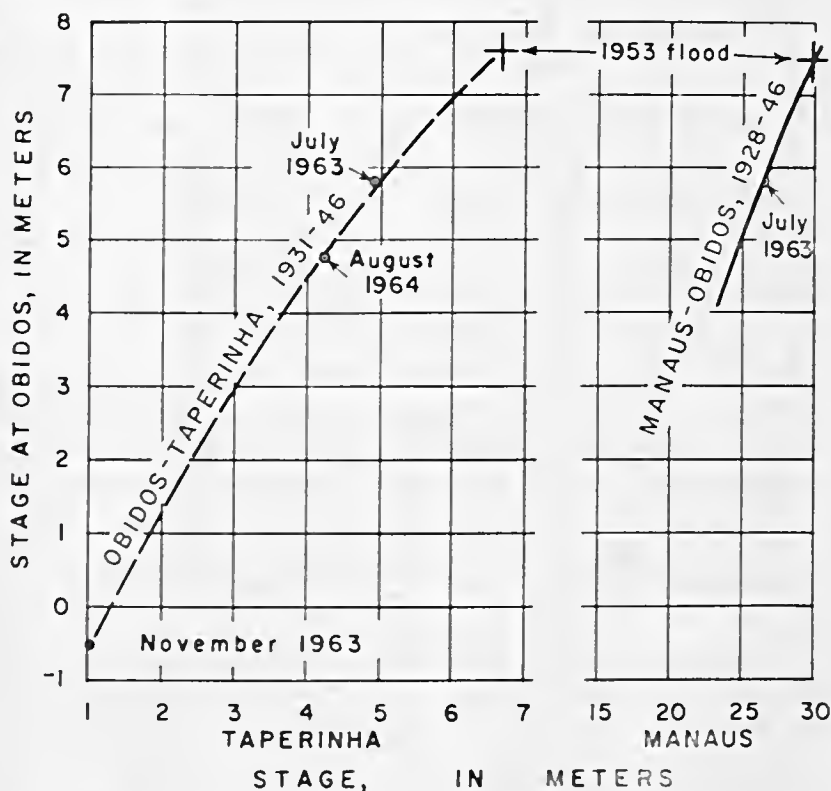


Fig. 1 — Concurrent readings on gages Obidos-Manaus-Taperinha.

Figure 1 shows the good agreement of the concurrent 1963-64 Obidos readings with those from

Manaus and Taperinha where daily gage readings were available. The stage graphs showing the re-

lationship of concurrent readings for the period 1928-46 (overlapping records Obidos and Manaus) and 1931-46 (Obidos and Taperinha) were prepared by plotting selected concurrent readings for the three gages and fitting the curves to the scatter plot. There can be no question that the Obidos gage datum was recovered with reasonable accuracy, as the concurrent readings 1963-64 lie on the curves developed from data taken in 1928-46 (1931-46 in the Obidos-Taperinha comparison). For example: the relationship curve Manaus-Obidos shows that a stage of about 7.5 meters would have occurred at Obidos at the crest of the great 1953 flood, which reached 29.7 meters at Manaus. Similarly, the Taperinha - Obidos relation curve shows that a stage of about 7.6 meters would have occurred at Obidos during the 1953 flood, which reached 6.65 meters at Taperinha. Discussion with Obidos inhabitants who remembered the 1953 flood and showed the survey party the level it reached in the vicinity of the gage location verified the approximate Obidos stage of 7.5 meters for the 1953 event. Thus, significant evidence indicates reliable recovery of the Obidos gage datum used in 1928-46.

A rating curve (curve showing relationship of stage to discharge) prepared for Obidos on the basis of

the three available measurements of discharge and other data is shown in figure 2.

Guidance in drawing the curve through the discharge measurements and extending it to the greatest known stage of 7.6 meters was obtained from a study of conveyance and slope. The slope computed by use of the Manning formula with a Manning coefficient (English units) of 0.020 (derivation of the Manning coefficient from a vertical velocity curve is explained later) varied among the three measurements as follows:

July 1963	8.75×10^{-6}
November 1963	1.74×10^{-6}
August 1964	5.65×10^{-6}

It is the author's opinion that the square root of the slope varies linearly with stage at and above the stage of the two higher measurements of discharge. Thus, the slope estimated for a stage of 7.6 meters at Obidos is 16.0×10^{-6} . The stage-conveyance relation for Obidos does not vary much with stage (conveyance, K, equals, in English units, $1.486 \frac{AR^{2/3}}{n}$

where A is cross-sectional area and R the hydraulic radius); hence the increase in discharge with stage is mainly a result of increase in slope through the Obidos nar-

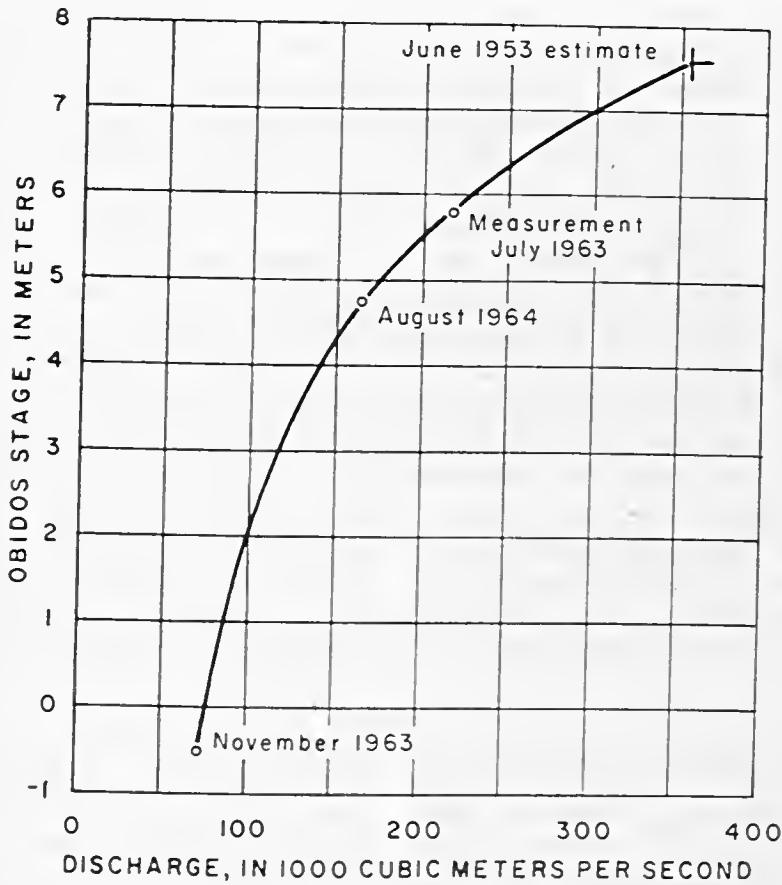


Fig. 2 — Stage-discharge relation — Amazon River at Obidos.

rows. An observation by Lecointe of the high velocity through the Obidos narrows concurrent with the crest of the flood of May 1918 (3.15 meters/second from float observation) supports the extrapolation of the stage-discharge relation to 250,000 cm at stage 7.6 meters. Figure 3 shows the small variation in cross section measured in the Obidos discharge measurements. The cross-sectional area

of the main channel for a 7.6 meters would be but 4,150 meters² larger (about 4 percent larger) than that of the discharge measurement of July 1963.

During the three trips for collection of reconnaissance data, limited time did not permit an investigation of the overflow situation at Obidos. Maps (see Figure 4) clearly show the area subject to overflow between the main chan-

nel opposite Obidos and the terra firme about 32 km south of Obidos. The flood plain, judging by available maps and air photos, is covered with shallow lakes, swamps, scrub trees, and grass, and the drainage channels and abandoned meanders indicate the localized flow directions during floods. A set of levels run from the water surface as far inland on the flood plain as limited time would permit shows the top of the natural levee and flood plain adjacent to the right bank of the main channel opposite Obidos to be about at elevation 6.9 meters (Obidos gage datum). Thus, significant overflow covering the entire flood

plain opposite Obidos would occur any time the Obidos stage exceeded 6.9 meters. It is of interest that the former Obidos gage observer (Mrs. Platt) made a notation in the gage records that overflow would begin at Obidos when the river level reached 7.5 meters.

Although overflow directly opposite Obidos might not begin until the river stage reached 6.9 meters, it is very likely that significant overflow would exist at a 6.9-meter stage through the channels and lakes (Lago do Poção, Lago Grande de Vila Franca, and connecting small lakes) occupying roughly a strip of the flood plain 15 km wide immediately adjacent to terra fir-

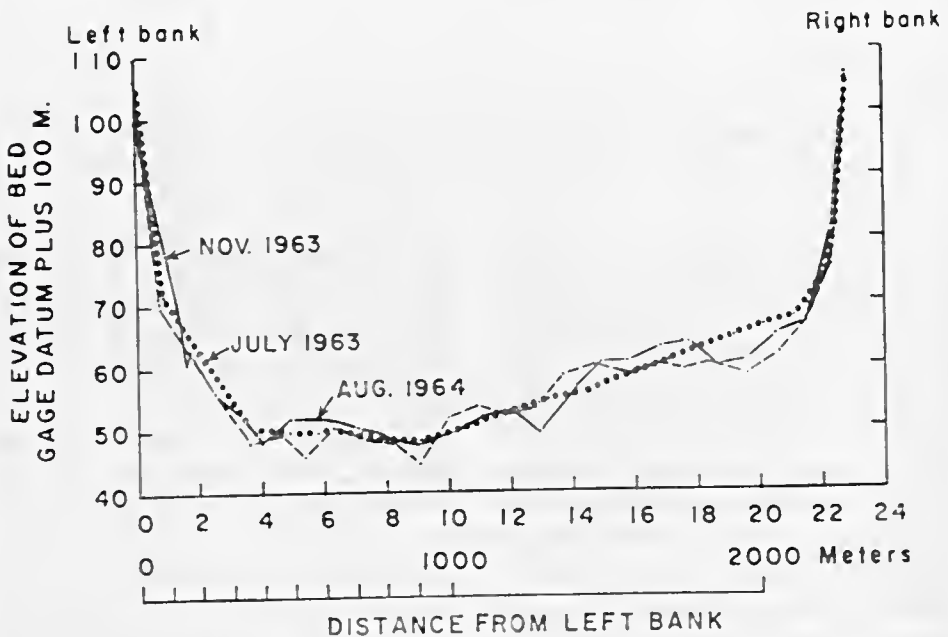


Fig. 3 — Measured cross sections from three discharge measurements.

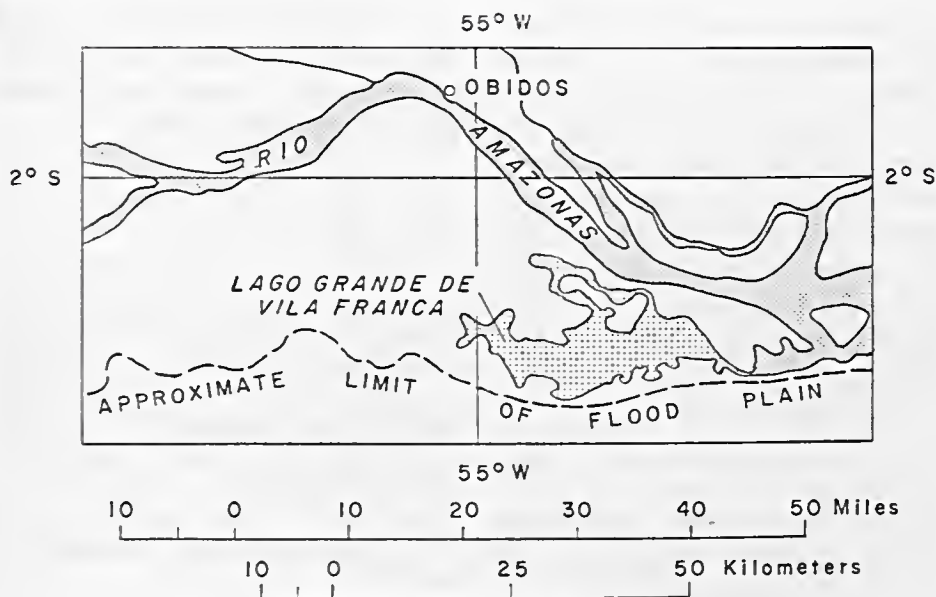


Fig. 4 — Map of Amazon River in vicinity of Obidos.

me. A computation of possible range in discharge over the flood plain at the stage (7.6 meters) of the 1953 flood was made by (a) assuming the worst possible hydraulic conditions of shallow depth, water-surface slope equal to the main channel water-surface slope, and maximum natural roughness and (b) assuming the best possible hydraulic conditions of average depth of overflow equal to 2 meters, water-surface slope increased 50 percent over the main channel slope, and minimum probable roughness (Manning coefficient 0.030). The result based on assumed worst hydraulic conditions showed that the overflow could be ignored without seriously affecting the accuracy of

the estimated maximum discharge. The computation based on best conditions showed that a flow equal to about 10 percent of the main channel discharge might bypass the main channel at a stage equal to that of the 1953 flood. It is likely that the actual overflow discharge in June 1953 was somewhere between the two results.

KATZER's interpretation of the overflow situation at Obidos is not favorable for accuracy of flow measurements. He wrote: "Unfortunately the narrows at Obidos is not suitable for this purpose as long as the entire quantity of water is to be determined, because only a part of the Amazon's total water passes at this point. Another

part flows into a number of arms in the lowland north of the Serra do Valaio and helps to fill the large lake, Lago Grande de Vila Franca, which forms a wide water zone with its numerous lagoons and their connecting channels. This water zone stretches like a bow-string across the main arm of the Amazon which bends north, and below whose zenith the city of Obidos is situated."

Several strips of overlapping aerial photographs taken on flight lines across the flood plain from east to west and north to south from the terra firme to the Amazon were available to the writer for study. It is unlikely that the overflow situation intimated by KATZER could exist. However, if great accuracy of measurement of the total discharge of a subsequent flood of the size of the 1953 event is desired, the overflow depths and current velocities should be measured and the quantity of flow computed. It is the writer's opinion that the quantity of flow bypassing the main channel at the stage equivalent to average annual discharge at Obidos is an insignificant percentage of the main channel flow.

Some questions may be raised about the fact that the two higher discharge measurements were made on a falling river stage and hence the measured flows may be

less than would occur at equal stage on the rising side of the hydrograph. A computation made by the Wiggin's formula,

$$\frac{Q_c}{Q_m} = \sqrt{1 - \frac{1}{US_c} \frac{dh}{dt}}$$

where Q_c = discharge corrected for changing stage; Q_m is discharge measured; U is velocity of flood wave (assumed equal to 1.3 times mean velocity); S_c is slope of energy gradient;

$\frac{dh}{dt}$ is rate of change of stage in feet per second,

showed the correction to be applied to the July 1963 measurement was less than 3 percent (which can be ignored in view of the reconnaissance nature of the work). The August 1964 measurement had a lesser correction computed for it.

Proof of tidal effect at Obidos was obtained by stage readings at short intervals during the November measurement. (The existence of tidal effect was a moot point based on previous investigations.) The graphs of stage readings taken at one-half-hour intervals on November 20 and 21, 1963, are shown in Figure 5.

It should be kept in mind that the readings were taken during one of the lowest flows of the Amazon at Obidos when the upstream

reach of tide effect would be a maximum. (During the period 1928-46 no stage reading of less than 0.05 meter was recorded. The mean stage of the November 1963 discharge measurement is -0.5 meter, or one-half meter lower than zero datum.) The effect of tide on the Obidos stage-discharge relation is considered insignificant by the writer.

On the basis of the recorded gage readings for the period 1928-46 and the rating curve of figure 2, mean monthly discharge has been computed as listed:

<i>Month</i>	<i>Average monthly discharge for period (1,000 cm)*</i>
January	110
February	140
March	170
April	215
May	240
June	240
July	205
August	165
September	120
October	90
November	85
December	95

* Average rounded to nearest...
5,000 cm

The computed annual mean discharge at Obidos for the period is

157,000 cm. The mean annual discharge computed for Obidos on the basis of the three discharge measurements and Obidos gage readings for the period 1928-46 is thus seen to be more than 50 percent greater than Parde's estimate of 90,000 to 100,000 cm.

Some observations on velocity distribution in selected verticals and in the complete cross section at Obidos are shown in Figure 6 and 7.

The point velocity observations for the vertical distribution of velocities observed on November 21, 1963, were measured while the corvette was anchored and should be reasonably free of errors caused by movements of the metering vessel during individual observations. Each point velocity observation is the average determined during a period of forty or more seconds. The effects of natural stream turbulence are evident in the scatter of the observations about the arbitrarily placed distribution graph. It is evident that, because of the large scale of the turbulence, each point velocity observation should have been derived from a meter run of much longer duration — perhaps as long as 4 minutes. From a study of data from 23 United States rivers ranging in depth from 2.4 ft. to 26.7 ft. (0.73 m to 8.1 m), Carter and Anderson determined that an obser-

vation period of 4 minutes for the 20-percent depth location will yield a mean point velocity within 2 percent of the probable true average. As predicted by turbulence theory, the effect of turbulence at the Obidos section is most pronounced in proximity to the channel bed and it decreases as the distance of observation point above the bed increases.

The vertical velocity curve data in Figure 6 and the several other vertical velocity distribution curves developed for other locations and dates at Obidos verify the essential correctness of the Geological Survey's standard procedure for computing the mean velocity in the vertical as the average of point velocity observations taken at 20 and 80 percent of the total depth. The

mean in each vertical for the Obidos discharge measurements of July and November 1963 was computed from the 20-and 80-percent depth observations—each corrected for movement of the measuring corvette during the period of observation, as explained in Geological Survey Circular 486. The mean in each vertical for the August 1964 measurement was obtained by applying an appropriate coefficient to the subsurface velocity.

The distribution of mean velocity in vertical across the Obidos measuring section for the high-flow measurement of July 1963 is shown on Figure 7. The distribution of velocities in the section is remarkably uniform, as would be expected from Geological Survey experience derived from thousands

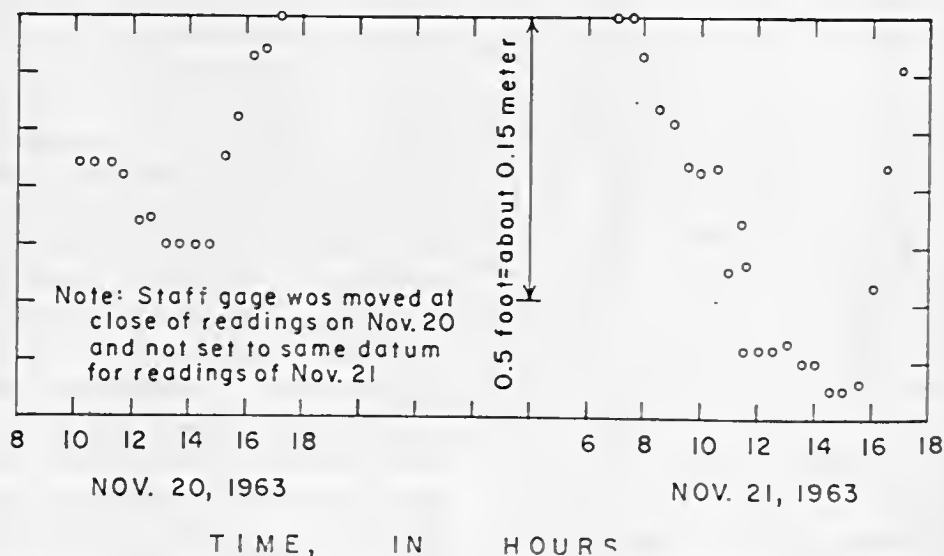


Fig. 5 — Graphs of stage readings showing tidal effect at Obidos at low flow.

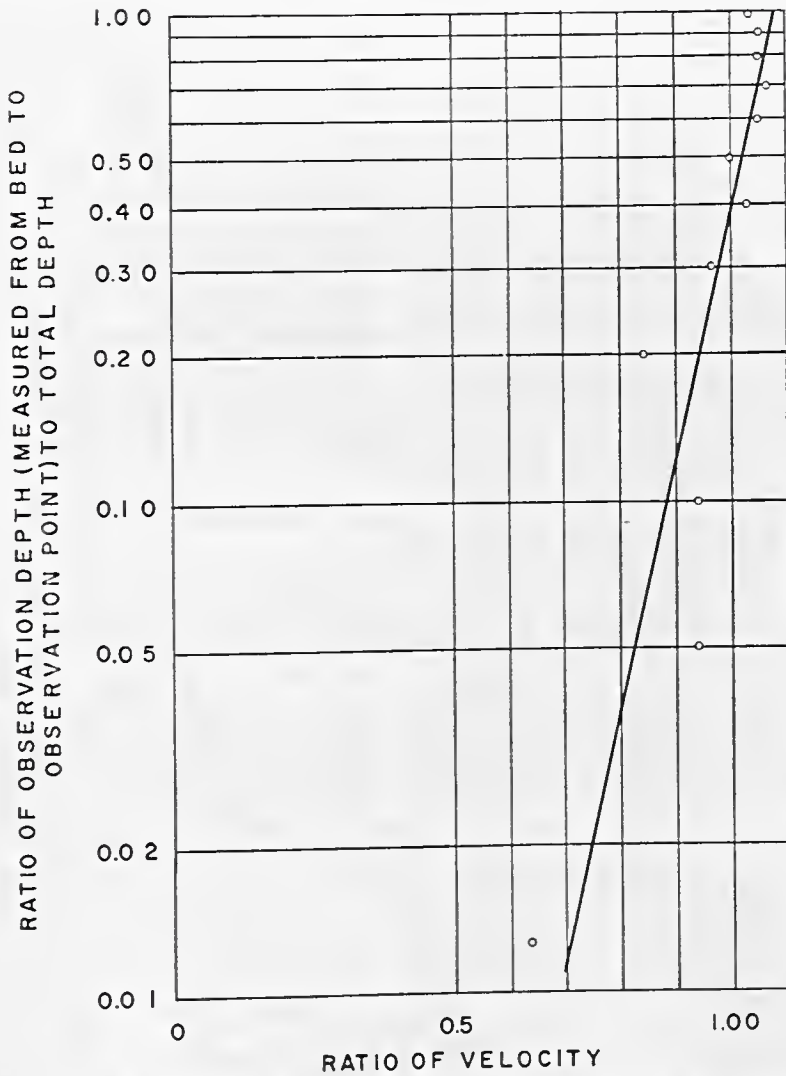


Fig. 6 — Distribution of velocity in a selected vertical at Obidos.

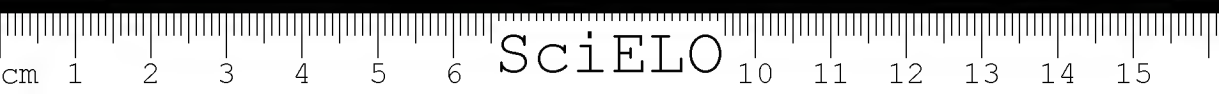
of discharge measurements made on deep, swift rivers in the United States with similar uniformity of measuring section and similar streambed conditions.

An analysis based on the vertical velocity distribution graph and

the logarithmic velocity distribution law for wide channels (smooth or rough):

$$\frac{v - V}{V \sqrt{f}} = 2 \log_{10} \left(\frac{y}{y_0} \right) + 0.88$$

where v is observed point velocity (all English units)



- V is mean velocity in vertical
 f is Darcy-Weisbach friction coefficient
 y is depth of observation (measured from bed)
 y_0 is total depth of measured vertical

yielded a Darcy-Weisbach friction coefficient of $= 0.008$, equivalent to a Manning roughness coefficient for the depth investigated of 0.019.

This indication of a relatively smooth bed is borne out by the bed profile shown by sonic soundings and the bed material samples obtained. A section of fathometer chart taken November 21, 1963, during a run up the approximate middle of the channel and crossing the general location of the measured cross section is shown on Figure 8.

The chart shows dunes with an approximate length of 200 meters. (The illustration is a drafted reproduction of the fathometer chart. The explanation of the short period fluctuations is unknown.) Experience with sand channels in the United States has led to assignment of Manning coefficients in the range 0.018 to 0.035 for such bed geometry. The size distribution of material determined from bed samples is discussed later.

QUALITY OF WATER

In contrast to the many published estimates of water discharge for the Amazon, there is little published information on the suspended sediment and dissolved solids loads carried by the flow. KATZER and STOLI have published a few analyses of suspended sedi-

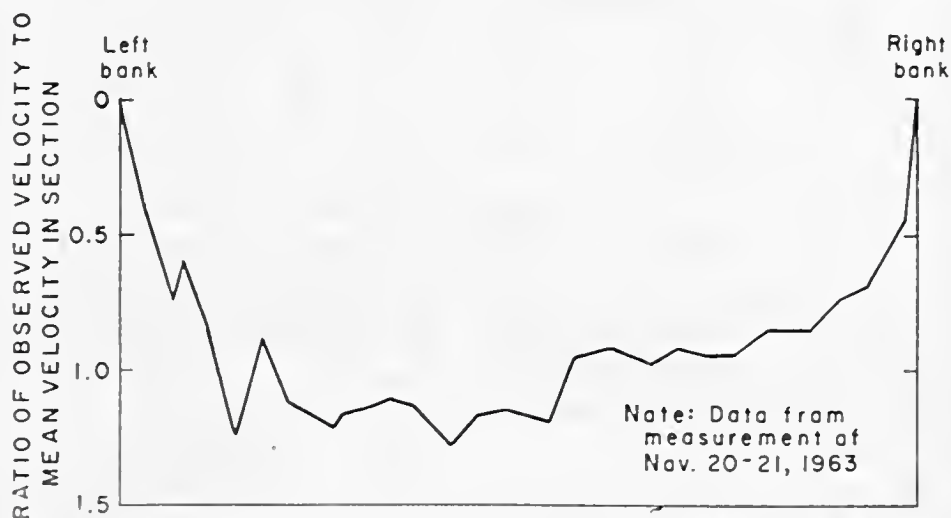


Fig. 7 — Distribution of mean velocity in cross section at Obidos.

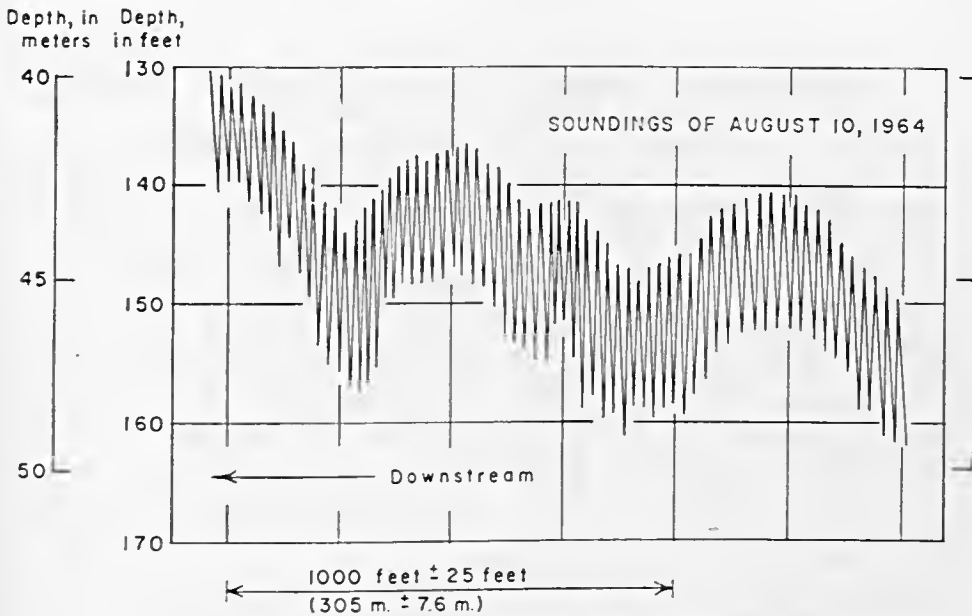


Fig. 8 — Section of fathometer chart taken near midstream and crossing general location of measuring section.

ment, total dissolved solids, and some other information on the chemical and physical nature of the Amazon water in the general vicinity of Obidos. PINTO is quoted by CAMARGO as having computed a mean daily discharge of suspended load at mouth of Amazon to be 3 million tons.

Undoubtedly, the lack of means for collection of suspended sediment samples from various depths at the relatively high flow velocities discouraged investigators from attempting to assess the mean annual suspended sediment discharge by Obidos. Similar difficulties would have discouraged attempts to collect samples of the material in place on the streambed.

The joint reconnaissance venture of 1963-64 was well equipped to collect water samples at any point in the measuring cross section at Obidos. Samples of the material on the top of any part of the bed could also be taken with an oceanographic clamshell type sampler or standard U.S. BM-54 sampler. The U.S. P-61 suspended sediment sampler (equipped with 3/16-inch-diameter intake nozzle), having an electrically controlled intake and closure valve, permitted water samples for analysis of suspended sediment to be taken at any location in the cross section of flow. Thus, the distribution of suspended sediment concentration from bed to surface could be deter-

TABLE 3

Concentration of dissolved and suspended material (ppm)
[mg/l], Amazon River at Obidos

Constituent	July 16, 1963	November 2 ^o , 1963	August 9, 1964
Discharge (cms).....	216,000	72,500	165,000
Silica (SiO ₂).....	7.0	9.0	9.0
Aluminum (Al).....	.67	.02	.15
Iron (Fe).....	.06	.06	.09
Calcium (Ca).....	4.3	10	3.9
Magnesium (Mg).....	1.1	.4	.6
Sodium (Na).....	1.8	4.2	1.8
Potassium (K).....	—	.4	.6
Bicarbonate (HCO ₃).....	19	32	16
Sulfate (SO ₄).....	3.0	6.4	1.0
Chloride (Cl).....	1.9	4.5	1.6
Fluoride (Fl).....	.2	0	0
Nitrate (NO ₃).....	.1	0	.1
Total dissolved solids.....	28	51	21
Hardness as CaCO ₃	15	27	12
Dissolved oxygen.....	5.8	5.6	5.4
Specific conductance.....	40	84	34
pH.....	6.5	7.1	6.5
Temperature (°F).....	83	86	83
Suspended sediment.....	89	60	110

mined at any selected vertical. A bathythermograph furnished temperature-depth profiles at desired verticals. Chemical-quality samples were taken with an oceanographic sampler consisting of an open tube that allowed flow through of water until it was closed, as desired, by ball-type valves.

The quality of water aspects of the investigation were conducted by Mr. F. C. Ames, Geological Survey, Denver, Colorado. Mr. Ames furnished Table 3, which shows the results of the three series of sam-

plings made at Obidos. The tabulated suspended-sediment concentrations are the calculated average concentration for the cross section. Suspended sediment samples were taken at many points in each vertical sampled, so that the distribution of suspended material in the vertical could be charted. In a personal communication (April 1966), Mr. Ames has furnished information, as follows, on the range of suspended-sediment concentrations measured in the cross section:

	July 1963	November 1963	August 1964
Upper portion of verticals	60 mg/l	50 mg/l	70 mg/l
Near the bed	300	280	340

As expected, the concentration of suspended sediment is high in the vicinity of the bed.

Ames reports (personal communication) this information on the bed material at Obidos:

"The median diameter of bed material averaged about 0.20 mm. The median diameters indicated by individual samples ranged from 0.15 to 0.25 mm. Only one to two percent of the bed material (by weight) was finer than 0.062 mm and only one or two percent was coarser than 0.4 mm."

KATZER reported total dissolved solids of 56 mg/l in a sample taken at Obidos June 30, 1896. Because the turbulent mixing and lack of major tributary inflow in the vicinity of Obidos (the discharge from the Rio Trombetas would have small effect) should guarantee uniformity of dissolved-solids concentration in a cross section of the stream, the minor differences in the four analyses can be attributed to seasonal variations. One would expect the total dissolved solids found by Katzer on June 30, 1896, to be more dilute than he reported unless the flow for that season was very low. The concentration of dissolved solids on August 9, 1964 (discharge 165,000 cm) if there were a relatively fixed inverse curvilinear relation between total dissolved solids and water discharge, would be expected

to be slightly higher than found on July 16, 1963, (discharge..... 216,000cm). The contrary findings, 21 mg/l and 28 mg/l, respectively, show the importance of seasonal variations in the proportions of total Obidos flow contributed by "white water" and "black water" tributaries. It is apparent that a minimum of one water sample per month collected over several years would be necessary to describe accurately the dissolved-solids load variation at Obidos.

The three determinations of mean concentration of suspended sediment in the Obidos cross section also show the need for many more samples to be taken during several years before one could calculate a mean annual concentration of suspended sediment. However, on the basis of reconnaissance results at Obidos, if the mean annual concentration were assumed to be 100 mg/l, one would arrive at a calculated mean daily suspended load at Obidos (using.... 157,000 cm) of about one-half that which Pinto computed for the mean daily load at mouth.

The dissolved oxygen content is close to saturation level at the observed stream temperature. Bathythermograph results showed no detectable variation of temperature in any of the verticals where observations were taken from surface to bed and return. The pH was

found to be as expected from the analyses reported by Sioli for the vicinity of Santarém.

ESTIMATED DISCHARGE AT MOUTH

The drainage area tributary to the Obidos location is about 5,000,000 sq km (square kilometers). The drainage area above the mouth is about 6,000,000 sq km, or an increase of about 20 percent over that for Obidos. If equal contribution of runoff existed for the basin above mouth, the mean annual discharge at mouth would be expected to be about 190,000 cm. However, there are several data that indicate the yield per unit drainage area from the approximately 1,000,000 sq km of drainage intervening between Obidos and the mouth to be less than that occurring above Obidos.

Only two large tributaries, the Tapajós and the Xingu, enter the Amazon downstream from Obidos. In August 1964, the gaging party measured the dry season discharge of the Tapajós at São Luís, location of the first rapids, about 300 km upstream from Santarém. The discharge was found to be 2,840 cm. A stage-discharge relation for the Tapajós gage at Fordlandia was drawn on the basis of the one discharge measurement, measured geometry of the high-

-flow cross section at São Luís, and a consideration of the apparent variation of water-surface slope with stage for the Tapajós location at São Luís. On the basis of available daily gage readings from the Fordlandia gage and the constructed stage-discharge relation, a mean annual discharge for the Rio Tapajós has been calculated as . . . 7,100 cm.

No measurement was made on the Xingu.

A low-water-season measurement made by the joint survey group on the Tocantins (not considered an Amazon tributary) at Marabá in October 1963 showed the discharge to be 1,500 cm. Using the cross-sectional area at Marabá that would be occupied by bankful discharge and an estimated mean velocity at bankful stage, the writer has calculated a bankful discharge of 33,000 cm. No stage records are available at Marabá. The mean discharge for the Tocantins was estimated, on the basis of the low-water measurement and the estimated bankful discharge, as 11,000 cm.

The Tocantins is not tributary to the Amazon (its basin has a common drainage boundary with the Amazon) but its estimated mean discharge and that of the Tapajós permit a "bracketing" of an estimated mean annual discharge for the Xingu. The sum of mean

annual discharges for Tapajós, Xingu, and minor tributaries between Obidos and the mouth is estimated to be 18,000 cm. On this basis, the partly estimated average annual discharge of the Amazon at mouth is 175,000 cm.

Estimates of the runoff from the intervening area between Obidos and the mouth based on the Thornthwaite potential evapotranspiration approach result in a discharge of about double that based on hydrometric data. The estimates based on hydrometric data are considered to be more reliable than those based on rainfall-runoff computations. The writer concludes that the most reliable value of average annual discharge for the Amazon at its mouth is 175,000 cm.

CONCLUSIONS

The results of the joint investigations show the previously published estimates of mean annual flow past Obidos to be much too low. The mean discharge computed on the basis of a stage-discharge relation developed from three complete discharge measurements and daily stage readings for the period 1928-46 is 157,000 cm. The great flood of 1953 which probably reached a state of 7.6 meters at Obidos is calculated to have discharged at 350,000 cm through the main channel with an indetermi-

nate quantity of overflow on the flood plain.

The observations of dissolved-solids suspended sediment and other water-quality parameters provide much more information on these aspects for the Obidos location than had been determined previously, but there is insufficient information to permit an accurate assessment of either the mean annual suspended load or the salt load discharge. The bed material samples and fathometer charts provide much insight into the nature of the streambed at Obidos.

The objective of the joint investigation to provide reconnaissance information on the flow and water quality of the Amazon was achieved. If more refined determinations of the average annual flow and water quality characteristics are needed, it will be necessary to conduct intensive investigations at Obidos and elsewhere in the basin. The maintenance of a river-stage gage at Obidos — above tidal effects during all but extremely low flow — would provide valuable information at small expense.

SUMMARY

Selected published estimates of the discharge of Amazon River in the vicinity of Obidos and the mouth are presented to show the great variance of available information. The most reasonable esti-

mates prepared by those who measured some parameters of the flow were studied by Maurice Parde, who concluded that the mean annual discharge is 90,000 to 100,000 cm (cubic meters per second). A few published estimates of discharge at mouth of 110,000 cm based on rainfall-runoff relationships developed for other humid regions of the world are available.

Three measurements of discharge made at the Óbidos narrows in 1963-64 by a joint Brasil-United States expedition at high, low, and medium river stage are referred to the datum used at the Obidos gage during the period of operation, 1928-46, and a relationship between stage and discharge prepared on the basis of the measurements and supplementary data and computations. Recovery of the original Obidos gage datum is verified by referring the 1963-64 concurrent river stages at Manaus, Obidos, and Taperinha to gage relation curves developed for Manaus-Obidos and Obidos-Taperinha for periods of concurrent operation, 1928-46 and 1931-46, respectively. Based on the stage-discharge relation and record of river stage for the period 1928-46 an average discharge of 157,000 cm is computed for the Obidos site.

The greatest known flood at Obidos, that of June 1953, is computed to have been a flow of

350,000 cm at stage of 7.6 meters in the main channel with an indeterminate amount of overflow which, under the best assumed overflow conditions, may have amounted to about 10 percent of the main channel flow. Overflow discharge at stage equivalent to mean annual discharge is judged of flow down the main channel.

Miscellaneous data collected during the flow measurements show that the tidal effect reaches upstream to Obidos at extremely low flows; the distribution of velocities in stream verticals is affected by large-scale turbulence; the standard procedure of basing mean velocity in vertical on the average of point velocities measured at 20 and 80 percent of the total depth is valid; and there is a low Manning roughness coefficient of 0.019 (English units).

Samples of suspended sediment taken with a point sampler at various depths in selected verticals show, for the Obidos site, a variation in concentration from 300 to 340 mg/l (milligram per liter) near the streambed to 50 to 70 mg/l in the upper portion of the verticals. Median diameter of bed material at Obidos averaged about 0.20 mm in a range of 0.15 to 0.25 mm. Analyses of water samples collected at Obidos in July and November 1963 and August 1964 are presented.

The reconnaissance measurements of 1963-64 provide a well-supported value of mean annual water discharge of Amazon River at Obidos and the mouth. Many more measurements of flow and water-quality characteristics are needed to obtain more exact values of discharge, suspended sediment, and salt loads.

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MOLUSCOS PLANORBÍDEOS DA AMAZONIA

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(Com uma figura no texto)

A fauna de planorbídeos da região amazônica é ainda muito mal conhecida, devido às naturais dificuldades de trabalho nessa vasta região e também ao escasso número de investigadores interessados nesse grupo zoológico. Considerando-se toda a área drenada pelo rio Amazonas e seus tributários, foram aí assinaladas até agora 11 espécies de planorbídeos, das quais 6 pertencem ao gênero *Biomphalaria* Preston, 1910, e 5 ao gênero *Drepanotrema* Fischer & Crosse, 1880.

1. *Biomphalaria straminea* (Dunker, 1848)

Esta é a espécie de *Biomphalaria* que tem sido encontrada em maior número de localidades e que ocupa a maior área de distribuição aparecendo na literatura amazônica sob as denominações de *Tropicorbis* (*Obstructio*) *paparyensis* (Baker, 1914), *Australorbis centi-*

metralis (Lutz, 1918) e *Armigerus* (*Tropicorbis*) *centimetralis* (Lutz, 1918). A sua sinonímia foi discutida por PARAENSE (1963). O reconhecimento da *B. straminea* na Amazônia deve-se principalmente a SIOLI (1953), que a coletou nas seguintes localidades: Estado do Amazonas: lago Calado, à margem norte do baixo Solimões, perto de Manacapuru; lagos Comprido e Matafome, no médio Madeira, perto de Três Casas; Estado do Pará: rio Cuminá, afluente da margem esquerda do Amazonas, perto de Óbidos; lago Salgado, à margem leste do rio Cuminá, cerca de 50 km ao norte de Oriximiná, na foz do Trombetas (fazenda Timbó); lago do Tracoá, à margem do rio Cuminá, em frente ao lago Salgado; lago do Tostão, à margem norte do rio Amazonas, entre Óbidos e Alenquer; lago Grande Ca-

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ruaí, em Caraubal, entre Parintins e Santarém; Santarém; Jacaré (Retiro Daniel de Carvalho), em frente a Aveiro; Pindobal, pôrto de Belterra; Fordlândia; lago Timbó, perto de Curi; rio Cupari, perto de sua foz e perto de Flechal; lagos Caxias e Curuçá, à margem direita do baixo Cupari; rio Aniperi, afluente da margem direita do rio São Manuel, perto de sua foz.

O material acima referido foi estudado por HAAS (1949 a, b, 1952), que o identificou ao *Tropicorbis (Obstructio) paparyensis*.

No Estado do Pará a *B. straminea* foi também assinalada em Belém (COSTA, 1952; PINTO & DESLANDES, 1953). No Estado do Acre foi coletada em Cruzeiro do Sul e Rio Branco (PARAENSE, não publicado). No Estado de Goiás foi encontrada em Arraias, à margem esquerda do rio do mesmo nome, afluente do rio da Palma que drena para o Tocantins através do rio Paranã (CUNHA NETO, comunicação pessoal).

Na localidade de Fordlândia, à margem direita do baixo Tapajós, a *B. straminea* transmite a esquistossomose mansonii no único foco até agora conhecido dessa parasitose na bacia amazônica, descoberto por MACHADO & MARTINS (1951). Estes autores examinaram 400 espécimes esmagados entre lâminas, com resultado negativo para *Schistosoma*. Resultados idênticos foram

obtidos por Maroja e por Sioli (MAROJA, 1953) e por mim, ao exame de 100, 900 e 5.000 espécimes, respectivamente. Experimentalmente obtive a infecção de 3 entre 28 espécimes expostos, cada um, a 10 miracídios de *S. mansonii* de Belo Horizonte.

A *B. straminea* ocorre na Venezuela, nas três Guianas, no Paraguai, no norte da Argentina e em todos os sistemas de drenagem do território brasileiro com exceção apenas da bacia do Uruguai, do lado oriental da bacia do Paraná e da área que drena para o Atlântico ao sul do paralelo 21°.

2. *Biomphalaria schrammi* (Crosse, 1864)

Na região amazônica esta espécie até agora foi encontrada apenas em Belém por mim próprio (PARAENSE, FAURAN & COURMES, 1964). Ela tem sido também assinalada nas Antilhas, na Guiana Francesa e no Brasil, onde tem o seu limite sul no Estado de São Paulo. Entre os seus sinônimos mais conhecidos contam-se *Planorbis janeirensis* Clessin, 1884 e *P. nigilabris* Lutz, 1918.

3. *Biomphalaria amazonica* Paraense, 1966

Esta espécie, que descrevi recentemente em material coletado pelo Instituto Nacional de Pesquisas da

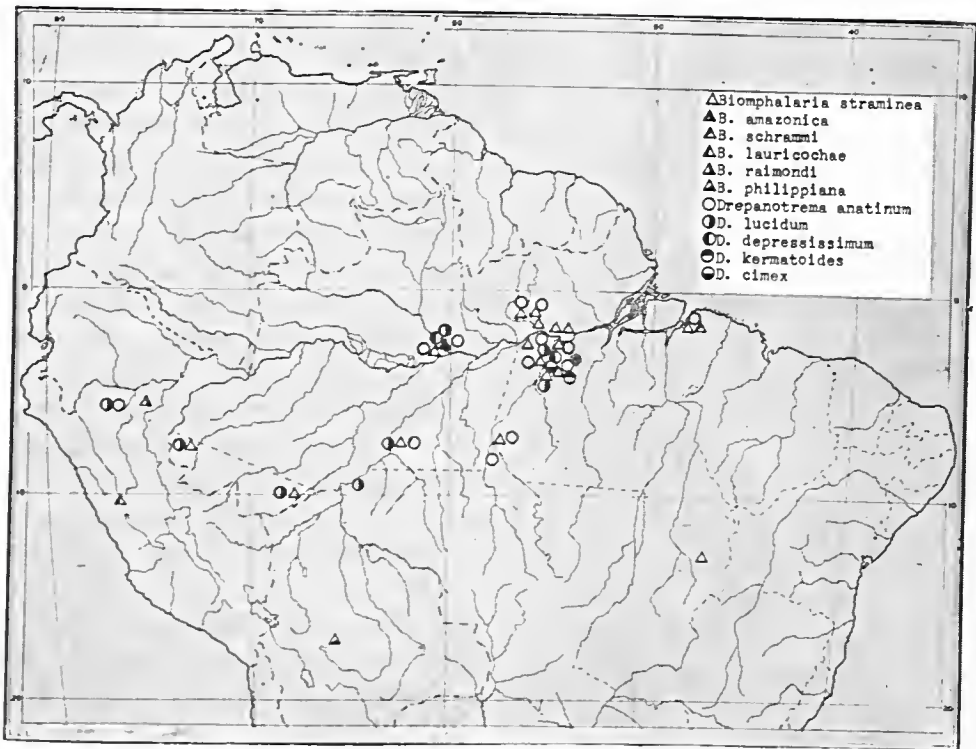


Fig. 1 — Distribuição aos planorbídeos até agora reconhecidos na região amazônica.

Amazônia, foi encontrada até agora apenas em Manaus e na ilha do Careiro, situada à margem direita do rio Amazonas, em frente à desembocadura do rio Negro. Seguramente deve ocorrer em outras localidades, o que será demonstrado por estudos futuros.

4. *Biomphalaria lauricochae* (Philippi, 1869)

Espécie do lago Lauricocha, nascente do rio Marañon, no Peru, foi descrita com base nos caracteres exclusivamente conquílio-

lógicos. São necessários estudos anatômicos para definição de sua verdadeira identidade. Segundo HARRY (1962), trata-se de provável sinônimo da *Biomphalaria andecola* (Orbigny, 1835) do lago Titicaca.

5. *Biomphalaria raimondi* (Philippi, 1869)

Este planorbídeo, como o anterior, também não está ainda bem definido. Foi coletado "em riachos das florestas da região do Peru chamada Pampa del Sacramento",

vasta porção da Amazônia peruana que se estende entre os rios Ucayali e Huallaga.

6. *Biomphalaria philippiana* (Dunker, 1848)

A descrição original desta espécie refere-se a material de Cochabamba, na Bolívia, situada nas origens de tributários dos rios Beni e Mamoré. Em 1953, o Dr. Ennio Luz coletou em Morretes (Estado do Paraná) espécimes de um planorbídeo que enviou a Lucena e que, a pedido deste (LUCENA, 1956: 92), foram determinados por BEQUAERT como *Tropicorbis philippianus* (Dunker, 1848). Mais tarde PARAENSE & DESLANDES (1958 b) estudaram exemplares pertencentes à mesma população de Morretes, tratando-os como *philippianus* por já ter sido este nome aplicado à referida população. De acordo com os dados de que disponho atualmente, este planorbídeo distribui-se pelos Estados do Paraná, Santa Catarina e Rio Grande do Sul, e manteve-se séria dúvida quanto a ser ele idêntico ao verdadeiro *philippianus* de Cochabamba. BARBOSA, BARBOSA & CARNEIRO (1958) estudaram, sob a denominação de *Tropicorbis philippianus*, um planorbídeo de Guayaquil (Equador) cuja anatomia é diferente da dos espécimes do sul do Brasil e assemelha-se à da *Biomphalaria peregrina* (Orbigny, 1835). Comparando conchas dos

espécimes estudados por PARAENSE & DESLANDES e por BARBOSA, BARBOSA & CARNEIRO com o material depositado no Museu Britânico, observou HUBENDICK (1962) que "o material tipo desta espécie no Museu Britânico é perfeitamente semelhante conchiliologicamente à concha figurada por PARAENSE & DESLANDES, 1958, a qual, entretanto, não é topotípica. O material determinado por MORRISON como *T. philippianus* e estudado por BARBOSA *et al.* 1958 obviamente não pertence à mesma espécie, mas é provavelmente idêntico ao *T. havanensis*."

Como se vê, a identidade da verdadeira *Biomphalaria philippiana*, a de Cochabamba, ainda precisa ser estudada pelos métodos modernos de investigação malacológica. Caso seja diferente da espécie do sul do Brasil, terá esta de receber outro nome.

7. *Drepanotrema anatinum* (Orbigny, 1835)

Foi coletado pela Expedição Stanford em um lago artificial em frente à Catedral de Belém (BAKER, 1914) e aparece nas Ests. 79 (Figuras 16-18) e 124 (Figs. 1-3) da monografia de BAKER (1945) com a indicação "Pará, Brazil", provavelmente referindo-se a Belém.

Em material coligido por SIOLI (1953) e identificado por HAAS

(1949 a, b, 1950, 1952) como *Gyraulus (Drepanotrema) anatinus*, aparece esta espécie nas seguintes localidades, quase tôdas comuns à *Biomphalaria straminea*: Estado do Amazonas: lago Calado, no baixo Solimões; lagos Comprido, Matafome e Paxiúba, no médio Madeira; Estado de Mato Grosso; rio Juruena, à margem direita; lago do Peri, no rio Juruena, perto da Barra do São Manuel; Estado do Pará: rio Cuminá, perto da fazenda Timbó; lago Salgado; rio Branco de Óbidos, na sua desembocadura no lago Mamuru; lago Grande Curuaí, em Caraubal; Santarém; Fordlândia; lago Curi; rio Cupari, perto de sua foz e perto de Flechal; lagos do Caxias e Curuçá, no baixo Cupari.

Entre o material enviado a êste Centro, para identificação, pelo Instituto Nacional de Pesquisas da Amazônia, tem sido reconhecido o *D. anatinum* em amostras de Manaus e da ilha do Careiro, Estado do Amazonas. A sua presença no Peru foi assinalada por BAKER (1945, Est. 124, Fig. 30), que apresenta a concha de um espécime de Yurimaguas (incorretamente grafada "Juminaguas"), localidade à margem esquerda do rio Huallaga, Departamento de Loreto.

O *D. anatinum* é encontrado, sob várias denominações, nas Antilhas, no México, na América Central e na América do Sul a leste dos Andes, chegando até a Argentina. A

oeste dos Andes encontrei-o no Equador.

8. *Drepanotrema lucidum* (Pfeiffer, 1839)

Foi coletado por SIOLI e identificado por HAAS (1949a, 1952), sob a denominação de *Gyraulus (Drepanotrema) schubarti* (Haas, 1938) na Fordlândia (Pará) e no lago Matafome, médio Madeira (Amazonas). SIOLI (1953) encontrou-o no lago Grande Curuaí, perto de Caraubal (Pará). Identifiquei-o em material da ilha do Careiro (Amazonas), de Cruzeiro do Sul e Rio Branco (Acre) e de Pôrto Velho (Rondônia).

No Peru foi assinalado por BAKER (1945, Est. 124, Figs. 29, 31, 32) em Yurimaguas, juntamente com o *D. anatinum*. O planorbídeo de Buena Vista, Santa Cruz (Bolívia), que aparece sob a denominação de *Drepanotrema paropseides* na Est. 124, Figs. 14-20, da monografia de BAKER (1945), parece pertencer realmente à espécie *D. lucidum*.

Esta espécie corresponde ao *D. melleum* (Lutz, 1918). Sua distribuição compreende a região das Antilhas e a América do Sul a leste dos Andes.

9. *Drepanotrema depressissimum* (Moricand, 1839)

Sob o nome de *Gyraulus (Drepanotrema) depressissimus*, foi iden-

tificado por HAAS (1949 a) no rio Cupari, perto de sua foz (Estado do Pará), em material coletado por SIOLI. No Estado do Amazonas tem sido encontrado na ilha do Careiro, perto de Manaus, em coletas do Instituto Nacional de Pesquisas da Amazônia, conforme identificação feita neste Centro.

O *D. depressissimum* foi assinado até agora nas Antilhas e no Brasil, distribuindo-se neste país desde o extremo norte até o Estado de São Paulo.

10. *Drepanotrema kermatoides* (Orbigny, 1835)

SIOLI coletou esta espécie no igarapé do Guaranazal, pequeno afluente do rio Cupari (Pará), que foi identificada como *Gyraulus (Drepanotrema) kermatoides* por HAAS (1949 b).

O *D. kermatoides* distribui-se pelo oeste do Brasil, através de Goiás e do oeste de Minas, na direção do Paraná, Santa Catarina e Rio Grande do Sul, estendendo-se para o Paraguai, Uruguai e Argentina. A oeste dos Andes ocorre no Peru e no Equador.

11. *Drepanotrema cimex* (Moricand, 1839)

Coletei esta espécie em Fordlândia (Pará). Sua distribuição compreende as Antilhas e, na América do Sul, comprovadamente o Brasil e o Uruguai.

A identificação da maioria das espécies acima referidas poderá ser feita sem dificuldade de acordo com as descrições conchiliológicas e anatômicas constantes dos trabalhos de PARAENSE & DESLANDES sobre *B. straminea = centimetralis* (1955), *D. anatinum* (1956 a), *D. lucidum = melleum* (1956 b), *D. depressissimum* (1957), *D. cimex* (1958 a), *B. philippiana* . . . (1958 b), *D. kermatoides* (1958 c), de PARAENSE, FAURAN & COURMES sobre *B. schrammi* (1964), e de PARAENSE sobre *B. amazônica* . . . (1966).

SUMÁRIO

Como contribuição ao inventário da biota amazônica, um dos principais objetivos deste Simpósio, são apresentados os dados existentes sobre a distribuição das espécies de planorbídeos da região Amazônica. Esta região é considerada aqui no seu sentido hidrográfico mais amplo, abrangendo toda a área drenada pelo rio Amazonas e seus tributários, mas não inclui as áreas convencionalmente consideradas como extensões da Amazônia, como por exemplo a zona Bragantina do Pará e a parte vizinha do Maranhão, onde ocorrem planorbídeos, inclusive transmissores da esquistossomose mansoni.

São as seguintes as espécies de planorbídeos assinaladas na Amazônia: *Biomphalaria straminea*

(Dunker, 1848), *B. schrammi* (Crosse, 1864), *B. amazonica* Paraense, 1966, *B. lauricochae* (Philippi, 1869), *B. raimondi* (Philippi, 1869), *B. philippiana* (Dunker, 1848), *Drepanotrema anatinum* (Orbigny, 1835), *D. lucidum* (Pfeiffer, 1839), *D. depressissimum* (Moricand, 1839), *D. kermatoides* (Orbigny, 1835) e *D. cimex* (Moricand, 1839).

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PRIMEIROS RESULTADOS DE PESQUISAS ETOLÓGICAS EM INVERTEBRADOS LÍMNICOS DA AMAZÔNIA

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Schlitz (Hessen), Alemanha

(Com 4 figuras no texto)

Em geral, distinguem-se vários grupos ecológicos-etológicos de larvas de Efemerópteros (NEEDHAM, TRAVER & HSU, 1935; *Wesenberg-Lund*, 1943), dos quais as larvas escavadoras provavelmente têm o comportamento mais diferenciado. Enquanto representantes do grupo dos "revolvedores" (sprawlers) (p. ex *Potamanthus*), que podem ser considerados como precursores das formas escavadoras, movimentam-se na lama fôfa em todos os sentidos sem deixar rastro nítido, as larvas escavadoras propriamente ditas produzem túneis irregulares no substrato, que se podem ramificar e que se desfazem pouco depois de serem construídos (*Ephemer*) (WESENBERG-LUND, 1943; SATTLER, no prelo), ou então os túneis não se ramificam, têm forma de U e são permanentes (*Polymitarcis*, *Tortopus*) (RÉAUMUR, . . . 1734/42; FRIC & VÁVRA, 1901).

As larvas escavadoras na literatura são geralmente indicadas sumariamente como devoradoras de lama e de minhocas (DESPAX, 1949). Isto, entretanto, não vale para a larva palaeotrópica *Povilla*, que mina em esponjas de água doce e em pau submerso. Ela reveste os túneis com uma secreção produzida pelos tubos de Malpighi e eliminada pelo ânus. Com movimentos respiratórios das brânquias a larva conduz uma corrente de água pelo túnel, da qual partículas comestíveis suspensas na água são filtradas. Isso acontece por meio de tufo de cerdas localizadas na cabeça e nas patas anteriores (HARTLAND-ROWE, 1953, 1958).

Pesquisas nas larvas neotropicais do gênero *Asthenopus* (SATTLER, no prelo), mostraram que, nelas, a evolução de devorador de lama para filtrador progrediu mais ainda. As larvas roem, com suas im-

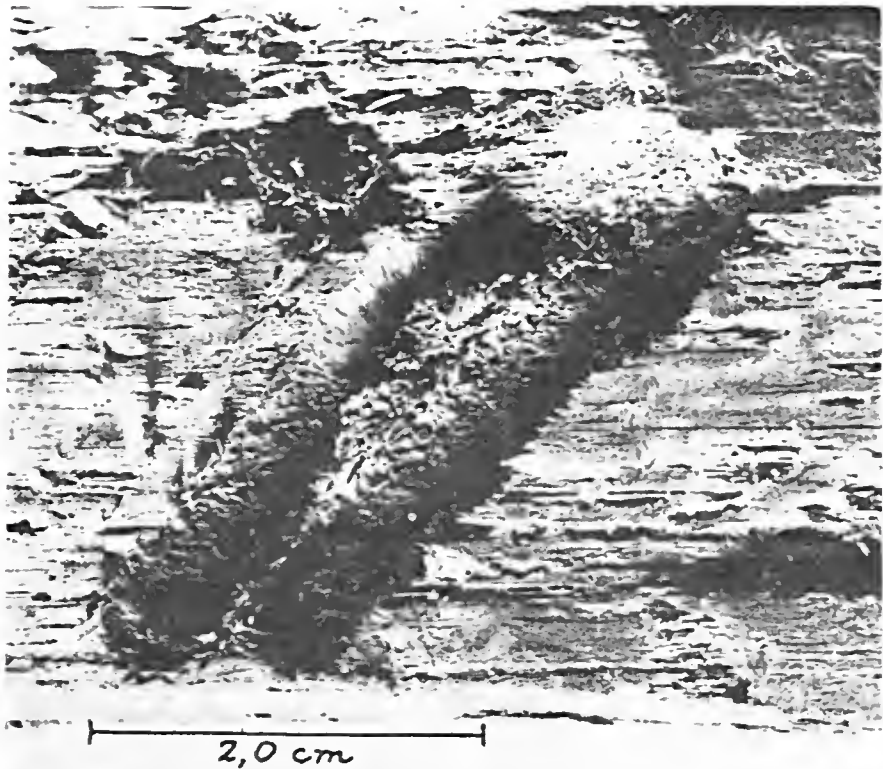


Fig. 1 — Túnel em forma de U, de *Asthenopus*, a parede divisória de lascas de madeira.

ponentes mandíbulas, a madeira submersa na água, construindo galerias cuja curva estreita em U provém da acumulação, entre os dois braços do U, de lascas roídas coladas com a secreção dos tubos de Malpighi (fig. 1). Trata-se, pois, de um verdadeiro trabalho construtivo e não só, como é costume, de uma escavação destrutiva do substrato. O aparelho filtrante consiste de longas cerdas em 8 tufo com forma de funil. Em cada lado do animal acham-se dois tufo na tí-

bia, um no fêmur da pata anterior e um na base do lado exterior da mandíbula (fig. 2). Todos os funis são dirigidos para frente contra a corrente de água respiratória e preenchem o diâmetro do túnel. Todas as cerdas dos funis possuem duas filas de finos pêlos, dirigidos para um só lado, e a distância entre um e outro mede ca. 4 μ . Com isso o efeito do aparelho filtrante torna-se bastante aumentado. A secreção produzida pela larva, não só cola as lascas da parede divisória,

mas reveste também as outras paredes da galeria, alisando-lhe irregularidades e evitando assim fendas entre as paredes e os tufo de cerdas, que possam perturbar a filtração.

A larva de *Asthenopus* pode, pois, por meio de sua atividade construtiva e com sua disposição morfológica com cerdas, ganhar minúsculas partículas comestíveis das águas geralmente cristalinas dos igarapés amazônicos, ficando ela mesma num abrigo seguro.

Com os mesmos princípios, porém de maneira completamente diferente, a larva do Tricóptero *Macronema*, que vive no mesmo bió-

topo, descobriu igual fonte de alimento. Esta larva também faz um abrigo, pelo qual a água, doadora de alimento, flui, e ela também dispõe de um aparelho filtrante. Cerdas especiais na cabeça e nas patas anteriores servem à alimentação.

Gêneros parentes afastados (*Holocentropus*, *Plectrocnemia*) somente constróem abrigos tubiformes e irregulares, feitos da secreção filiforme das glândulas labiais e ampliados em frente em forma de um funil para captura. Gêneros parentes mais próximos de *Macronema* (*Rhyacophylax*, *Hydropsyche*, *Diplectrona*) fazem tubos de

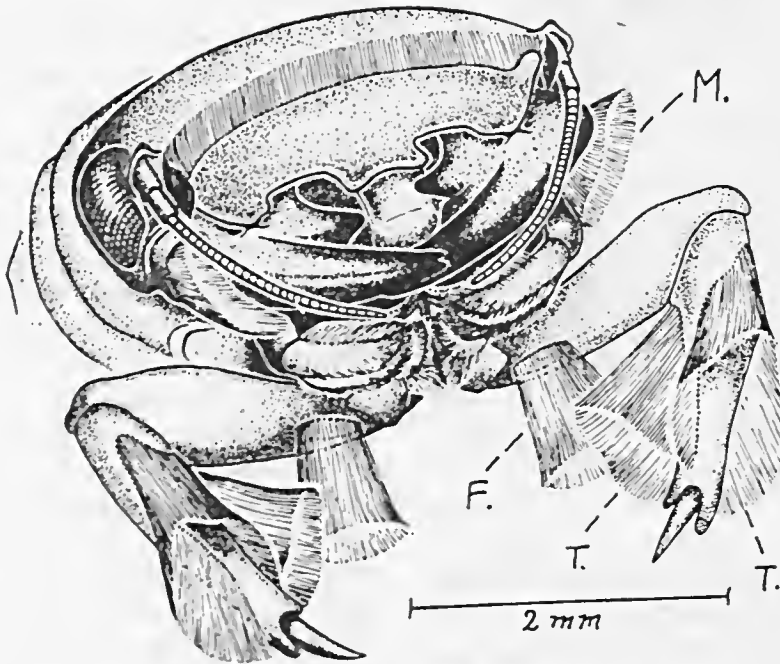


Fig. 2 — Larva de *Asthenopus*, vista diagonalmente de frente, mostrando o aparelho filtrante (F, T, M = tubos de cerdas, F = do fêmur, T = da tibia, M = da mandíbula).

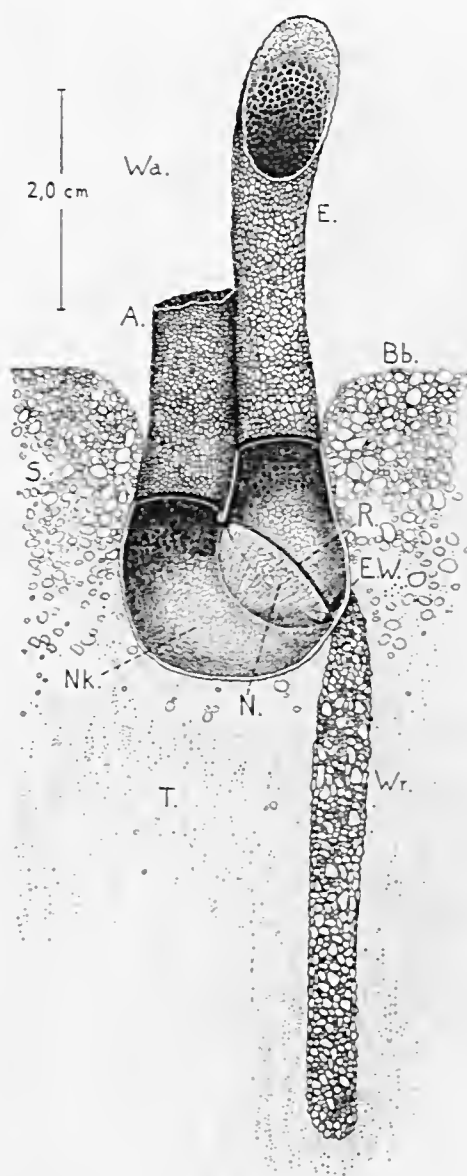


Fig. 3 — Abrigo da larva de *Macronema* (A. = chaminé de saída de água, Bb. = solo do igarapé, E. = chaminé de entrada, EW. = entrada do tubo de moradia, N. = teia, NK. = câmara para teia, R. = moldura da teia, S. = areia, T. = argila, Wa. = água, Wr. = tubo de moradia).

secreção e material heterogêneo, que têm em frente, em vez de funil, uma teia plana de malhas retangulares (ca. $300 \times 200 \mu$) muito regulares.

O tubo e a teia de *Macronema*, entretanto, evoluíram para uma das construções de animais mais complicadas, que conhecemos (SATTLER, 1963). Do simples tubo de *Rhyacophylax* etc. desenvolveu-se um sistema de quatro tubos (com chaminé para entrada, outro para saída da água, câmara para teia, tubo de moradia), cuja parte inferior está metida no solo do igarapé e que é colado com areia e secreção das glândulas salivares (fig. 3). As duas chaminés estão dispostas de tal maneira, que na embocadura de entrada age a pressão total P_z da água corrente do igarapé e na embocadura de saída age somente a pressão estática P_s . Da diferença das pressões $P_z - P_s$ resulta, que pelos tubos e pela teia estendida na sua câmara constantemente flui água (SATTLER & KRACHT, 1963). A teia é construída pelo mesmo princípio dos gêneros parentes; tem também malhas retangulares de uma extrema regularidade, que parecem ser feitas à máquina (fig. 4). Mas são tão minúsculas, que não menos do que 630 — 4.300 delas cabem numa malha de *Rhyacophylax*; medem ca. $2-4 \times 14-24 \mu$. Os poros deste aparelho filtrante têm, pois,

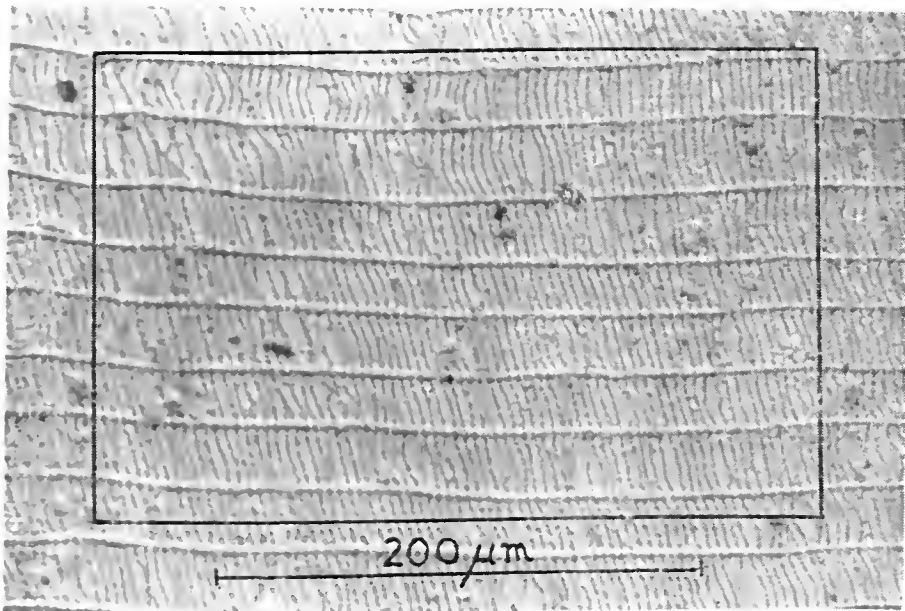


Fig. 4 — Parte da teia de *Macronema*, o retângulo marcado mostra em comparação o tamanho de uma malha da teia de *Rhyacophylax*

tamanho correspondente ao da larva de *Asthenopus*. Os tufos de cerdas na cabeça e nas patas anteriores de *Macronema*, que seus parentes não possuem, apesar de terem semelhança com as de *Asthenopus*, não servem à filtração mas para apanhar as partículas comestíveis da teia.

Para ter uma idéia do tripton orgânico (partículas de origem orgânica transportadas pela água corrente) levado das águas de igarapés amazônicos, foram tiradas amostras de água de um lugar, onde os dois tipos de larvas vivem um ao lado do outro, e passadas por um filtro membranoso de poros com $0,45 \mu$ (SATTLER, 1963). Disso resultou que 1 cm^3 desta

água só continha 4 partículas com diâmetro maior de 100μ , 208 partículas entre 100 e 30μ , mas 12.925 partículas entre 30 e 3μ . Estas partículas da última categoria, que não obstante o número relativamente grande delas, não turvam a água dos igarapés amazônicos, representam evidentemente a base de alimentação dos dois tipos de larvas.

Agradecimentos — As pesquisas foram realizadas, em parte, com auxílio do Conselho Nacional de Pesquisas, Rio de Janeiro, ao qual dirijo agradecimentos.

RESUMO

É estudado o comportamento construtivo e a alimentação de

duas larvas aquáticas de insetos, (*Asthenopus*, Ephemeroptera, e *Macronema*, Trichoptera). Os dois animais representam termos finais bastante diferenciados de duas progressões evolucionárias etológicas-morfológicas. A sua contemplação comparativa aqui efetuada tem sua justificação pela maneira, pela qual êstes animais com os mesmos princípios, mas com técnica bem diversa, acharam como fonte de alimento o "Nanno-Tripton" orgânico dos igarapés amazônicos.

SUMMARY

Building-behaviour and way of feeding of two aquatic insect-larvae (*Asthenopus*, Ephemeroptera, and *Macronema*, Trichoptera) are dealt with. Both are the strongly modified final members of two ethological-morphological lines of evolution. The comparative consideration of them, which is performed in this paper, is justified by the fact that both have made accessible the organic "nanno-tripton" of the forest-creeks in the Amazon-region as a food-source in principally equal ways but the quite different technics.

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ORIENTATION OF AMAZONIAN FISHES TO THE EQUATORIAL SUN

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(With 8 text-figures)

Some of the most challenging problems in modern biology are concerned with the orientation of animals in time and in space. A great deal of research of a merely descriptive nature is still needed in this field, but some experimental studies of the sensory mechanisms involved in orientation have yielded results as surprising as the discovery of time-compensated sun-compass orientation in the honeybee (FRISCH, 1950), in birds (KRAMER, 1950), and in fish (HASLER, HERRALL, WISBY & BRAEMER, 1958).

Many fish are known to undertake long distance migrations in the ocean and some even home to particular spawning sites. Examples are the many species of salmonids, the eel, and the tainha (*Mugil brasiliensis*). While in the salmon the olfactory sense appears to play an important role in detecting the home stream (WISBY & HASLER, 1954), and probably also

the spawning ground, olfactory orientation can not explain adequately the directed movements of fish in the ocean. Therefore, orientation by visual means was considered to be a likely hypothesis, and has been studied in field and laboratory experiments since 1955 at the Laboratory of Limnology, Wisconsin, under guidance of Prof. A. D. Hasler. Field experiments showed that white bass (*Roccus chrysops* Raf.) oriented towards the spawning ground significantly better when released under sunny conditions than under a cloudy sky. In addition, it was discovered that centrarchid fish, which were trained to swim into a compass direction, depended on the sun in maintaining this direction throughout the day and that they could allow for the sun's daily movement (HASLER *et al.*, 1958).

All earlier experiments about sun-orientation of vertebrate ani-

mals had been made in higher northern latitudes where the sun's apparent daily movement around the horizon (the sun's azimuth curve) is relatively uniform and where a uniform rate of changing the angle of orientation to the sun's azimuth (at 15 degrees per hour) would allow the animal to remain oriented into one compass direction. Moreover, in contradiction to an early theory about bird navigation which emphasized the importance of the sun's changing altitude (MATTHEWS, 1955), several experimental results seemed to disprove an effect of the sun's height on the orientation of birds (HOFFMANN, 1954; RAWSON & RAWSON, 1955; KRAMER, 1955; SCHMIDT-KOENIG, 1961), and it became customary to speak about "sun-azimuth-orientation". This simplified concept of orientation to the sun's azimuth had to be re-examined after experiments by BRAEMER (1959, 1960), and after results with cichlids from the Amazon at the equator (HASLER & SCHWASSMANN, 1960).

To illustrate one of the major problems for sun-orientation in the tropics, Fig. 1 shows the sun's movement from sunrise to sunset at a place in the northern hemisphere (50°N) and at the equator when the sun's declination is 10°S (22 March and 19 October). The hourly intervals in the azimuth

curve of the sun are rather uniform at 50° N, but they are quite different at the equator where there is little change in the sun's azimuth during morning and evening and a more than 100° change during the two hours around noon. If a sun-compass animal compensated for the sun's azimuth movement at a uniform rate of approximately 15°/hour, it could not be oriented into a compass direction at the equator. In addition, the direction of the sun's azimuth movement reverses itself twice during the year in the tropics. Near the equator, it changes from clockwise in late March to counterclockwise, and becomes again clockwise in late September. Sun-compass animals which live in the tropics must be able to allow for the sun's movement in the two different directions at different times of the year.

Subsequent experiments with fish demonstrated that the sun's altitude was of importance and that it influenced the change of the conditioned angle to the sun's azimuth (BRAEMER & SCHWASSMANN, 1963; SCHWASSMANN & HASLER, 1964), confirming and extending the earlier results by BRAEMER (1959). It could also be shown how the rate of change of the sun's altitude determined the rate of change of the trained horizontal orientation angle in young



centrarchid fish at first exposure to the sun (SCHWASSMANN & HASLER, 1964). The duration of daylight which changes considerably throughout the year at higher latitudes was found to influence the rate of change of the trained angle to the sun in centrarchid fish (SCHWASSMANN & BRAEMER, 1961). This factor can be of no importance near the equator because the day length here is a constant twelve hours all year.

Sun-compass behavior in fish depends on a circadian clock mechanism, continuously synchronized with the natural day by sunrise and sunset which can be replaced in experiments by the onset and termination of artificial light. Shifting the "on" and "off" times in the light cycle results in a pre-

dictable shift of the compass direction to which the fish had been trained (BRAEMER, 1959). In constant artificial light, the orientation rhythm was found to continue, but the period length was now slightly different from 24 hours (SCHWASSMANN, 1960).

The present paper describes experiments on sun-compass orientation of fish from the Amazon region which illustrate and partially answer some of the problems in the tropics.

METHODS

The apparatus for training and testing fish in a metal tank of 1.60 meter diameter with slanted walls which is filled with water and which prevents the fish inside from seeing any landmarks on the hori-

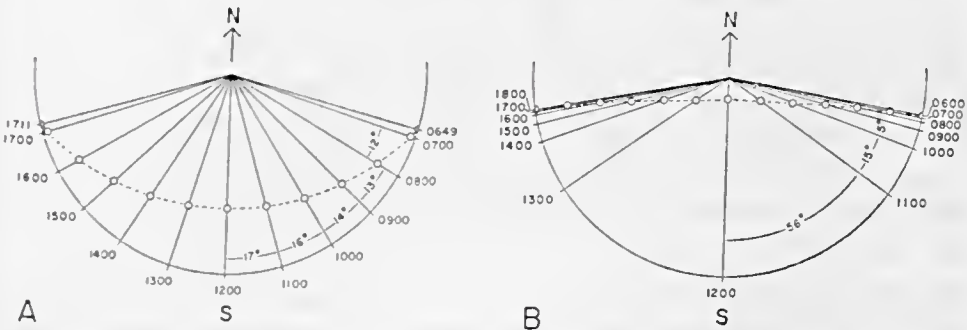


Fig. 1 — Hourly positional changes of the sun at 10° S declination for a latitude of 50° N in A, and at the equator in B. An observer, stationed in the center of the half-circles would see the zenith (center of the sky) directly above and the horizon represented as the periphery. The sun moves across the sky at a constant speed of 15° /hour. At a low inclination of the sun's arc (A), the azimuthal position of the sun changes at a fairly uniform rate. At the same time of year, the rate of change of the sun's horizontal projectory (azimuth) is highly alinear at the equator (B) because of the high inclination of the sun's arc.

zon (Fig. 2). Sixteen metal boxes are arranged in a circle inside the tank, their openings pointing outwards. They are covered by a circular plate and cannot be seen by the fish upon release from the center where it is held captive in a cylinder of transparent plastic. Releasing the fish is done remotely by a lever underneath which causes the plastic center cage to recess into the well. Observation of the fish is accomplished by two observers through four concentrically mounted periscopes. In order to prevent orientation to marks within the tank, the latter is rotated between trials. For training, only one of the sixteen boxes is open and always points into the same compass direction. Training is repeated daily at the same time for usually 10 to 20 minutes, until the fish has apparently learned, to relate the position of the one open box, in which it can hide, with the sun's position at this time of day. During later testing all sixteen boxes are open and tests are conducted at different times of the day. Every test consists of at least five trials and the observers record the exact place at which the fish swims over the margin of the cover plate before entering a box. Some experiments at Belém were made utilizing a large mirror to reflect the sun into the tank, whereas the real sun was blocked

from the view of the fish by a large sunshade (Fig. 2).

The fish species used were the following cichlids: *Cichla auratus* s. Heckel, *Crenicichla saxatilis* L., *Varu amphiacanthoides* Heckel, and *Aequidens portalegrensis* Hensel. In addition, experiments are reported with *Anableps microlepis* Mueller & Troschel, and the North American centrarchid *Lepomis cyanellus* Rafinesque. All fish were immature and between five and eight centimeters long.

RESULTS

1) *Orientation to the equatorial sun* — Once a fish has been trained for a few weeks to swim at a certain angle to the sun, and always during the same ten minutes every morning, it is then tested at different times of day. Two different modes in the behavior have been found. The great majority of trained fish will swim into the same compass direction. Because of the daily movement of the sun, these fish alter the angle of swimming in relation to the sun's azimuth position continuously. This behavior is called time-compensated sun-compass orientation. Sometimes a fish will swim at the same angle to the sun, to which it had been trained, also at other times of the day; it will not allow for the sun's movement with time. Such "azimuth constancy" is rare

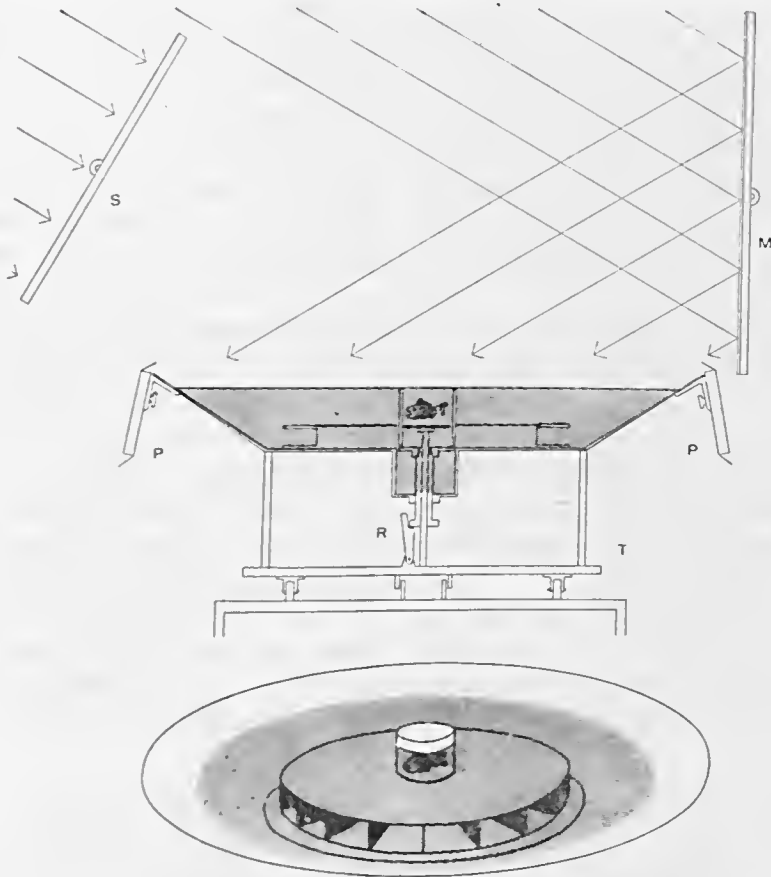


Fig. 2 — Training and testing apparatus shown in testing condition. The fish is held captive inside the plastic cage in the center of the water-filled tank. The release mechanism (R) causes the center cage to recede into the well, liberating the fish which can swim into any direction and will seek cover in one of sixteen open boxes. Two of four periscopes (P) for observation are shown. The turntable with the tank is rotated after every trial. For some experiments the sun was blocked by a shade (S) and reflected into the tank by a mirror (M).

under the real sun, but is usually found when the real sun is replaced by an electric light bulb.

For the first behavior, the commonly observed sun-compass orientation, it remains to be shown that the fish actually utilize the

position of the sun only, and that their compass constancy is not caused by some other factor unknown to us. In order to demonstrate if the sun was the important external reference, a large mirror was used in 1962 at Belém. As a re-

sult, the orientation of all the cichlids used in these experiments was 180° reversed (Fig. 3). The angle between mean direction of the scores and the real sun in A is the same as the one between mean direction and reflected sun in B. The mirror worked so effectively that it was employed to test the influence of the sun's altitude on the orientation of these fish. Changing the apparent altitude of the sun could easily be accomplished by tilting the mirror in its horizontal axis. The results have been reported in detail elsewhere (BRAEMER & SCHWASSMANN, 1963).

Having established the sun's position as the effective external reference in the orientation behavior of the fish, justifies recording of

individual test scores as angles to the right or left of the sun and the data can be presented in this manner with the sun's position kept stationary and indicated as a straight line (Figs. 4, 6, 7). A compass direction is represented in these graphs as a curved line which is computed from the sun's azimuth curve during the time of the experiments. If a fish would swim accurately into this compass direction, its scores should follow this latter curve.

Usually, the orientation of one trained fish is not very accurate; the mean direction of a test often deviates from the compass direction and the scatter around the mean is great. However, when a great number of scores from tests

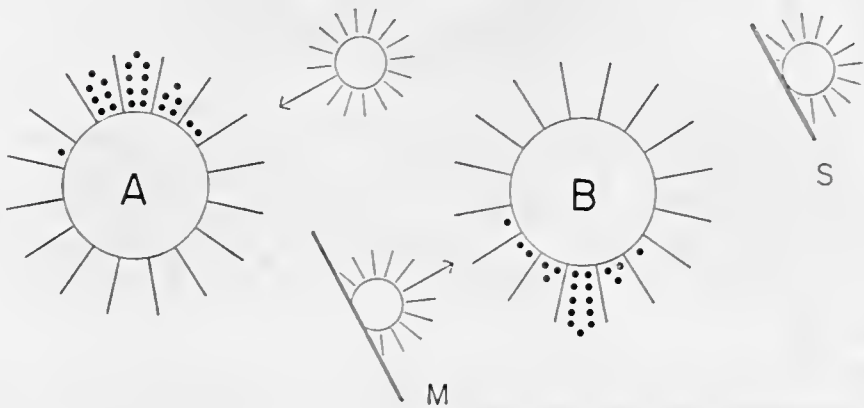


Fig. 3 — A mirror experiment. A: directional scores of five cichlids under the real sun. B: scores under the reflected sun. Immediately after the tests in A, the view of the sun was blocked by a shade (S) but the sun was reflected by the mirror (M) into the tank. All fish swim at approximately the same angle to the mirror image of the sun in B, as they swam to the real sun in A, but reversed in compass direction by 180° . The experiment demonstrates that the sun is the only external reference point in the orientation of these fish. Data by Braemer & Schwassmann (1963)

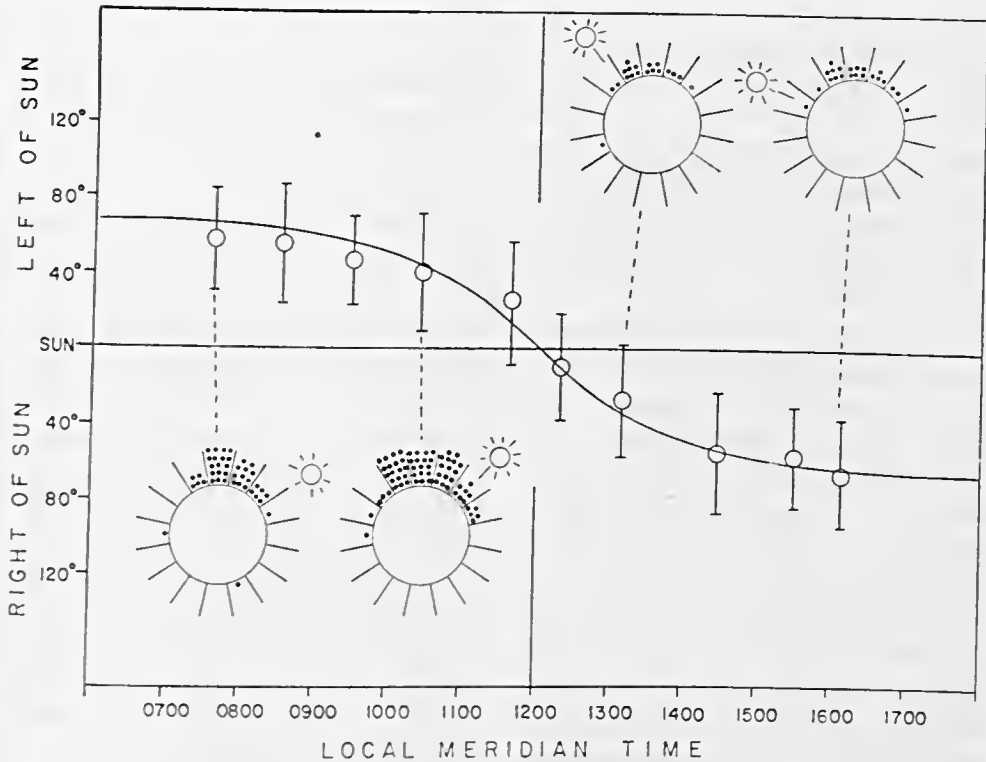


Fig. 4 — Sun-compass orientation of six cichlid fish at the equator during June and early July 1962. The daily pattern of angular change over the entire day to the sun's azimuth can be seen. All scores of the six fish falling into each hourly interval were averaged, and the mean was plotted (circles), with its standard deviation (vertical bars), as angle to the right or left of the sun's azimuth position (straight horizontal line). The procedure is exemplified for four of the ten means (scatter diagrams showing all scores and the sun's position at this time). The curved line indicates how a compass direction changes in relation to the sun's azimuth with time of day. If the fish allowed precisely for the sun's azimuth movement, their recorded means should follow this line
 Data computed from 402 scores. From experiments
 by Braemer and Schwassmann (1963).

of several fish is averaged, the combined results show a good fit to the theoretical curve. This is shown in Fig. 4 where a total of 402 scores of six cichlid fish was used. These fish were tested throughout the day from 31.5. to 7-7-1962 at Belém. All test scores falling into

each hourly interval were pooled and the common mean with its standard deviation is indicated. The rate of angular change to the sun is small during morning and evening hours but is great during the two hours around noon. Similar data have been presented by

SCHWASSMANN & HASLER (1964). Very few experiments have been done at the equator during the time of the equinoxes when the sun's noon position approaches the zenith (HASLER & SCHWASSMANN, 1960); and it was found that the fish did not orient as well under a very high sun.

2) *Innate and learned behavior in the sun-compass of fish* — Another experiment in collaboration with BRAEMER in Wisconsin during 1958 yielded results of far-reaching significance (BRAEMER, BRAEMER & SCHWASSMANN in prep.). Green sunfish and Portcichlids were reared from the egg in artificial light for several months until they had reached a size suitable for experiments on sun-orientation. These fish never experienced any natural daylight, but their regime of artificial lighting was continually adjusted to the changing times of sunrise and sunset at 43° N. During early September, the fish were trained at local noon in a darkened room to swim towards an electric light bulb, simulating the sun. They were tested subsequently out-of-doors under the sun in the morning and afternoon. In these tests, they compensated for the movement of the sun correctly according to season and latitude, although they had never seen the sun, or its apparent daily movement, previously (Fig. 5).

All green sunfish swam south which corresponds to the sun's position at noon, the time of previous training towards the light (Fig. 5, A₁-A₂). The behavior of the equally treated cichlids was different from that of the North American sunfish. At least the diagram B₁ shows a bimodal distribution. A few scores point towards the sun, indicating that the fish had not changed the trained angle. A concentration of scores in the southern sector corresponds to the behavior of the sunfish. In addition, many scores fall into the northern sector. A bimodality seems also indicated in diagram B₂ from the afternoon test but the two modes are not clearly separated, possibly obscured by some "constant-sun-angle" scores towards the sun.

The orientation behavior of the cichlids can be analyzed in the following way: In the northern temperate zone, the sun moves in a clockwise direction through the southern part of the sky, its position at noon is South. Sun-compass fish, like the *Lepomis*, compensate for this movement by changing the angle of swimming to the sun in a counter-clockwise manner. In the southern hemisphere, the direction of the sun's movement, as well as that of the compensating angular change of compass fish to the sun, are the reverse. If the movement of the sun were to be com-

compensated for in the "wrong" direction, if sun motion and the fish's compensating angular chan-

ge had the same sign, the change in orientation angle of the fish would be added to, instead of sub-

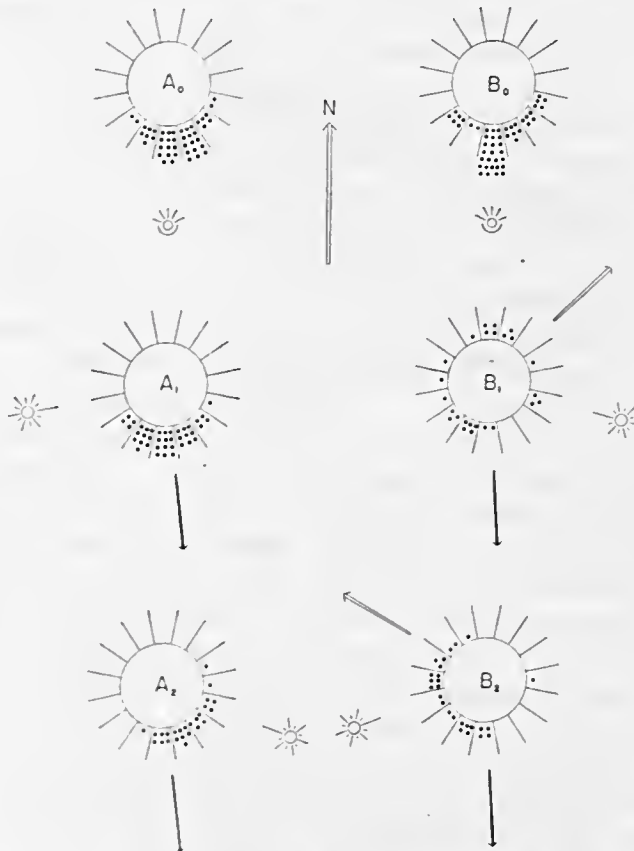


Fig. 5 — Demonstration of the innateness of sun-compass behavior. The orientation behavior of six North-American sunfish is shown on the left (scatter diagrams $A_0 - A_2$) and contrasted with the behavior of six equally treated tropical cichlids on the right ($B_0 - B_2$). A_0, B_0 : scores at the training time under the electric light; A_1, B_1 : orientation scores at first exposure to the sun, afternoon and morning respectively; A_2, B_2 : second tests under the sun, morning and afternoon respectively. The mean directions from the control tests under the electric light are indicated as solid arrows in the four lower diagrams. In B_1 and B_2 the direction to be expected for a compensation of the sun's movement in the "wrong" direction is marked by the open arrow. Data from experiments by Braemer and Schwassmann.

tracted from, the amount which the sun had moved around the horizon in azimuth. In this case, the compass direction which the fish indicates would be continually changing. The cichlids apparently also compensate for the movement of the sun, otherwise all scores should point towards the sun, but they change the orientation angle to the sun in both directions, clockwise as well as counter-clockwise. The compass directions, are indicated in B_1 and B_2 , and the results seem to conform to the hypothesis outlined above.

The results are evidence that sun-compass orientation in fish is basically an inherited behavior pattern, requiring no learning of the sun's movement. In addition, the apparent necessity for tropical cichlids to learn in which direction the sun is moving seems of biological significance. Later experiments have confirmed the innateness of sun-compass behavior in the green sunfish (SCHWASSMANN & HASLER, 1964). Experiments which illustrate the "two-direction ability" of cichlids are reported in the following pages.

The ability of cichlid fish from the Amazon to learn to accommodate their orientation behavior to a reversed sun movement was demonstrated by transporting them, after training and testing at Belém, to Madison, Wisconsin (43° N) during

1961. The orientation of two fish at Belém in late May is shown in Fig. 6 A, where the sun's movement was counter-clockwise and the fish's angular change occurred in a clockwise manner. In early June the two fish were tested at 43° N (Fig. 6, B) where they continued to change their angle to the sun as they did at the equator previously. After five days exposure to the sun out-of-doors, and one 15 minute period of re-training in the morning to an electric light indoors, one of the two fish appeared to have learned and accommodated for the locally correct direction of the sun's movement (Fig. 6, C). The other fish lost its oriented behavior during the five days of outdoor exposure and a brief re-training was ineffective. Confirmation of these results was obtained by data from two more cichlids which had been brought from Belém to 43° N where they were trained to swim towards an electric light at noon. In the first tests under the real sun of 43° N they scored like the two cichlids in Fig. 6, B, but after two weeks of partial exposure to the local sun one had completely reversed the direction whereas the other now seemed undecided and showed scores according to the two different modes of compensating angular change, similar to the inexperienced cichlids in Fig. 5, B. These and further data

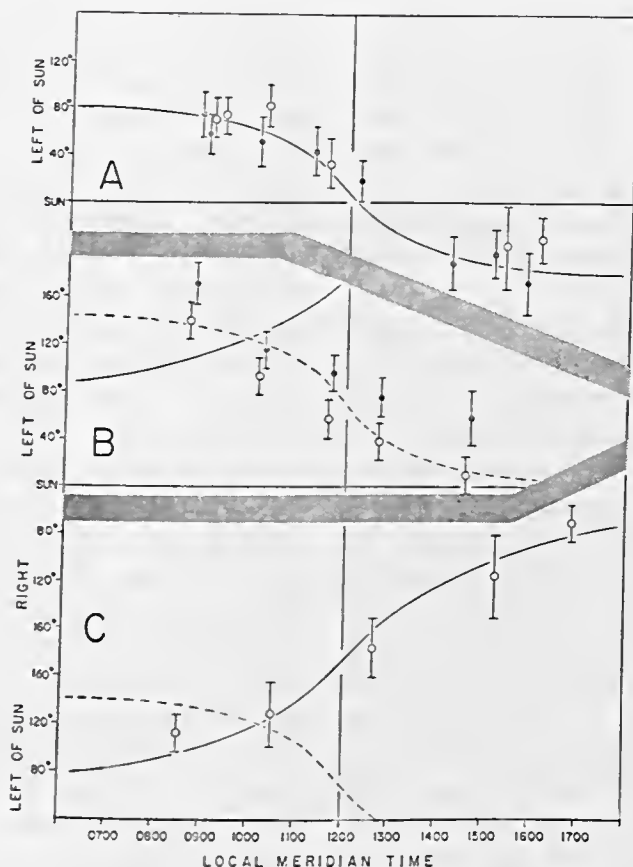


Fig. 6 — Data which demonstrate the ability of cichlids to accommodate their compass orientation to a sun movement in the reverse direction. The mean directions with standard deviations are plotted as in Fig. 4 (filled and open circles for the two different fish) and each was computed from a minimum of five scores. A: pattern of angular change to the counter-clockwise movement of the sun at Belém in May 1961. B: the orientation of the same fish after transport to 43° N in early June under a clockwise sun movement. C: the pattern of angular change to the clockwise moving sun is "locally correct" in one of the two fish after five days exposure to the sun. The solid curve indicates a compass direction under the local sun movement, the dashed curves in B and C indicate the pattern of angular change to the sun at Belém.

were reported earlier (SCHWASSMANN, 1962). The experiments reported above were made at a time when the sun's altitude curves

were quite similar at both locations; at least the noon position of the sun was of the same height. Since the day at 43° N was considerably longer than 12 hours, the fish were kept in an artificial light cycle with 12 hours, light, except for the day of exposure to the local sun.

To test the two-direction concept in the sun-orientation of cichlids further, and to compare it with the apparently hereditarily fixed single direction of compensation in centrarchids, experiments were designed which enabled training of fish to a sun apparently moving in the opposite direction. The experiment did not require transporting the fish over long distances and also left the daily sun arc unaltered except for the reversal of direction. This was accomplished by mounting a tank on a turn-table which had fastened to its underside an excentrically mounted ring gear. This gear was driven by a constant speed motor with reduction box and final pinion which, as a unit, remained stationary in azimuth but was sliding in and out radially because of the ring-gears excentricity. The resulting rotation was in the same direction as the sun's movement, but at exactly twice its azimuth velocity (Fig. 7, B). Sufficient reference marks inside the turning tank, in addition to the usual single training box,

were provided so that the fish inside had opportunity to relate their successive positions with the sun. Fig. 7, A shows the orientation of two *Cichlaorus severus* cichlids which were brought from Belém to Madison, Wisconsin. They had been kept in natural daylight and were trained during early September 1962 to swim towards the sun between 0700 and 0800 hours. They compensated locally correct for the sun's movement (Fig. 7, A, 1-2). After five sunny (and more cloudy) days inside the azimuth-reversal apparatus, they were tested again and had now reversed the direction in which they changed the orientation angle to the sun (Fig 7, A, 1-3). They allowed for the sun's movement as it was at this time of year (autumnal equinox) at the same latitude in the southern hemisphere.

3) *Sun-compass orientation of fish in nature* — Few experiments with fish have been made which investigated if sun - orientation might be involved in movements to a spawning ground, or towards "home", after experimental displacement, during a certain phase of active migration. Simple displacement and release at a distant place might not always yield conclusive data, since additional factors could provide orientational cues, like odors, landmarks, etc. Better directed orientation under a sunny

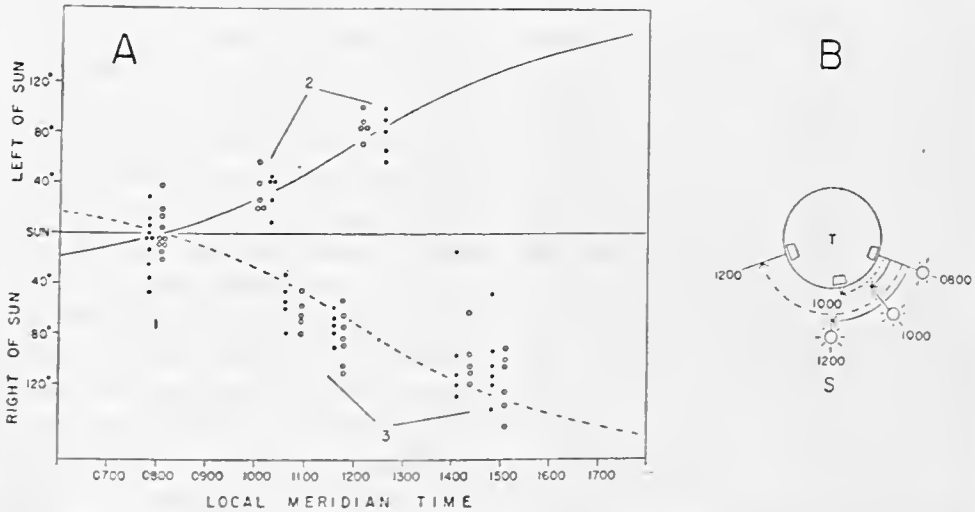


Fig. 7 — Experimental reversal of the direction of the sun's movement at 43° N latitude. The principle of the azimuth-reversal apparatus is shown schematically in B. At 0800 hours the open training box inside the tank (T) is in line with the sun's azimuth. At 1000 and at 1200 hours, since the tank has been rotated at twice the sun's azimuth velocity, the open box has traveled twice as much as the azimuth of the sun, simulating a sun movement in the opposite direction. In A is shown the orientation behavior of two cichlids from the Amazon, after training at 0800 hours (tests 1). They changed the orientation angle correctly for the clockwise sun movement (1. to 2.). After five sunny days of treatment in the azimuth-reversal apparatus, they had reversed the direction of angular change to the sun and allowed for a movement of the sun as it was correct for the southern hemisphere (1. to 3.).

sky than under cloudy conditions is an indication for the sun's importance in guiding the fish (HASLER et. al., 1958; WINN, SALMON, & ROBERTS, 1964). If the direction of "homing" after release is shifted by the amount predicted by a phase-shift of the fish's time sense (conditioning the fish in a delayed or advanced artificial light cycle for several days), sun-orientation can be assumed to be the orienting mechanism (WINN et. al., 1964). If the fish are sufficiently small, they can be tested in a circular

tank where possible environmental cues other than the sun seem to be eliminated. GROOT (1965) used this method to investigate the orientation of sockeye smolt during their seaward migration and the data indicate that the sun plays at least a certain role in the orientation of these salmonids.

Experiments in the field with fish, of which some natural tendency to swim in a certain compass direction is known, are promising. They have the great advantage that no directional training is ne-

cessary. One experiment of this kind was done in 1964 at Salinas, Pará, with *Anableps microlepis*. Previous studies on a large population of these fish near Salinas had shown that they form schools, the size and compactness of which depends on the age and sex of the fish. Adult females were observed in loose groups of from two to ten, the smaller males and younger females in groups of five to twenty. These schools of large and medium sized *Anableps* swam along the beach in open water and in bays and river outlets. They were never found in very deep water but stayed close to shore. Most striking was their change in behavior during the later part of every rising tide, day or night, when these fish literally stranded themselves on the beach with every incoming wave, often being left on the sand by the receding water. A similar behavior of moving close to shore with every rising tide was thought to be correlated with increased feeding activity, since many shore insects are trapped by the rising water. Studies of the Salinas population demonstrated an obvious purpose of the cyclic behavior. During March of 1962, at the time of the high tides of the equinoctial syzygies, many hundreds of the fish entered in this manner through an 80 meter long channel

into a large brackish water lagoon. With every rising tide, day or night, the fish concentrated in large numbers at the channel entrance. At about the time of highest water level, the fish reversed this movement and had left the lagoon before the channel had become dry. Inside the lagoon, many large schools of often more than a hundred newly born and up to seven centimeter long *Anableps* were found. The small fish did not leave the lagoon until a considerably later date. The lagoon obviously served as breeding ground for this *Anableps* population. Later observations were made during April 1964, when the tidal change in water level was insufficient to flood the channel leading into the lagoon. Now only a few *Anableps*, seven to ten centimeters long, were found inside, but all the larger fish outside still showed the same behavior of concentrating at the channel mouth with every rising tide.

These fish seemed ideally suited for sun-orientation tests because of their strong directional tendency and also because of the known outstanding performance of their visual system, especially of the aerial portion of the "amphibious" eye (SCHWASSMANN & KRUGER, 1965). The orientation tank was placed on a high sand dune near the lagoon so that the horizon was

occluded by the rim of the tank. Since large *Anableps* could not be accommodated in the apparatus, five immature fish, eight to ten centimeters in length, were captured out of a larger school which displayed consistently strong swimming in an E-N-E direction. This was the generally observed tendency of the entire population corresponding to the direction of channel and lagoon. Time of capture was the 26-4-1964, 1730 hours, during rising tide which had begun around 1400 hours. After overnight storage in individual covered containers, the fish were tested the following morning shortly before high tide level, and again in the late afternoon during the early part of the next rising tide. Bad weather prevented further testing and there was from 50 to 70% cloudcover during the tests. In these trials all fish showed a strong preference for the E — and N-E sector (Fig. 8, A, B). Three of these fish could be tried again after

sunset and under complete cloud-cover with beginning heavy rain before it became completely dark. They now displayed random scattering in their orientation, although it was still the time of rising tide (Fig. 8, C). Equally disoriented behavior was noted in three small *Anableps* from a different population inside a nearby bay which were captured during falling tide and tested immediately.

The results show that *Anableps* can utilize the sun's position as directional reference when other means of orientation are excluded, and that they are capable of time-compensated sun-compass behavior. When the sun was in the East in the morning, they swam towards it, whereas they swam away from it in the late afternoon, thus maintaining one compass direction. No orientation seemed possible without the presence of the sun in the artificial environment of the testing apparatus.

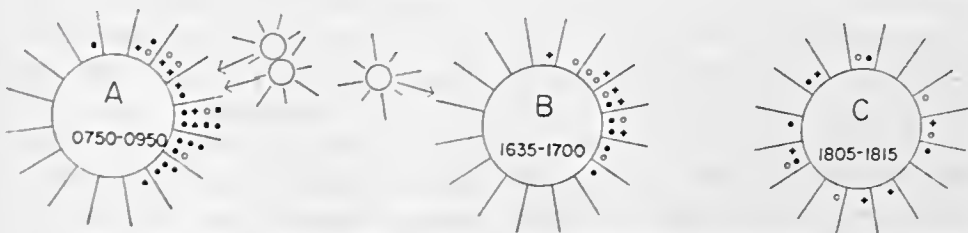


Fig. 8 — Sun-orientation of five *Anableps* at the equator. A: Scores during the morning, B: scores in the late afternoon, both tests under 50-70% cloudcover. C: apparent random behavior after sunset and in heavy rain. The sun's position is indicated in A and B; North is up. Each fish is indicated by a different symbol.

DISCUSSION

The fish species used in the experiments are mostly non-migratory and usually inhabit small bodies of water; they were chosen because of the easiness with which they could be maintained in captivity and trained to compass directions. That all the investigated species were found to be capable of time-compensated sun-orientation, together with the evidence about the innate nature of the basic pattern to alter the angle of swimming to the sun with time of day, makes it appear likely that sun-orientation plays an important role in the directional movements of fish in nature. Of further significance should be the considerable accuracy of this compass orientation which is noted when many data of several fish are averaged, as compared to the performance of an individual fish. Most species that undertake long distance migrations are schooling and usually migrate together in large numbers.

Major difficulties were envisaged in sun-orientation for animals living in the tropics, where not only the sun's movement occurs along a very steep arc but where also the direction of movement reverses itself twice during the year. It could be demonstrated that South American cichlids can compensate for the sun's movement in either di-

rection, and that they are able to learn to accommodate for a sun movement in the opposite direction within a few days.

Sun-compass orientation in fish is the expression of an endogenous circadian rhythm. The poor accuracy, usually apparent in the recorded directional performance of trained fish, is certainly not a true measure of the precision of the involved time sense. Another species of fish from the Amazon, the gymnotid *Gymnorhamphichthys hypostomus* Ellis, exhibits a high degree of precision of its endogenous rhythm when a different parameter, the daily onset of activity, is used for its measurement (LISSMANN & SCHWASSMANN, 1965).

It is not known how important the sun-compass might be for the orientation of fish in nature. Its usefulness seems to be limited to times of day with sunshine. Certainly, other means of orientation must also be important, since many fish migrate in an apparently oriented manner also at night. That the sun can become an important reference for orientation when other directional cues are excluded, was shown by the experiments with *Anableps*. The behavior of *Anableps* is of additional interest, because it not only resembles the peculiar spawning behavior of the California grunion (*Leuresthes tenuis* Ayres), but the

urge to return to the original place of birth (at least in the observed population) is reminiscent of the homing behavior of salmon. It might well be possible that similar principles of early imprinting and orientation are involved.

Acknowledgements — Most of the experiments reported here were part of the author's thesis work on sun-orientation of fishes, conducted under the guidance of Prof. A. D. Hasler at the Laboratory of Limnology, University of Wisconsin, and supported by the National Science Foundation (G-3339) and the Office of Naval Research (NR-301-903). The orientation studies on *Anableps* were made while the author was a post-doctoral fellow of the Public Health Service and affiliated with the Department of Anatomy, University of California, Los Angeles. Research support was obtained from the Office of Naval Research (NR-301-790) and the National Science Foundation (GB-2796). The Museu Goeldi, Belém, provided necessary facilities and services for the experiments near the equator. The azimuth-reversal apparatus was built by Mr. E. Hanson of the Department of Zoology, University of Wisconsin. The data shown in Figs. 3, 4, and 5 were obtained in collaboration with the late Dr. Wolfgang Braemer.

SUMMARY

Fish can orient into compass directions by using the sun's position as external reference and by making allowance for its daily movement. Reflecting the sun from a

large mirror, it could be demonstrated that the sun was the only environmental reference point in this orientation. Under the very steep sun arc at the equator, correlated with a greatly alinear rate of the sun's movement around the horizon, the compass-orientation of cichlids from the Amazon is as precise as the sun-compass of fish at higher latitudes. Very little change of the orientation angle to the sun's azimuth is observed during morning and evening hours; practically all angular change occurs during the two hours around noon.

Raising centrarchid and cichlid fish from the egg in conditions of artificial light, gave evidence that the basic feature of sun-compass behavior, the tendency to alter the angle of swimming to the sun with time of day, must be considered an innate behavior pattern. In the North-American centrarchids also the direction in which this angular change to the sun occurs appears hereditarily fixed, whereas the tropical cichlids need to learn the direction in which the sun moves around the horizon. About five days of exposure to a sun movement, in a direction opposite to that which the cichlids had learned previously, suffices to cause the fish to reverse the direction of changing its orientation angle to the sun.

Anableps from a population which displayed strong directional swimming during rising tide were found to orient to the sun and to allow for its daily movement when they were deprived of other means of orientation.

SUMÁRIO

Os peixes são capazes de se orientarem no espaço usando como referência a posição do sol, tomando em consideração o seu movimento diurno ("sun-compass orientation"). Com a reflexão do sol, usando um grande espelho, foi possível demonstrar que o sol é o único ponto de referência externa usado nesta orientação.

Em condições equatoriais onde a inclinação do sol aproxima o zênite e, em consequência, o movimento solar segue uma trajetória horizontal não linear, a orientação dos ciclideos amazônicos é tão precisa como a dos peixes em latitudes maiores. Durante a manhã e a tarde, os peixes quase não mudam o ângulo de orientação ao azimute solar, mas durante as duas horas antes e depois do meio-dia a mudança angular é considerável.

Baseado no fato de que peixes (*Centrarchidae* e *Cichlidae*), criados em laboratório sob luz artificial desde o ovo, têm a capacidade de se orientarem ao sol, levando

em consideração o movimento solar, concluímos que este tipo de orientação é inato. Nos *Centrarchidae* norte-americanos, a direção em que a mudança do ângulo ao sol se efetua, também parece ser hereditária, enquanto que nos ciclideos tropicais os peixes precisam aprender em que direção o sol move ao redor do horizonte. Expondo os ciclideos ao movimento solar oposto ao previamente aprendido por cerca de cinco dias é suficiente para que eles revertam a direção em que eles alteram o ângulo de compensação.

Os tralhotos de uma população que demonstraram marcada tendência em nadar numa certa direção durante a maré enchente são também capazes de se orientar ao sol levando em consideração o seu movimento, quando desprovidos de outros meios de orientação.

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SÔBRE O BALANÇO METABÓLICO DE IÔNIOS INORGÂNICOS DA ÁREA DO SISTEMA DO RIO NEGRO

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O abastecimento de elementos nutritivos inorgânicos para os organismos terrestres vem primeiramente do solo. Além disso têm importância a alimentação através de precipitações. Em certas regiões temos o fenômeno do abastecimento com elementos nutritivos transportados pelo vento. Além disso é necessário a indicação do abastecimento particular de compostos nitrogenados formados pela atividade microbológica utilizando nitrogênio atmosférico. O cálculo quantitativo destes abastecimentos naturalmente é difícil. Todavia, o balanço dos elementos nutritivos é de alto interesse.

Um fator importante no balanço dos elementos nutritivos é a perda desses elementos por lixiviação em uma dada região. Em parte estes elementos alcançam camadas inferiores do solo onde formam compostos insolúveis não tomando mais parte na circulação biogênica

dos elementos nutritivos. Outra parte é carregada pelas águas correntes superficiais, enquanto que provavelmente a maior parte é arastada, com a água de percolação, a água freática com a qual aparece nas fontes e é eliminada, da região, com os córregos e rios. As condições para este transporte são muito favoráveis na bacia do rio Negro em virtude das elevadas precipitações (segundo o Atlas Pluviométrico do Brasil de 1948, alcançam 1.500 a 3.500 mm). Outrossim, existem vastas regiões com solos permeáveis; e há solos cujas características físicas e químicas apresentam pouco poder de absorção de elementos nutritivos. Finalmente, observando a bacia do rio Negro, vê-se que é coberta por extensa rede de afluentes, o que permite uma conexão efetiva entre o solo e a água. Os problemas dessa comunicação entre o solo e água foram pesquisados por SIOLI e

KLINGE e são citados em diferentes publicações básicas (SIOLI, 1951, 1955 a, 1955 b, 1960 e 1964; SIOLI & KLINGE, 1962).

Nesta coerência é que estamos realizando pesquisas sobre as quantidades dos elementos de importância biológica que o rio Negro transporta para fora de sua bacia. Representam eles as reservas em nutrientes para o crescimento da vegetação que são liberadas nos solos daquela região progressivamente.

Êsses trabalhos estão concentrados na foz do rio, perto da cidade de Manaus, onde realizamos registros ecográficos do perfil do rio e determinações de velocidade da correnteza. Com êsses dados fomos possível calcular sua vazão, que em 13-4-66 atingiu a..... 27.000 m³/s.

Para pesquisas químicas coletamos amostras de água pouco aci-

ma da cidade a fim de evitar a poluição.

Outrossim foram realizadas em 13-4-66 pesquisas químicas, cujos resultados multiplicados pela vazão forneceram dados sobre as quantidades de elementos transportados por segundo naquele dia, como também a perda de elementos nutritivos inorgânicos no mesmo dia e por quilômetro quadrado de sua bacia.

Em fevereiro, março e abril, em oito diferentes dias, realizamos as mesmas pesquisas; os dados químicos indicaram apenas pequenas diferenças das realizadas em 13-4-66, não sendo por isso seus dados aqui referidos. A amostra de 13-4 vai mais pormenorizada porque nesta data o rio apresentava uma vazão aproximadamente média; por isso mesmo os resultados terão talvez um valor mais generalizado.

TABELA

	Concentração em µg/l	Transporte em kg/s	Transporte t/dia	Transporte g/dia/km ²
N total.....	357	9,7	840	1 300
N (NH ₄ ⁺).....	15	0,40	35	54
N (NO ₃ ⁻).....	17	0,46	40	61
N Orgânico.....	325	8,8	765	1 180
P total.....	7,0	0,19	17	26
P (PO ₄ ³⁻).....	4,9	0,13	11	18
Fe total.....	370	10	860	1 300
Fe diss.	280	7,6	660	1 000
Fe não diss.	90	2,4	200	300
Ca ⁺⁺	360	9,7	840	1 300
Mg ⁺⁺	230	6,2	540	830

Das análises químicas evidenciou-se inicialmente serem pequenas as concentrações de substâncias, principalmente de fósforo total e fósforo de fosfatos que se apresentaram extremamente baixas; sensivelmente baixas são também as concentrações dos compostos de nitrogênio, o cálcio e o magnésio. Digno de nota apresentou-se a quantidade de ferro, superando por si a soma dos alcalino-terrosos, estando êste fenômeno em correlação com as características geoquímicas e edáficas da bacia que em sua maior parte está pobre em cálcio. Da concentração total de ferro somente 3/4 estão em dispersão iônica, enquanto que 1/4 distribuídos em forma não ionizada acham-se em suspensão, ou seja incorporados em outras substâncias.

A bacia do rio Negro apresenta uma área de aproximadamente... 650.000 km² (determinação planimétrica usando-se o mapa do Brasil de 1964, da escala 1: 5 000 000, editado pelo IBGE, Divisão de Cartografia), e em 13-4-66 transportou elementos na ordem de 840 t de nitrogênio total; 17 t de fósforo total e 1.380 t de alcalino-terrosos. O fluxo desses elementos diariamente, por quilômetro quadrado é calculado em : 1.300 g de nitrogênio total; 26 g de fósforo total; 1.300 g de ferro total e 2.100 g de cálcio e magnésio.

Objetivamos continuar estas observações por um período mais prolongado, pelo menos um ciclo anual inteiro, intensificando o trabalho também por comparações entre bacias de diferentes afluentes a serem estudadas separadamente.

Os dados que apresentamos são análises preliminares sobre o balanço dos elementos inorgânicos nutritivos da bacia do rio Negro, pois os trabalhos estão agora iniciados e não podemos por enquanto positivar o porque das condições especiais dessa bacia.

SUMÁRIO

Pesquisas hidrográficas e químicas estão sendo realizadas no rio Negro, perto da cidade de Manaus, para determinação das quantidades absolutas dos elementos da importância biológica que êle transporta. Estas pesquisas desenvolvem-se em duas partes distintas: 1) hidrográficas, para determinação da velocidade da corrente e registro ecográfico da profundidade. Êstes resultados permitirão calcular a vazão do rio; 2) Químico-analíticas, para determinação do N, P e Fe sob vários aspectos particularmente Ca e Mg.

Em 13-4-66, as análises químicas apresentaram os seguintes resultados para os vários aspectos químicos do N, Fe e P e para os alcalinos-terrosos (Ca e Mg). Devemos assinalar as diminutas concentra-

ções encontradas para os mesmos: a concentração do ferro foi de 370 $\mu\text{g}/\text{l}$, é digna de atenção, superando pouco a dos alcalinos-terrosos, que se apresentaram com 360 $\mu\text{g}/\text{l}$ aproximadamente. O Fe não dissolvido constituiu $\frac{3}{4}$ da concentração total desse elemento, estando o restante em dispersão iônica. A concentração do N, como amônia, foi de 15 $\mu\text{g}/\text{l}$. Como nitratos, 17 $\mu\text{g}/\text{l}$ e como N orgânico, 325 $\mu\text{g}/\text{l}$.

O fósforo como fosfatos, esteve presente em pequena quantidade — 4,9 $\mu\text{g}/\text{l}$ — enquanto a concentração total de P chegou à atingir a quantidade de 7,0 $\mu\text{g}/\text{l}$.

Em 13-4-66, em uma das determinações feitas, a vazão do rio Negro foi determinada em..... 27 000 m^3/s . O fluxo total diário dos elementos, apresentou os seguintes valores: Nitrogênio total, 840 t (sendo 35 t como N de amônia e 40 t sob a forma de nitratos); Fósforo total, 17 t (sendo 11 t sob a forma de fosfatos); Ferro total (com 860 t); Cálcio (840 t); Magnésio (com 540 t), respectivamente.

Com relação à área da bacia do rio Negro que é aproximadamente de 650 000 km^2 , calculamos a partir dos dados analíticos, referidos acima, que a vazão diária de elementos químicos nesta bacia por km^2 é de: nitrogênio total, 1 300 g; nitrogênio orgânico, 1.180 g; fós-

foro total, 26 g; ferro total, 1.300 g; cálcio, 1.300 g; magnésio 830 g.

SUMMARY

Hydrographical and chemical observations were carried out in Rio Negro near Manaus to determine the amount of elements of biological importance transported by the river. The hydrographic work included determinations of current speed and echographic depth recording. The data thus received permitted the calculation of the amount of water effluent out of the basin of the Rio Negro. The chemical determinations were extended to nitrogen, phosphorus, and iron, each in different components, and to calcium and magnesium.

On 13th of April 1966, for instance, the following data in a water sample from Rio Negro were found: 370 $\mu\text{g}/\text{l}$ of total iron, almost the concentration of earth alkalines present in 360 $\mu\text{g}/\text{l}$. Only one fourth of the total iron is not dissolved, three fourths are suspended. Ammonia-nitrogen was found in a concentration of 15 $\mu\text{g}/\text{l}$. The amount of nitrate-nitrogen is... 17 $\mu\text{g}/\text{l}$, and of organic nitrogen 325 $\mu\text{g}/\text{l}$. The sample contains phosphate-phosphorus in a concentration of 4,9 $\mu\text{g}/\text{l}$, and total phosphorus in 7,0 $\mu\text{g}/\text{l}$.

The out-flow of the Rio Negro basin on 13th of April 1966 was calculated to 27.000 m^3/s . The efflu-

ence of elements per day was as follows: total nitrogen: 840 t, ammonia-nitrogen: 35 t, nitrate-nitrogen: 40 t, total phosphorus: 17 t, phosphate-phosphorus: 11 t, total iron: 860 t, calcium: 840 t, magnesium: 540 t.

The area of the basin of the Rio Negro is approximately 650 000 km². The effluent of elements per square-kilometre per day was calculated as follows: total nitrogen: 1.300 g, organic nitrogen: 1.180 g, total phosphorus: 26 g, total iron 1.300 g, calcium: 1.300 g, magnesium: 830 g.

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