



Gonzalo Fernández de Oviedo y Valdés (kneeling) presenting a copy of his first published work (*Claribalte*) to the Duke of Calabria, to whom the book was dedicated. The illustration appears as the frontispiece of *Claribalte* (Editorial Juan Venao, Valencia, 1519). Courtesy *Real Academia Española de la Lengua*.

Ichthyology of the Lakes of Nicaragua: Historical Perspective

JAIME VILLA

Scientific study of Nicaraguan freshwater fishes did not begin until Günther described the first species from Lake Nicaragua in 1864, but actual accounts of several interesting fishes were written as early as the sixteenth century by the first historians of the New World. These accounts ranged from hearsay to rather detailed (for their time) descriptions and first-hand observations on the form and life of some species. In some cases these observations or conclusions have been doubted for many decades but confirmed and elaborated in recent years. Therefore I believe it may be of interest to examine the early chronicles.

The first of the early historians was Captain Don Gonzalo Fernández de Oviedo y Valdés (1478–1557) hereinafter referred to as Oviedo, who presented a wealth of information on the plants and animals of the New World. Due to the general lack of familiarity of ichthyologists with this historian, a few words about his life and works seem appropriate.

Oviedo was born in Madrid in 1478 and was raised in the courts of several prominent noblemen at the time Spain was in an agitated political state and on the way to becoming a world power. One of the men he met during his youth was Christopher Columbus. His life is almost as interesting as his chronicles on the New World, where he first arrived in 1514 and was to hold several important positions, such as Governor of El Darién (Panamá) and of Cartagena, and Captain of the Fort of Santo Domingo (Hispaniola). As a result of his involvement in many political intrigues he was jailed after being nearly knifed to death in 1522 (Ballesteros, 1958). He was a very important and influential man in his time, and left us many written works on topics as varied as etiquette, chivalry (a novel), weapons and coats of arms (he was granted one in 1525), politics, catalogues of Spanish rulers, etc.

His most important works to us, and to America in general, are his Indian chronicles, which Oviedo wrote at the request of the Spanish king, Charles V. He first produced a "short version" (written from memory) titled *De la Natural Historia de las Indias*, or *Sumario de la Natural y General Isteria de las Indias*, first published in Toledo, Spain (Oviedo, 1526¹). The *Sumario* (as it is best known today) dealt mostly with Cuba, Hispaniola and other islands, and some parts of the American mainland, such as Panamá and the route to the newly discovered "Southern Sea" (Pacific Ocean).

As with the following and most extensive book, his approach was geographical, historical and political, but entire sections were devoted to plants and animals. The latter accounts were vivid and nearly always first-hand (which he

often separated from hearsay); they were strongly influenced by the writings of Pliny, but these he sometimes doubted and even criticized.

Oviedo's greatest work, in my opinion, is the *Historia General y Natural de las Indias, Islas y Tierra-Firme del Mar-Océano*, which incorporated much of the material in his *Sumario*. It consisted of 50 books; the first 19 were published in 1535, the twentieth in 1557, shortly before his death the same year in Santo Domingo, and the following books remained in manuscript form until they were published by the Spanish Historical Academy nearly three centuries later (Oviedo, 1851–1855; *vide* Amador de los Ríos, 1851). The importance of this work was immediately recognized, and it quickly became a "best seller" which was translated into French, Italian, Arabic, German, Turkish, Latin and Greek (Amador de los Ríos, 1851; Miranda, 1950). Many other languages have since followed, and several recent reprints are available². The *Historia* has been recognized as one of the great works of its time.

Oviedo writes about the lakes of Nicaragua in Chapter IV of his book XLII. His "Laguna de Lenderi" can be identified as Lake Masaya, where he found only small fishes:

"... ni en él hay pescado de ningun género, sino unos pescadicos tan pequeños como cabo de agujetas, que no se pueden comer por ser tan menudos mejor que en tortillas de huevos ..."

"Yo le pregunté al cacique que por qué no echaban en aquel lago algunos buenos pescados, traydos de algunas partes, é me respondió que muchas veces se avia probado para que se multiplicassen é tuviessen qué comer, é que luego se mueren é hieden, y el agua los sube ençima de sí, é aun la dañan; é por esso, como cosa muy experimentada, no curan dello."

It is clear, from the preceding quotation, that the natives often tried introducing fishes in some lakes. Astorqui (1967) has suggested human introduction as the possible origin of the ichthyofauna of Lake Masaya, an opinion with which Villa (1968) concurred. It may also help to explain the presence of fishes in other volcanic lakes whose shores, as Oviedo notes, were heavily populated:

"Todas estas lagunas é lagos están poblados en las costas de mucha gente, en espeçial de los chorotegas ..."

¹There are at least three recent editions of the *Sumario*: a Spanish edition (1950), one in English (1959), and a facsimile edition (1969).

²I have not been able to examine the original (1535, 1557) edition due to its extreme rarity. Therefore the quotations that follow are taken from the 1851–1855 edition, generously lent to me by the Banco Central de Nicaragua; this edition is reputed to be complete and textual. A later edition was published in 20 volumes by the Editorial Guaranía, Paraguay (1945), and is reputed to be a word-by-word copy of the 1851–1855 edition.

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Although Oviedo was told that the natives' efforts to introduce fishes were unsuccessful, this may have been only partly true; it would be expected that many of the fishes died due to improper handling, whereas others (perhaps only a small part of them) survived to populate these lakes.

Oviedo's "Laguna del Diria" is now known as Lake Apoyo, and

"... esta es de agua salada como la mesma mar, é tiene mucho pescado é muy bueno ..."

Presently Lake Apoyo's water is slightly saline, and four species³ of fishes have been collected: *Cichlasoma citrinellum*, *C. managuense*, *Melaniris sardina* and *Poecilia sphenops*.

The "Laguna de Managua" of Oviedo is clearly not today's Lake Managua, but probably Lake Tiscapa or Lake Asososca (of Managua). Neither of these, however, quite conform to Oviedo's description in being "square". Of this lake Oviedo only reports that fishes are plentiful and good.

Two additional lakes, which remain to be identified, are near León: Teguacínabie and Tecuañavete, but no fishes were mentioned from these.

The most interesting part of this section concerns the great lakes of Nicaragua. The bulk of the discussion was centered on whether there were two or more lakes. Oviedo reviews past arguments and gives his opinion: there are two or more, but being connected with one another, and with the sea, they should be considered as only one lake. He was the first one to claim a marine origin for some of the fishes of this lake, including sharks and sawfishes:

"... é aun hay otra raçon para ello muy perentoria, y es que hay pescados muy grandes en ella que son de la mar, é della entran en la laguna, asi como tiburones é lagartos muchos é cocatriges ..."

His main argument for a connection with the "Mar del Norte" (Caribbean Sea) was the discovery of a large dead sawfish on the shores of Lake Nicaragua:

"È lo que tengo en más é confirma mi opinion é me ha hecho estar firme en ques toda una agua é comunicable con la mar, es quel año de mill é quinientos é veynte y nueve yo hallé en la costa desta laguna, en la playa, en la provincia de Nicaragua, un pescado muerto que la mesma agua debiera aver echado fuera: el qual nunca hombre vido ni es muerto sino en la mar, é llamanle *peixe vigüela*, ques aquel que trae por hoçico alto en el extremo de la mandíbula superior aquella feroçissima espada llena de colmillos muy agudos (en ambos filos) puestos á trechos. È son grandísimos pescados, y yo le he visto tan grande, que un par de bueyes con una carreta tienen assaz carga en tal pescado ... y este que digo que hallé muerto fuera de la laguna no podia ser sino que entró por el dicho desaguadero; é aunque era de más de doce piés de luengo, era pequeño, porque aquella espada era pequeña é no mayor que palmo é tres dedos, é no más ancha en lo más ancho ó en su nascimiento que dos dedos ..."

In Book XII, Chapter III, Oviedo gives essentially the same description under the heading for the *peixe vihuela* (previously spelled *vigüela*), or sawfish.

As Thorson *et al.* (1966) pointed out, Oviedo's idea of the Caribbean origin of the shark and sawfish of Lake Nicaragua was criticized by Belt (1874) and by Gill and

Bransford (1878); but now, more than four centuries later, Oviedo's idea is considered correct.

An additional item of interest is Oviedo's contention that Lakes Managua and Nicaragua were broadly united during his time. Presently they are united by Río Tipitapa, but for the first hundred or so meters the river seeps underground, thus preventing fishes from moving from one lake to the other. Although Oviedo apparently did not see it, he reports that the lakes were connected, and that during the summer (dry season) the water level in the channel was chest high or less:

"... donde dicen que desagua en la [Laguna] de Granada [Lake Nicaragua], es aquello alli estrecho, y en verano está tan baxo que un hombre lo atraviessa de costa á costa, dándole el agua á los pechos ó más abaxo; é aquel passo o el caçique se llaman *Itipitapa*."

If this report is correct, it would help explain the similarity of the ichthyofaunas of the two lakes. (See Villa [1976] for further discussion.)

Writers after Oviedo paid much less attention to the natural history but concentrated mostly on the geography, history and politics of the New World. Nevertheless, some brief references to Nicaraguan freshwater fishes may be found. A few examples can be cited.

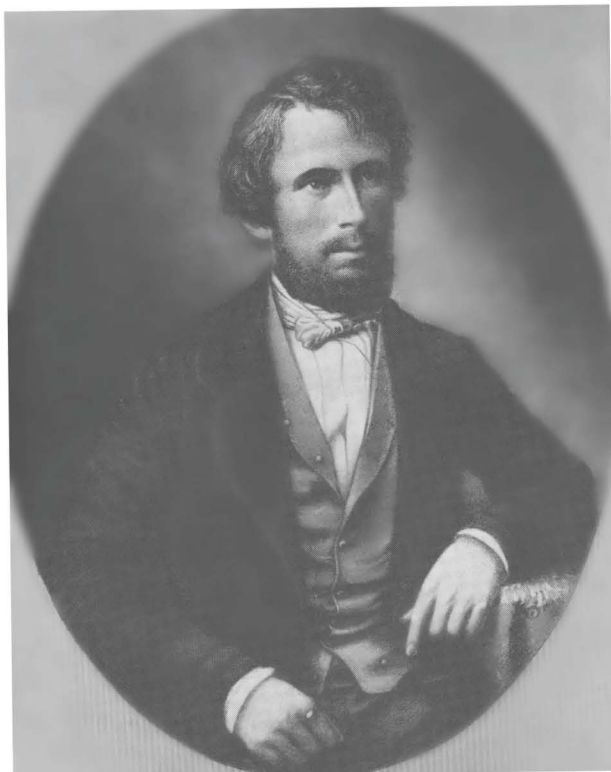
Zaragoza (1894) attributes to Spanish cosmographer-historian, Juan López de Velasco, an extensive manuscript prepared between 1571 and 1574, first published in book form as *Geografía y Descripción Universal de las Indias* (López, 1894). "Las Indias" in this case included not only America but also part of China, Japan, New Guinea, the Philippine and Solomon Islands, etc. López writes matter-of-factly (as opposed to Oviedo's amazement with the things he saw) and possibly he never came to America. He says (p. 318) only that there are "many fishes" in Lake Managua, and (p. 322) that in Lake Nicaragua there are "Many fishes, and a kind of very large tarpon" ("Sábalo"). Of Laguna Lindyri he says (p. 322) that "there is no kind of fish nor any other living thing" ("en ella no hay ningún género de pescado ni otra cosa que viva"). Of this particular lake (Masaya), as we have mentioned, Oviedo said there was no kind of fish *but* some as little as "Cabo de aguejeta". Velasco may have used Oviedo's earlier work and copied it incompletely, as certain sections appear to paraphrase it; nevertheless, the mention of absence of fishes is not devoid of interest.

At a time when England and the United States had cast their eyes upon Nicaragua as a possible route for an interoceanic canal, Ephraim George Squier (1821–1888), a New York engineer, ethnologist, diplomat and writer, visited Nicaragua as "Charge D'Affaires of the United States to the Republics of Central America." His two years (1848–50) in Nicaragua produced two important works: "*Waikna, or Adventures on the Mosquito Shore*" (published under the pseudonym of Samuel A. Bard, in 1855) and "*Nicaragua; its People, Scenery, Monuments and the Proposed Interoceanic Canal*" (Squier, 1852⁴). The latter work, in two volumes, contains references to Nicaraguan freshwater fishes.

Squier (1852, vol. 1, pp. 175–77) visited what he called "Laguna de Salinas," which he thought to be Lenderi [Lake Masaya], but referred to Oviedo's "Laguna del Diria." This reference, his mention of its waters being "slightly salty to the taste" and his later visit to Lake Masaya (*vide infra*) sug-

³A new species of cichlid, *Cichlasoma zaliosum*, is reported from Lake Apoyo in this volume (Barlow and Munsey).

⁴The original 1852 edition was superseded by a one-volume edition in 1860, with a slightly different title, upon which a Spanish translation by Luciano Cuadra (1970) was based.



EPHRAIM GEORGE SQUIER

gests that he visited Lake Apoyo. Here he only "observed some small fishes." He also visited "Lake Nihapa", which is not the present Lake Nejapa, but Lake Asososca of Managua, where he observed that "it abounded in fish . . . for they swarmed along the edge of the water and at the foot of the cliffs."

He could not, of course, refrain from referring to the presence of sharks and sawfish in Lake Nicaragua, after a lengthy translation of Oviedo's account.

"The statement that sword-fish [sawfish] have reached the lake seems somewhat apocryphal, although it should be observed that Oviedo is usually very accurate in matters of this kind. It is, however, a fact that sharks abound in the lake. They are called "tigrones" [tiburones] from their rapacity. Instances are known of their having attacked and killed bathers within a stone's throw of the beach at Granada; and I have myself repeatedly seen them from the walls of the old castle, dashing about, with their fins projecting above the water. Great varieties of fish are found in Lakes Nicaragua and Managua, which are extensively caught and used by the people residing on their shores." (Squier, 1852, vol. 1, p. 196).

There are several passing references to freshwater fishes throughout Squier's *Nicaragua*, but his account of the "sardina" fishing should be singled out.

"At one point bushes were planted in the lake [Managua], like fish wears, between which women were stationed with little scoop nets, wherewith they laded out myriads of little silvery fishes, from the size of a large needle to that of a shrimp, which they threw into kettle-shaped holes, scooped in the sand, where in the evening light, leaping up in their dying

throes, they looked like a simmering mass of molten silver. These little fishes are called *sardinas* by the natives, and are cooked in omelets, constituting a very excellent dish, and one which I never failed to order whenever I visited Managua. The first travelers in Nicaragua mention this novel fishery as then practised by the aborigines, and it has remained unchanged to the present hour" (Squier 1852, vol. 1, p. 412).

Squier visited Lake Masaya and again quoted Oviedo's account mentioning small fishes, of which Squier (1852, vol. 2, p. 18) says that they "are the same with those called *sardines* at Managua, and which I have described in another place."

That Squier's writings stimulated the interest of many people is well known. Gill and Bransford (1878) referred to some of these paragraphs, and Meek (1907) described the *sardina* as *Melaniris sardina*, and quoted Squier in full.

The first scientific descriptions of fishes from the great lakes of Nicaragua were published by Albert [Carl Ludwig Gotthilf] Günther (1830–1914), of the British Museum of Natural History. These were based on specimens obtained by Osbert Salvin and Fredrick Godman, who travelled extensively in Central America, and by John Dow, Captain of the Panama Railway Company, who also collected numerous fishes and presented them to the Smithsonian Institution (see Gill, 1863) and to the Zoological Society of London. The latter specimens were subsequently transferred to the British Museum.

Heros labiatus (*Cichlasoma labiatum*), from Lake Nicaragua, was the first species to be described from the great lakes (Günther, 1864a) and, in addition, to be illustrated in a color plate. A second article (Günther, 1864b) contained four additional new species from Lake Nicaragua: *Eleotris longiceps* (*Gobiomorus dormitor*), *Heros citrinellus* (*Cichlasoma citrinellum*), *H. nicaraguensis* (*C. nicaraguense*) and *H. dovii* (*C. dowi*).

The fifth volume of Günther's "Catalogue of the Fishes in the British Museum" also appeared in 1864 (Günther, 1864c) and contained the description of *Pimelodus* (= *Rhamdia*) *nicaraguensis* based on a specimen collected by Capt. Dow in Lake Nicaragua. The sixth volume appeared in 1866 (Günther, 1866a) and contained two additional species from the same source, *Gambusia nicaraguensis* and *Poecilia dovii*. The latter species was also based on specimens from Mexico and Guatemala, and has been considered synonymous with *Poecilia sphenops* (Regan, 1907 and subsequent workers), but is considered a valid form by Astorqui (1972).

Additional new species were briefly diagnosed by Günther (1866b) in a paper read before the Zoological Society of London and elaborated in a later monograph (Günther, 1869). Due to the brevity of the diagnoses and the more extensive descriptions which appeared in the latter monograph, the publication date of these species is generally considered to be 1869.

Günther's (1869) "Account of the Fishes of the States of Central America" was the most extensive paper on the subject. It contained descriptions of the collecting localities, including lakes Managua and Nicaragua, a historical account of previous collections and publications, a general list of the fishes known in the area (some 300, including marine and estuarine forms) and extensive zoogeographic considerations, in addition to the descriptions of most of the species and illustrations of many forms.

The zoogeographic considerations were interesting, and not greatly different from those of today (e.g., Miller, 1966). Günther stressed the similarities of Atlantic and Pacific ichthyofaunas and, before geologists could provide adequate proof, he postulated that both oceans were connected in the past. He considered the great lakes of Nicaragua as remnants of a previous marine channel, an idea partly shared with previous workers (see Thorson *et al.*, 1966, for a review) which to this date has not been completely discarded.

A descriptive account followed the zoogeographic essay, where the following new species were described from Lakes Managua and Nicaragua:

Günther's (1869) Usage	Present Name	Locality
<i>Heros multispinosus</i>	<i>Herotilapia multispinosa</i>	L. Managua
<i>Heros longimanus</i>	<i>Cichlasoma longimanus</i>	L. Nicaragua
<i>Heros erythraeus</i>	<i>Cichlasoma labiatum</i>	L. Managua
<i>Heros loboichilus</i>	<i>Cichlasoma labiatum</i>	L. Managua
<i>Heros managuaensis</i>	<i>Cichlasoma managuaense</i>	L. Managua
<i>Neotroplus nematopus</i>	<i>Neotroplus nematopus</i>	L. Managua
<i>Pimelodus managuaensis</i>	<i>Rhamdia managuaensis</i>	L. Managua

In spite of Günther's contributions, the ichthyofauna of the great lakes remained rather poorly known (6 species from Lake Managua, 9 from Lake Nicaragua). A substantial contribution was made by Gill and Bransford in 1878. Dr. John Bransford, U.S.N. (1846–1911), in connection with the proposed canal route through Nicaragua, collected not only amphibians and reptiles, but also many noteworthy fishes in Lake Nicaragua and the Río San Juan. The fishes were deposited in the Academy of Natural Sciences of Philadelphia. Theodore Nicholas Gill (1837–1914), a well known American ichthyologist, apparently wrote most of the article and used Dr. Bransford's notes. The product was a "Synopsis of the fishes of Lake Nicaragua," published in the Academy's Proceedings for 1877 (Gill and Bransford, 1878).

Gill and Bransford briefly described the physiography of Lake Nicaragua and reviewed previous literature, including a good free translation of extracts of Oviedo's accounts, and they criticized his idea that marine forms had entered Lake Nicaragua from the Caribbean ("The worthy chronicler must not be judged too harshly for his assumptions respecting the communicability between the sea and the lake, because of the presence of sawfish and other marine types. In our days naturalists have based their hypotheses and classifications upon even less data and in spite of known facts").

The presence of marine forms is thus explained by Gill and Bransford (pp. 179–180):

"They may have resulted (1) from the intrusion of the saltwater types into the fresh waters, or (2) from the detention and survival of the salt-water fishes in inlets of the sea that have become isolated and gradually become fresh-water lakes. On the whole, it appears more probable that the latter is the case. By the uplift of the land, an inlet of the Pacific Ocean might have been shut off from communication from the ocean, and the character of the water would be soon changed by the copious showers of that tropical country. The shark, sawfish, megalops, and other species mostly found in the sea, had, however, time to accommodate themselves to the altered conditions, and in this connection it must be remembered too, that most of the types in question are known to voluntarily ascend high up streams and even into fresh water. The numerous rapids of the river discharging

from the lake discourage, however, the idea that the species enumerated have voluntarily ascended that river and entered the lake. The concurrence of the fresh-water fishes with others and their entrance into the lake from the surrounding streams would be merely a question of time."

The above paragraph was cited by C. W. Hayes (1899), a geologist with the U.S.-Nicaragua Canal Commission, as support of his theory for the Pacific origin of the great lakes of Nicaragua, which was essentially the same as Gill and Bransford's.

It is not easy to explain why Gill and Bransford supposed a Pacific origin for *Eulamia nicaraguaensis*, since in their original description they considered it "closely related to *Eulamia milberti* [the Caribbean sandbar shark] and the kindred species." Later, according to Hayes (1899), Gill told him that the Lake Nicaragua sharks are "specifically identical with those found in the adjacent portions of the Pacific, but distinct from those found in the Caribbean Sea." There are no similar statements in any of Gill's papers.

Gill and Bransford's synopsis contains 21 species, of which 5 were not previously known from Lake Nicaragua and seven were new to science, as follows:

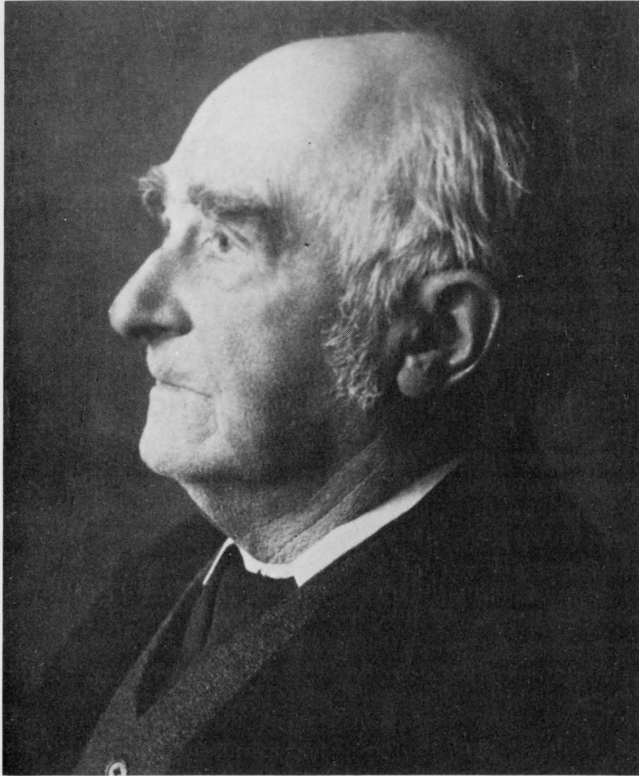
Gill and Bransford's (1878) Usage	Present Usage
<i>Chirostoma guatemalensis</i> [nec Günther]	<i>Melaniris sardina</i>
<i>Opisthonema libertatis</i> [nec Günther]	<i>Dorosoma chavesi</i>
<i>Megalops</i> _____	<i>Tarpon atlanticus</i>
<i>Chalcinopsis dentex</i> [nec Günther]	<i>Brycon guatemalensis</i>
<i>Pristis antiquorum</i> [nec Latham]	<i>Pristis perotteti</i>
<i>Heros rostratus</i>	<i>Chiclasoma rostratum</i>
<i>Heros basilaris</i>	<i>Chiclasoma citrinellum</i>
<i>Heros balteatus</i>	<i>Cichlasoma nicaraguaense</i>
<i>Heros centrarchus</i>	<i>Cichlasoma centrarchus</i>
<i>Neotroplus nicaraguaensis</i>	<i>Neotroplus nematopus</i>
<i>Bramocharax bransfordii</i>	<i>Bramocharax bransfordii</i>
<i>Eulamia nicaraguaensis</i>	<i>Carcharhinus leucas</i>

A collection of fishes from two Nicaraguan localities (Lake Nicaragua and "40 miles above the mouth of the Río San Juan") was made by Dr. Louis F. H. Birt and sent to the United States National Museum in 1888, where it was studied by David Starr Jordan (1851–1931). Jordan published a short note about the specimens (Jordan, 1889), recording 14 species, eight of them new to the great lakes basin:

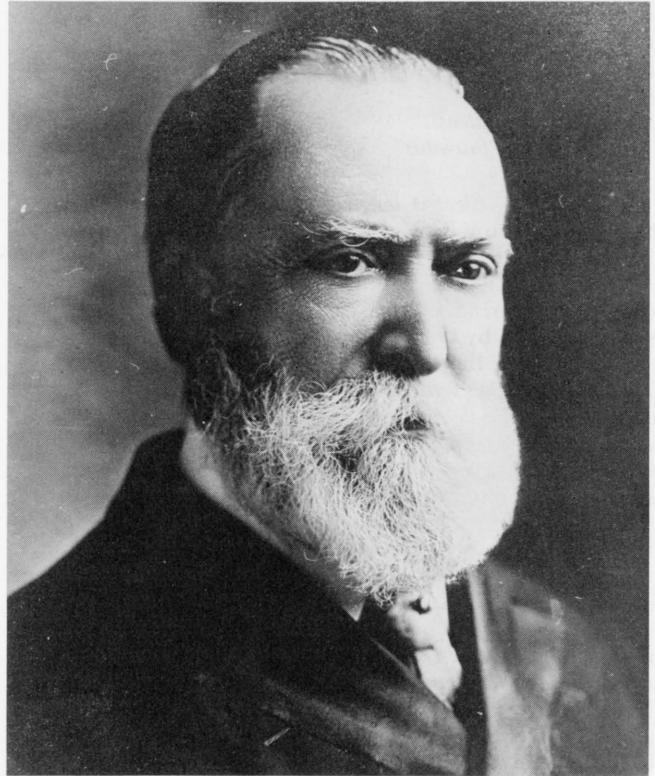
Jordan's (1889) Usage	Present Usage
<i>Ailurichthys filamentosus</i>	<i>Bagre filamentosus</i> ⁵
<i>Anacyrtus guatemalensis</i>	<i>Roeboides guatemalensis</i> ⁶

⁵This species apparently has not been reported again from Lake Nicaragua. Regan (1907) cited Jordan's (1889) record, which was also accepted by Miller (1966) and by Villa (1971a). Curiously enough, the two most recent major papers on the fishes of the great lakes basin (Meek, 1907; Astorqui, 1972) excluded this species without comment.

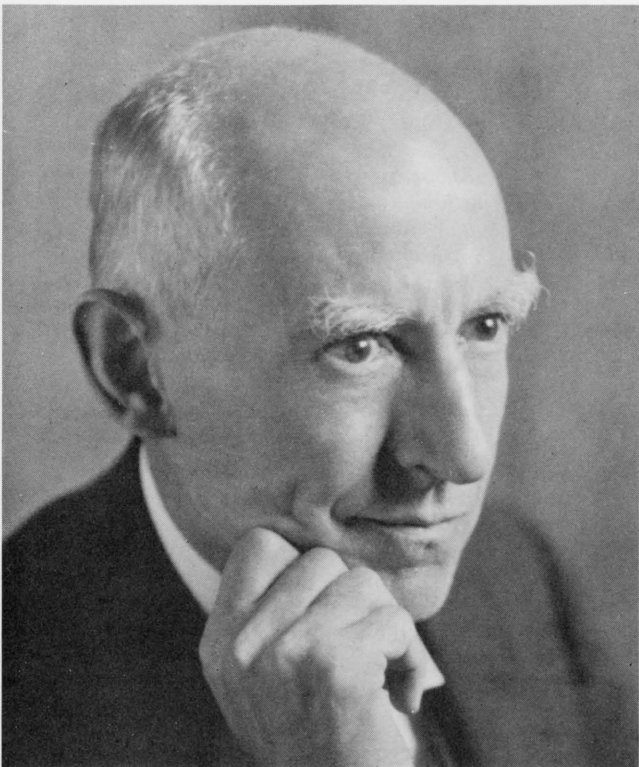
⁶This species was hesitantly reported ("This specimen was with the others, but it is not included with the memoranda of Dr. Birt's collection") and it was excluded from the list of additions to the basin's ichthyofauna, while *Chalcinopsis dentex* (previously recorded by Gill and Bransford, 1878, p. 188) was included. Since *Anacyrtus* (= *Roeboides*) *guatemalensis* is known to be present in Lake Nicaragua, it seems probable that the specimen came from this locality but was excluded from Birt's memoranda.



ALBERT GÜNTHER



THEODORE NICHOLAS GILL



CHARLES TATE REGAN



SETH EUGENE MEEK

The "Big Four" of early ichthyologists who worked with fishes of Nicaraguan lakes.

<i>Heros aureus</i>	<i>Chiclasoma</i> _____
<i>Heros friedrichsthalii</i>	<i>Cichlasoma friedrichsthalii</i>
<i>Heros motaguensis</i>	<i>Cichlasoma friedrichsthalii</i>
<i>Heros nigrofasciatus</i>	<i>Cichlasoma nigrofasciatum</i>
<i>Rhamdia guatemalensis</i>	<i>Rhamdia</i> _____
<i>Tetragonopterus fasciatus</i>	<i>Astyanax fasciatus</i>

In addition, *Eleotris longiceps* Günther, described from Lake Nicaragua, was recognized as *Philypnus dormitor* (*Gobiomorus dormitor*).

In 1879, C. Lütken transferred *Eulamia nicaraguensis* to the genus *Carcharias*, basing this action on notes and sketches taken by Ørsted in 1848.

In 1896 the first part of an important work by D. S. Jordan and B. W. Evermann (1853–1932) appeared: “*Fishes of North and Middle America*.” It was completed in 1900, and it consisted of four parts with 3400 pages and 292 plates. Over 3200 species were described, many of them new to science. There has not been a comparable work published since then, and its importance to American fish systematics is too well known to merit further elaboration. Not much was added to the knowledge of the fishes of the great lakes of Nicaragua, however. Many of the descriptions of these species were copied or adapted from previous publications, and some of the keys for identification (*i.e.*, Cichlidae) were unworkable even then. An updated summary checklist followed (Jordan, Evermann and Clark, 1930).

Jacques Pellegrin, of the Museum d'Histoire Naturelle de France, published a comprehensive revision of the cichlid fishes (Pellegrin, 1904), including anatomical and taxonomic aspects. Pertinent to this review, *Heros multispinosus* was recognized as belonging to a new genus, which he named *Herotilapia*. Pellegrin included *Cichlasoma managuense* and *C. friedrichsthalii* in the synonymy of *Heros motaguensis* (= *Cichlasoma motaguense*), but presently they are considered as valid. Many of the Nicaraguan species presently assigned to *Cichlasoma* (such as *citrinellum*, *dowi*, *labiatum*, *nicaraguense*, etc.) were assigned to *Heros*.

A more widely accepted arrangement of the American cichlids was published only a year later (1905) by C. Tate Regan (1878–1943) in England. Among the Nicaraguan species, he separated *Cichlasoma managuense* and *C. friedrichsthalii* from *C. motaguense*, synonymized *Neetroplius nicaraguensis* with *N. nematopus* and *Heros basilaris* with *C. citrinellum*, and described *C. maculicauda*, although the latter species was not yet known from Nicaragua.

In 1906 the *Pisces* section of *Biologia Centrali-Americana* began to appear (in separate fascicles), and it was completed in 1908. This work was also written by Regan (1906–08), and is comparable with Günther's (1869) “*Fishes of the States of Central America*.” To this day it remains the only comprehensive work on the freshwater species of Middle American fishes. It is a good critical review of previous literature and collections, and many distributional records were included. No new species were described from Nicaraguan lakes, but many were illustrated for the first time (*e.g.*, *Cichlasoma balteatum* [= *C. nicaraguense*], *C. friedrichsthalii*, *C. centrarchus*, *C. rostratum*, *Poecilia sphenops*, *Rhamdia nicaraguensis*, and *R. managuensis*).

Seth Eugene Meek (1859–1914), an Ohio-born zoologist, is a familiar name to students of Middle American freshwater fishes. He explored the streams of central and western United States, Mexico and Central America, and studied their fishes. He is perhaps best known for his papers on Mexican freshwater fishes (Meek, 1904, etc.) and, with

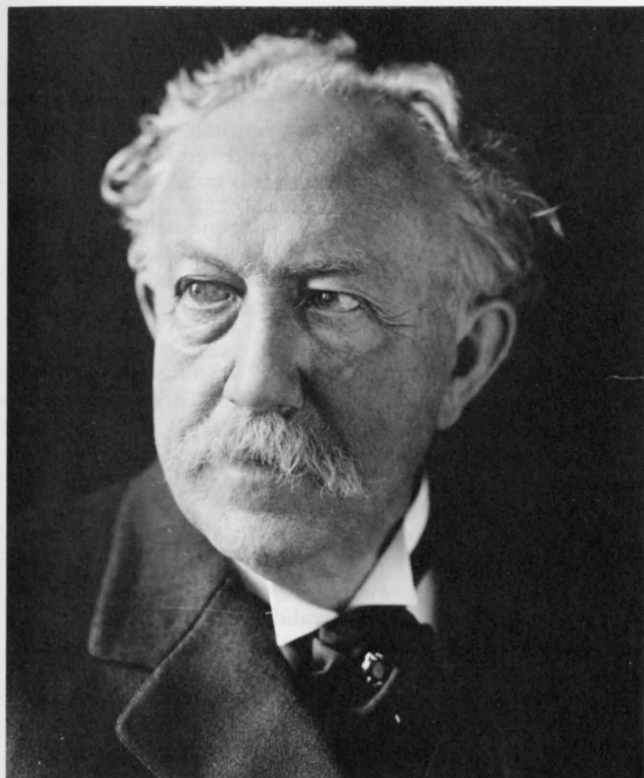
Samuel F. Hildebrand, also prepared several volumes of the fishes of Panama (Meek and Hildebrand, 1916, 1923–28).

In March, 1906 Meek visited Nicaragua and made noteworthy collections in Lakes Managua, Nicaragua, Tiscapa, Apoyo, and small *lagunas* associated with the first two, such as San Francisco, Jenicero (= Genízaro) and Cisplaya. He was assisted by several people while collecting, notably by Dioclesiano Chaves, taxidermist and later Director of the Museo Nacional of Nicaragua, after whom he named a new species of the clupeid genus *Dorosoma*. Meek's “*Synopsis of the fishes of the great lakes of Nicaragua*” was published a year later (Meek, 1907) and was to be the most comprehensive work on the subject for more than 60 years. He included 35 species, nine of them described as new to science, of which 4 are presently considered valid. His list, updated, is as follows:

Meek's (1907) usage	Present usage
<i>Carcharhinus nicaraguensis</i>	<i>Carcharhinus leucas</i>
<i>Pristis antiquorum</i> (nec Latham)	<i>Pristis perotteti</i>
<i>Lepisosteus tropicus</i>	<i>Lepisosteus tropicus</i>
<i>Rhamdia managuensis</i>	<i>Rhamdia managuensis</i>
<i>Rhamdia nicaraguensis</i>	<i>Rhamdia nicaraguensis</i>
<i>Ramdia barbata</i> , new	<i>Rhamdia barbata</i>
<i>Astyanax nasutus</i> , new	<i>Astyanax nasutus</i>
<i>Astyanax aeneus</i>	<i>Astyanax fasciatus</i>
<i>Brycon dentex</i>	<i>Brycon guatemalensis</i>
<i>Bramocharax bransfordii</i>	<i>Bramocharax bransfordii</i>
<i>Bramocharax elongatus</i> , new	<i>Bramocharax bransfordii</i>
<i>Roeboides guatemalensis</i>	<i>Roeboides guatemalensis</i>
<i>Dorsoma chavesi</i> , new	<i>Dorosoma chavesi</i>
<i>Tarpon atlanticus</i> (?)	<i>Tarpon atlanticus</i>
<i>Paragambusia nicaraguensis</i>	<i>Gambusia nicaraguensis</i>
<i>Poecilia sphenops</i>	<i>P. dowi</i> and <i>P. sphenops</i>
<i>Melaniris sardina</i> , new	<i>Melaniris sardina</i>
<i>Pomadasys grandis</i> , new	<i>Pomadasys boucardi</i> (?)
<i>Cichlasoma managuense</i>	<i>Cichlasoma managuense</i>
<i>Cichlasoma dowii</i>	<i>Cichlasoma dowi</i>
<i>Cichlasoma granadense</i> , new	<i>Cichlasoma citrinellum</i>
<i>Cichlasoma citrinellum</i>	<i>Cichlasoma citrinellum</i>
<i>Cichlasoma dorsatum</i> , new	<i>Cichlasoma labiatum</i>
<i>Cichlasoma erythraeum</i>	<i>Cichlasoma labiatum</i>
<i>Cichlasoma lobocheilus</i>	<i>Cichlasoma labiatum</i>
<i>Cichlasoma centrarchus</i>	<i>Cichlasoma centrarchus</i>
<i>Cichlasoma rostratum</i>	<i>Cichlasoma rostratum</i>
<i>Cichlasoma longimanus</i>	<i>Cichlasoma longimanus</i>
<i>Cichlasoma nigratum</i> , new	<i>Cichlasoma maculicauda</i>
<i>Cichlasoma nicaraguense</i>	<i>Cichlasoma nicaraguense</i>
<i>Cichlasoma balteatum</i>	<i>Cichlasoma nicaraguense</i>
<i>Neetroplius nematopsis</i>	<i>Neetroplius nematopus</i>
<i>Herotilapia multispinosa</i>	<i>Herotilapia multispinosa</i>
<i>Philypnus dormitor</i>	<i>Gobiomorus dormitor</i>

In an effort to popularize Meek's (1907) *Synopsis*, Chaves translated it into Spanish and had it published by the Tipografía Nacional of Nicaragua in 1913. The translation was rather poor and the edition was limited⁷ but, as Astorqui (1967) pointed out, it was the only paper on Nicaraguan fishes in the Spanish language. For this reason it was reprinted by the Revista Conservadora in 1967, but no effort

⁷Copies of this edition are extremely scarce. The national Library and the National Museum of Nicaragua have none; I examined a copy through the courtesy of Sr. José Luengo of the Oceanographic Institute of the Universidad de Oriente, Venezuela.



DAVID STARR JORDAN



BARTON WARREN EVERMANN



CARL H. EIGENMANN



HENRY WEED FOWLER

Four more prominent men who contributed to the pioneering stages of Nicaraguan lake ichthyology.

was made to polish Chaves' translation nor, for that matter, to proof-read it adequately.

In a following paper (also dated 1907 but stamped "Issued Jan. 3 1908"), Meek (1908) reported on a small collection sent by Chaves which included 6 species. Although none of them were new, some of them represented new localities of zoogeographic interest, being the first species reported from Lago (= Laguna) de Asososca and Lago de Guila (the latter shown by Villa, 1971a to be Laguna Xiloá). The new localities were as follows: *Cichlasoma managuense* and *Neotrophus nematopus* from Xiloá; and *C. citrinellum* and *Philypnus* (= *Gobiomorus*) *dormitor* from Asososca and Xiloá. Three species were also reported from Lake Managua (*Brycon dentex* [= *B. guatemalensis*], *C. citrinellum* and *C. rostratum*), which Meek (1907) had already included in the Lake Managua ichthyofauna in his earlier *Synopsis*.

Meek reaffirmed his earlier (1907) doubt on the distinctness of *C. rostratum* from *C. longimanus*, but again refrained from considering them synonymous. It is interesting to note that at this time both species are considered valid, and that no other species have been recorded from Lake Asososca, although *C. managuense* is conspicuously present there.

Meek's (1908) Lake Asososca (Fig. 1) requires clarification. There are two Nicaraguan lakes with the same name, one in Departamento de Managua, south of Lake Managua and one in Departamento de León, east of Lake Managua. I have collected in both lakes and have found them sharing two species, *Cichlasoma citrinellum* and *C. managuense*, but I have not found *Gobiomorus dormitor* in Lake Asososca of León, which Meek found in Lake Asososca of Managua. In addition to this negative evidence, I have spoken at great length with Miss Crisanta Chaves, Director Emeritus of the National Museum of Nicaragua, who vividly recalls her late father's journeys. She says Sr. Chaves obtained fishes in Lake Asososca of Managua, not in León. Lake Asososca of Managua has been easily accessible to collectors for several decades, being the main drinking-water supply of the city of Managua, whereas Lake Asososca of León has had access only in recent years. Available data point to Lake Asososca of Managua as the lake upon whose fishes Meek (1908) reported. Since there is no record of fishes from Lake Asososca of León, it is not out of place to list *Cichlasoma citrinellum* and *C. managuense* here, on the basis of a collection I made from that lake and deposited in the Museo de Zoología, Universidad de Costa Rica. A third species, of the genus *Tilapia*, is said to have been introduced in about 1966 by the Ministerio de Agricultura de Nicaragua, but I did not collect any examples of this species.

The first part of the "Fishes of the Western North Atlantic" appeared in 1948. Henry B. Bigelow and William C. Schroeder wrote the section on sharks, where *Carcharhinus nicaraguensis* was given full specific status (Bigelow and Schroeder, 1948). The similarity with *C. leucas* was noted, and *C. nicaraguensis* was considered a landlocked representative of the former species. In a later paper, however, Bigelow and Schroeder (1961) studied new material and suggested that these nominal species are identical. This contention was fully documented by Thorson *et al.* (1966). The second part of the "Fishes of the Western North Atlantic" dealing with the sawfishes, etc., was also written by Bigelow and Schroeder (1953). *Pristis perotteti* was illustrated and described, based in part on Lake Nicaragua specimens.

In 1908 Carl H. Eigenmann and Fletcher Ogle published a list of characin fishes in the U.S. National Museum and in

Indiana University. The Nicaraguan material was collected by Bransford and Birt. Eigenmann and Ogle (1908) described *Astyanax rutilus nicaraguensis* as a new subspecies (which Eigenmann [1921] raised to specific status), and recorded *A. rutilus oerstedii*. It is not yet clear whether these 2 forms represent the wide-ranging and variable *A. fasciatus*, which may be a "catch all" for several taxa.

"I doubt very much whether specimens of *fasciatus* and *mexicanus*, *rutilus*, *oerstedii* and *aeneus*, if freshly collected, similarly preserved, and mixed in one heap, could be separated specifically" (Eigenmann & Ogle, 1908).

In addition, *Bramocharax bransfordii* was illustrated for the first time, and *Roebooides guatemalensis* was listed from the Río San Juan.

In a revision of several clupeid genera, including *Dorosoma*, Regan (1917) listed *D. chavesi* from lakes Managua and Nicaragua.

Fowler (1923) reported a specimen of *Lepisosteus tropicus* from Lake Managua.

Robert Rush Miller revised the genus *Dorosoma* in 1950. He recognized *D. chavesi* as a valid species and pointed out similarities with *D. smithi*, suggesting parallel evolution. In comparing small samples of *D. chavesi* from lakes Managua and Nicaragua he noted differences, but refrained from considering them as different subspecies because of the size of the samples. In 1954, Miller discussed the type locality of the tropical garfish or "Gaspar" (*Lepisosteus tropicus*), usually referred to as "Panama." However, he concluded that the species does not reach farther south than the Guatemala-El Salvador border on the Pacific and the tributaries of the Río San Juan in Costa Rica on the Atlantic versant. Later (Miller, 1966) he modified the limits to the Río Negro, Golfo de Fonseca, on the Pacific. This last paper is one of the most interesting ones recently published on Central American freshwater fishes (along with that of Myers, 1966).⁸ Miller provided a checklist of more than 450 species, with revised distributional statements for all the species.

The 1960's brought increased interest, once more, in the Nicaraguan lakes and their fishes, as two ichthyologists focused on the area. Spanish priest Ignacio Astorqui, S. J., seeking material for his thesis research, came to the Colegio Centro America (which he would later direct), ideally situated on the northwestern shore of Lake Nicaragua. In 1960, he and his then-professor, Luis René Rivas, made extensive fish collections throughout Nicaragua, especially in the great lakes basin. Their specimens, or part of them, were later deposited in the Gulf Coast Research Laboratory (Ocean Springs, Mississippi). Astorqui's first published papers, which appeared in the leading Nicaraguan newspaper "La Prensa," were popular accounts of the shark, garfish, etc. these were later reprinted in the "Revista Conservadora" (Astorqui, 1967). Astorqui's thesis, after acceptance by the University of Miami, was translated into Spanish and published in the "Revista de Biología Tropical."

Astorqui's (1972) "Peces de la cuenca de los grandes lagos de Nicaragua" is the most comprehensive paper on the subject to this date. It includes 45 species belonging to 16 families, has keys for the identification of most species and

⁸A new contribution to the zoogeography of the San Juan ichthyofauna is provided in this volume by W. A. Bussing.

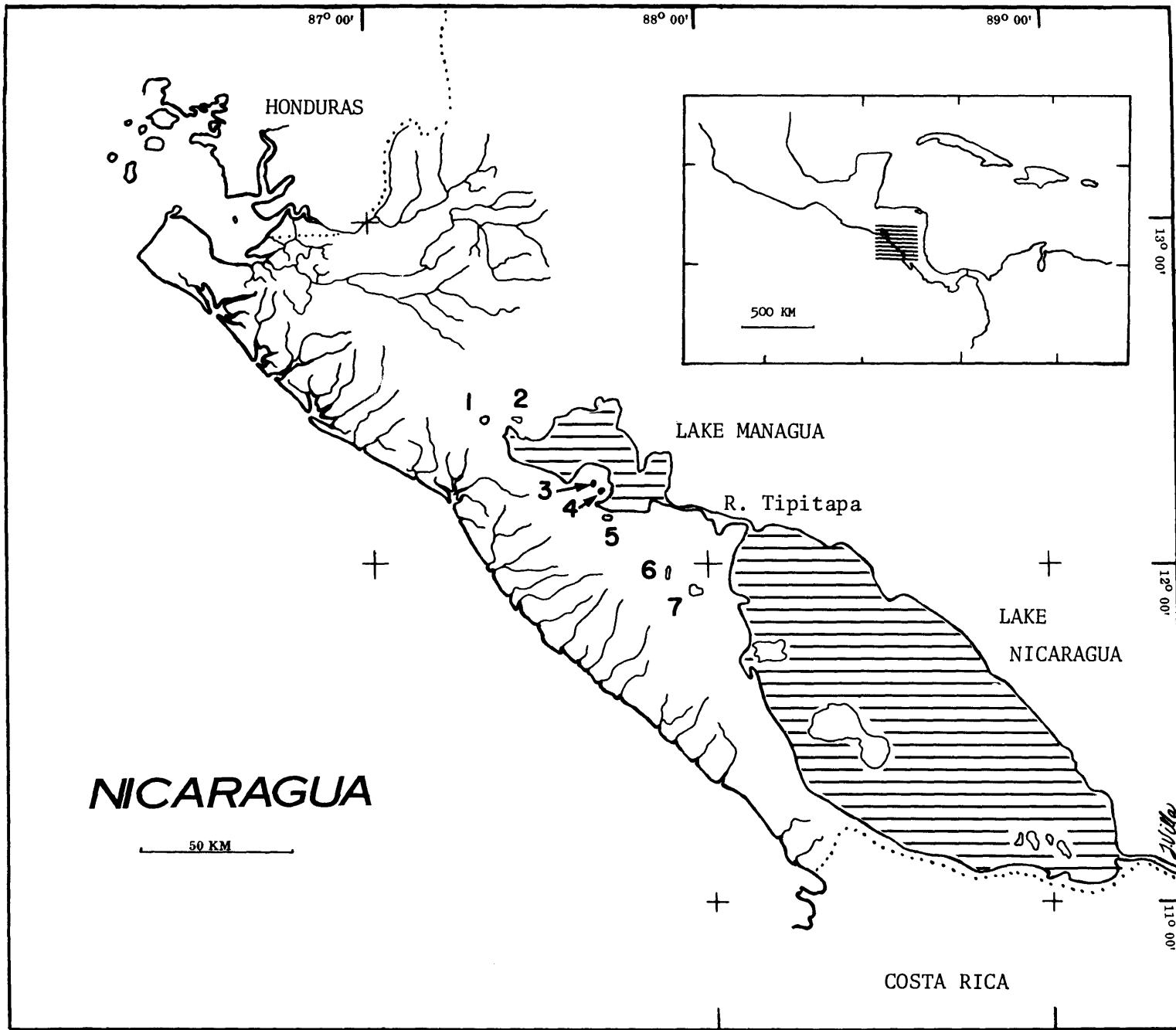


FIG 1. The Pacific Versant of Nicaragua, including the Great Lakes. Crater Lakes are: (1) Asosca (León), (2) Monte Galán, (3) Apoyeque, (4) Xiloá, (5) Asosca (Managua), (6) Masaya, (7) Apoyo.



IGNACIO ASTORQUI

detailed measurements, proportions and counts, which make it a useful reference work.⁹

Astorqui's treatment of the *Rhamdia* catfishes is quite conservative, basically the same as Meek's (1907). He examined specimens of *Dorosoma chavesi* from lakes Managua and Nicaragua and found differences between the two populations, as Miller (1950) had, but he did not evaluate them. Without explaining why, he used names such as *Mollienisia* and *Xenophallus* (instead of *Poecilia* and *Neoheterandria*), in spite of Rosen and Bailey's (1963) revision. In his treatment of the cichlids he ignored three species described by Meek (1907) from lakes Managua and Nicaragua (see Villa, 1976).

These remarks, however, do not detract from the importance of his contribution to the ichthyology of Nicaragua. He added several species, not previously reported there, to the fauna of the great lakes: *Pristis pectinatus*, *Rhoadsia eigenmanni*, *Hyphessobrycon tortuguerae* (tentative identification), *Bryconamericus ricae*, a *Hemibrycon* (also tentative), *Xenophallus* (= *Neoheterandria*) *umbratilis*, *Alfaro cultratus*, *Poeciliopsis gracilis*, *Cichlasoma maculicauda* (which Meek [1907] had described from Lake Nicaragua as *C. nigratum*), *Synbranchus marmoratus*, *Centropomus parallelus*, *Rivulus isthmensis*, and *Gymnotus carapo* (actually *G. cylindricus*). He invalidated or questioned the validity of several nominal species, including *Bramocharax elongatus* (later synonymized with *B. bransfordii* by Rosen, 1970), *Cichlasoma lobochilus*, *C. erythraeus*, and *C. nigrofasciatum* (I do not agree with his opinion that the latter is actually *C. spilurum*, but I consider it a valid species).

⁹An enlarged Spanish edition, published by Publicaciones Nicaraguenses, S.A., Managua (179 pp., dated 1974) was received too late to include in this paper.



THOMAS B. THORSON

At about the same time Father Astorqui was completing his collecting (1960), Thomas B. Thorson of the University of Nebraska came to Nicaragua to study the physiology of the bull shark, *Carcharhinus leucas*. His first paper (1962) dealt with the body fluids of freshwater examples of this species, compared with those of three marine species of sharks. Osmoregulation in freshwater sharks and sawfish was treated in a review article (Thorson, 1967), and two papers on shark body fluids appeared later (Thorson and Gerst, 1972; Thorson, Cowan and Watson, 1973), as well as one by Cowan (1971) on serum proteins of *C. leucas*.

Thorson's most important paper on the Lake Nicaragua shark population (Thorson *et al.*, 1966) included morphometric studies, comparisons between specimens from different localities, the origin of freshwater populations, and movements between the lake and the Caribbean Sea. The idea of a landlocked population had been briefly questioned earlier (Thorson, 1964), and actual movements between the lake and the sea, in part monitored by ultrasonic tagging (Thorson *et al.*, 1969), were finally documented (Thorson, 1971). The first report on Thorson's study of the sawfish, *Pristis perotteti*, a paper on the rostral teeth of that species, appeared in 1973. An updated appraisal of the Lake Nicaragua shark population and a discussion of the sawfish can be found in this volume, as well as several papers by Thorson's associates (D. E. Watson, N. H. Jensen and R. E. Tuma).

In 1962, M. R. Urist collected serum from the bull shark in Lake Nicaragua and the Río San Juan and compared various chemical parameters of the freshwater form with those of marine bull sharks and the tarpon.

My studies on fishes from the great lakes basin were part of a broader survey of lower vertebrates in Nicaragua, and although I had made sporadic collections in the early 1960s'

I was influenced by Astorqui, Bussing and Thorson to collect more systematically. A study of the fishes of Lake Xiloá revealed strong affinities with those of the great lakes, from which they probably originated (Villa, 1968, 1971b). In the popular and semipopular literature I reported two fishes then unknown from Lake Nicaragua, *Gymnotus cylindricus* and *Belonesox belizanus* (Villa, 1970a and 1970b). A "Synopsis" of the freshwater fishes from Nicaragua was originally prepared in response to the need of a handbook for the ichthyology course at the Universidad Nacional de Nicaragua (Villa, 1971a) and plans to update the third provisional edition are proceeding slowly.

Histochemical studies have been conducted by G. Gerzeli and his associates on the osmoregulatory function of the rectal glands of the shark and sawfish of Lake Nicaragua as compared with those of marine elasmobranchs (Gerzeli and De Stefano, 1968; Gerzeli *et al.*, 1969; Gerzeli *et al.*, this volume). This work has been based on field collections made by G. F. De Stefano when he was on the faculty of the Universidad Nacional Autónoma de Nicaragua at Leon in the late 1960s and early 1970s. Earlier, Oguri (1964) had also noted morphological and histological differences between the rectal glands of marine sharks and those of the bull shark of Lake Nicaragua.

Behavioral studies on fishes of the lakes of Nicaragua did not strictly begin until the late 1960s' with the arrival of George W. Barlow and his students from the University of California at Berkeley. Barlow and his group, concentrating on the family Cichlidae, have studied a number of species from several of the lakes. Although their primary focus has been on behavior, they have also given attention to taxonomy and other areas. Since 1973, seven papers have been published by Barlow and his group on their work in Nicaragua (Barlow, 1973; Baylis, 1974; McKaye and Hallacher, 1974; Noakes, 1973; Noakes and Barlow, 1973a and 1973b; Webber, Barlow and Brush, 1973). Five additional papers appear in this volume, four of them on the ichthyofauna, including those by senior authors Barlow, K. R. McKaye and T. Lim.

Jack D. Burke, together with his colleagues from the Medical College of Virginia, is studying ultrastructural, biochemical and immunological features of sharks and sawfish taken from both fresh and salt water. The first results of this study (Burke, 1974) indicate uniform hemoglobin characteristics in freshwater and marine *Carcharhinus leucas*.

In 1971, the Fisheries Division of the *Instituto de Fomento Nacional* (INFONAC) of Nicaragua began a three-year *Programa de Investigación de los Recursos Pesqueros del Lago de Nicaragua*. Its objective was to evolve a rational plan for the development and management of the Lake's fisheries resources. INFONAC biologists have collaborated with fisheries biologists of the United Nations Food and Agricultural Organization (FAO), volunteers of the United States Peace Corps and investigators from several universities. The papers in this volume by S. Martínez, K. W. Koenig, R. J. Beatty and W. D. Davies resulted from this program and the results of the program itself are presented in the final report of the project (INFONAC, 1974), which is also reprinted here.

S. Y. Lin, D. Riedel, A. H. Hagberg and R. W. Ellis, as fisheries experts for the FAO/UN, have contributed to the knowledge of lake fisheries by investigations conducted for the Nicaraguan government, and two of Riedel's papers (1965, 1972) are reprinted in this volume.

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