INTRODUCTION

The large river shrimps occurring in the United States are well known locally, because of their size and huge claws, and one species is of some commercial value. Nevertheless, the literature on these interesting crustaceans is so incomplete and scattered that identification of the various species by non-specialists has been impossible. The river shrimps are members of the palaemonid genus *Macrobrachium*, closely related to the little freshwater grass or “glass” shrimps of the genus *Palaemonetes*. There are several other genera in the family Palaemonidae, including *Palaemon* and *Leander*, but these usually occur only in the sea. Some of the species are found characteristically among the creatures which comprise the microcosomes of the sargassum. Recently, Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie of Leiden, working at the U. S. National Museum, made a thorough systematic revision of the American members of the Palaemonidae. This work is now awaiting publication by the Allan Hancock Foundation, and I am indebted to Dr. Holthuis for much of the information on the taxonomy and systematics of the genus *Macrobrachium*, and for the details on which the key to the species north of the Rio Grande is based. Since Dr. Holthuis’ comprehensive work is a purely systematic treatment, this...
paper will summarize what is known of the ecology and distribution of this genus in the waters north of the Rio Grande.

The literature on river shrimps in the United States is surprisingly meager, and several of the species remained unfigured before the author's note in the Progressive Fish-Culturist (1947). Disregarding the casual systematic and distributional notes on the various species, there are but four important papers on the Macrobrachiums of the United States. The first of these is Schmitt's (1933) distributional notes on all four species. This was followed by McCormick's papers (1933, 1934) on the anatomy of Macrobrachium obione. A few years later, Gunter (1937) published the results of a preliminary study of the life history of the same species.

Genus Macrobrachium Bate

The generic name *Palaemon* is common in earlier literature, including Ward and Whipple (1918, p. 845). Another name formerly used for this genus is *Bithynus*, which was favored by Rathbun (1902) More than a hundred species of *Macrobrachium* are recognized, occurring throughout the tropical regions. Twenty-six species are known from the Western Hemisphere, but only four have been recorded north of the Rio Grande. On the whole, the species are partly euryhalin, but there is no entirely marine species although the adults of many species invade bays, and the larvae of some Indo-Pacific species have been found in the sea. Without doubt this occurrence in bays accounts for the widespread distribution of many species, which have been able to spread through many river systems from bay to bay (Gunter, 1937), or through the dispersal of their larvae, which may be more tolerant of higher salinities than the adults. It is possible, especially on the Gulf Coast, for strictly freshwater organisms to migrate from river to river via stream confluences at the deltas since late Pleistocene time (Price, 1942). Some species are exclusively fresh water in habit. It is of interest to note that while many marine animals, including such decapod Crustacea as the blue crab, *Callinectes sapidus*, frequently invade freshwater, very few fresh water organisms, once established in this environment and spawning therein, return to the sea. Exceptions of course are the anadromous fish such as salmon and sturgeon. The gizzard shad, *Dorosoma cepedianum* (Le Sueur) of the eastern and middle United States is a partially anadromous species (Gunter, 1945) with completely landlocked populations and others which invade brackish waters, behaving in this respect like some populations of *Macrobrachium*.

The principal characters of the genus *Macrobrachium* are as follows: the carapace bears a prominent rostrum, and has two spines, the antennal spine on the anterior margin below the orbit, and the hepatic spine, obliquely below the antennal spine, well behind the anterior margin of the carapace. There is a short, well developed branchiostegal groove from the anterior margin of the carapace to the hepatic spine. There are two pairs of spines on the dorsal surface of the telson and two pairs on the posterior margin. The mandible bears a three jointed palp. The eyes are well developed, with a black cornea. The first two pairs of legs are chelate, and the second chelipeds are usually large in the adult (hence the generic name *Macrobrachium*), and spiny. The last three pairs of legs are simple.

The species found in the United States may be determined according to the following key:
1. Carpus (i.e., "wrist" jt.) of second chelipeds as long as, or longer than, the merus (preceding jt.)
Carpus of the second leg or cheliped distinctly shorter than merus, right and left chelipeds subequal. Both fingers provided with a single large triangular tooth. Rostrum arched over eye, tip directed upwards, four to six teeth dorsally behind orbit

2. Chelipeds similar, subequal, with straight fingers; rostrum somewhat arched, two to four teeth dorsally behind orbit
Chelipeds dissimilar, larger one heavier, with inflated palm, fingers of smaller chela arched, gaping; rostrum comparatively straight, with 12-15 small teeth dorsally, 4-5 behind the orbit

3. Dorsal teeth of rostrum continued out to tip, two behind orbit, ventral teeth more or less regularly spaced along rostrum; chelipeds large, strong, fingers covered by velvet or felt-like pubescence, with single large proximal tooth and small denticles behind
Distal tip of rostrum without spines dorsally and ventrally, 3-4 teeth dorsally behind orbit; chelipeds small, fingers naked or with scattered tufts of setae, with small, equal teeth proximally

MACROBRACHIUM ACANTHRUS (Wiegmann)

This species is readily separable from the others by the long slender, cylindrical carpus and chela, and the presence of but two teeth on the

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Figure 1. Chela and rostrum of a, Macrobrachium acanthurus; b, M. carcinus; c, M. obione; d, M. olfersii.
rostrum behind the orbit. The fingers are covered with a felt-like growth of fine setae, which are usually covered with mud. In life, this species is a generally olive green color, shading to blue on the edges of the abdominal pleura and the uropods. There is a broad, brownish orange stripe along the median dorsal surface of the abdomen. Specimens measuring 120 to 150 mm. from tip of rostrum to tip of telson are commonly found, and the chelipeds are about half again as long, i.e., 180-225 mm. An adult male is thus about fifteen inches in total length from telson to tip of the extended cheliped. The largest male in the U. S. National Museum collection measures 166 mm. from rostrum to telson. The females are somewhat smaller, and ovigerous specimens ranging from 36 to 110 mm. have been noted.

The range of this species is from St. Simon Sound, Georgia, to Rio Grande do Sul, Brazil, and the West Indies. It is found in Florida from St. Augustine to Coconut Grove, in Mississippi at Ocean Springs and Biloxi, in Louisiana at Lockport and near Grand Isle, and occurs in Texas along the coast in the bays from Palacios to the Rio Grande, and as far as Sioux Plantation, 97 miles up the Rio Grande.

**Macrobrachium acanthurus**

Figure 2. Lateral view of *M. acanthurus*, two fifths natural size.

After the heavy rains of September, 1946, this shrimp appeared in freshwater ponds around Rockport, Aransas County, in some numbers, evidently from the Aransas River drainage. There are several specimens in the collection of the Game, Fish and Oyster Commission at Rockport, most of them brought in by fishermen from the local bays. One ovigerous female was taken from Aransas Bay on September 10, 1935, another on Oct. 1, 1946.

**MACROBRACHIUM CARCINUS** (Linnaeus)

According to Dr. Holthuis, the name *Macrobrachium jamaicense*, by which this species was formerly known, should be abandoned in favor of the Linnaean name.
This is the largest and most spectacular species found in North America, and the most easily recognized, since the carpus of the cheliped is always short regardless of the age of the animal. In life it is a handsome creature. The general dorsal color is dark brown with rich opaque cream mottling on the sides, shading into a light olive green on the edges of the pleura and the legs. The large chelipeds are greenish, with brown-black tubercles and pale orange articulations. The outer uropods are dark, almost black-green, the inner are opaque cream. The telson is dark green but not as dark as the outer uropods. The largest measured specimen, a male, is 233 mm. from rostrum to telson. The second cheliped is not as long in proportion to the body as in M. acantburus, and is but slightly longer than the body. It is much heavier than in the preceding species, however, and the large triangular teeth of the fingers are conspicuous.

*Figure 3. Lateral view of M. carcinus, about three tenths natural size.*

Because of its spectacular size, this crustacean is usually saved when caught, and specimens can be found in almost every town on the Texas coast, crammed into a two quart or gallon jar, displayed in restaurants and sporting goods stores. The range of this species is from St. Augustine, Florida, to Santa Catharina, Brazil, and the West Indies. It is found in several places in Florida, from St. Augustine to Miami and Big Pine Key, and in Texas from Matagorda Bay to the Rio Grande, but it has not been recorded from intervening localities. It is often taken in Texas rivers at considerable distances from the bays, and there are records from the Colorado River near Austin, San Marcos River near San Marcos, San Antonio, the Nueces River (it seems to be common in Lake Corpus Christi near Mathis, the water supply reservoir for Corpus Christi), the Rio Grande at Brownsville, and Devils River, Valverde County.

A specimen taken alive in Aransas Bay on October 10, 1946, was kept alive in an aquarium for two days. It appeared to be an alert and intelligent
creatures. When poked at with a pencil, it would reach beyond the pencil for the hand that held it, a somewhat disconcerting maneuver. The long chelipeds of these shrimp enable them to reach anywhere about themselves, and they are difficult to pick up alive without tongs or forceps. Several specimens of *Macrobrachium carcinus* taken from bay waters were observed to have small barnacles on the carapace. These appear to be young specimens of *Chelonibia patula* (Ranzani), a species often found on crabs and on the Diamond Back Terrapin.

**MACROBRACHIUM OHIONE** (Smith)

The shape of the tip of the rostrum, prolonged to a dagger like point, separates this species from the other three found in the United States. It is also the only species of the four in which the females are larger than the males. The second chelipeds are comparatively small in comparison with those of the other species. They are about as long as the body and rather slender. In the adult the fingers of the chelae bear a few small teeth or spinules on the proximal half. The general color is pale gray flecked with small blue spots; the uropods are pale blue. Females of this species occasionally attain a size of 100 mm. (102 being the largest known), and ovigerous specimens ranging from 34-90 mm. have been observed (Mc Cormick). The largest male noted by Gunter (1937) was 68 mm.

This species is the only endemic member of the genus in North America, and is found from Avoca, North Carolina, to Aransas Bay, Texas, and has been recorded from the following localities:

North Carolina—Avoca, Bertie Co., Newport River, Carteret Co.
South Carolina—Cooper River, Edisto River below Dawkwo River.
Georgia—Savannah, Chatham Co., entrance to Altamaha River, Satilla River, Umbrella Creek.
Alabama—Pinto Island, Mobile Bay, early May, 1929. (Fiske M. D. Burkenroad).
Mississippi—Greenville, Washington Co., Milliken's Bend and Vicksburg, Warren Co., Passa-
goula, Jackson Co., Baldwin Lodge, Hancock Co.
Arkansas—Fort Smith, Sebastian Co., Red River.
Ohio—Ohio River at mouth of Great Miami R., S. W. Hamilton Co., mouth of White Oak Creek, Braddock, Scitoto Co., Perry To., Lawrence Co., White River below mouth of Missisqam River, Washington Co. (All Ohio records supplied by Mr. Milton B. Trautman, who reports that this shrimp is taken abundantly in S. W. Ohio only in the spring.)
Illinois—Cairo, Grand Tower, Chester, Shawneetown, lower Kaskaskia River (Luce, 1933).
Missouri—St. Louis, Hillcrest, Jefferson Co.
Indiana—Cannelton, Lawrenceburgh.
Oklahoma—Clear Lake, McCurtain Co.
Texas—Trinity River near Magnolia Point, Long Lake near Palestine, Big White Oak Bayou near Houston, Colorado River near Austin, Onion Creek 10 mi. west of Austin, Lavaca River, Mesquite Bay, Copano Bay, Aransas Bay as far south as Harbor Island.

This shrimp is especially widespread and common in southern Louisiana, where it is of undetermined importance as an item of food. Inasmuch as it is sold by individuals from door to door and directly to retail markets, there is no information available on the numbers caught or as to seasonal variations in the population. McCormick (1934) reported a small fishery for this species at Chester, Illinois, but that fishery seems to have been abandoned in recent years and the Illinois Natural History Survey has no information on its present commercial use in that state. Gunter (1937) suggested that the fishery in Louisiana amounted to several thousand pounds a year at that time. According to the Report of the Louisiana Conservation Commission for 1914-16, which incidentally contains what is evidently the
first published photograph of *Macrobrachium ohione*, the annual value of this fishery was then $150,000. Luce (1933) reports its use as fish bait in the Kaskaskia River, Illinois.

In Louisiana the fishery is carried on during the summer months. Traps constructed of slats, similar to lobster pots (which have the advantage of allowing the young to escape), are the usual gear employed for catching the shrimp. They are baited with raw meat, fish or cottonseed.
cake. Cottonseed cake is sometimes placed in holding cages after the shrimp are caught to convince possible customers that more repulsive bait has not been used. In Illinois, the shrimp were caught by "sets" of green willow and cottonwood branches stuck into the mud near the river bank and broken over. In the lower river the young are found in shallow water, and the traps are set in deeper water in Louisiana. Individuals are often caught with pole and line by fishermen.

According to Gunter's notes (1937) on this species, the spawning season in the lower Mississippi area occurs from about April to July. Ovigerous females were taken from April 14 to July. It appears that a fairly large percentage of females do not bear eggs during the breeding season. The shrimp were found in bay water ranging from 1.38 to 14.24 °/00, without apparent effect on the development of the eggs. There is some indication that this species reacts unfavorably to high turbidity. If high turbidity during flood periods interferes with respiration of these shrimp it may explain their frequent appearance in bays during such seasons of the year.

MACROBRACHIUM OLFERSII (Wiegmann)

Unlike the foregoing species, the chelae of the second chelipeds of this species are unequal in size. Regenerated chelae are smaller but of the same shape as the originals. The larger chela is broad, rather flat, with well bowed fingers, and the outer surface of the palm is adorned with numerous fish-hook like spines which are directed forward. The narrow, finely toothed rostrum is a distinctive character. This is a small species: males measure up to 90 mm. and ovigerous females from 30 to 65 mm.

This species ranges from Florida, through Central and South America from Vera Cruz, Mexico to Santa Catharina, Brazil. In the United States it is found only at Davenport Park, Alcazar Pool and Old Waterwork Pool, St. Augustine, Florida. Obviously its occurrence in Florida is far outside its normal range, and it is somewhat of a mystery. Schmitt (1933) suggested that it may have been introduced accidentally. Oddly enough, two other species, M. acanthurus and M. carcinus, are also found in the Alcazar Pool.

GENERAL COMMENTS

As Ortmann (1902) pointed out more than forty years ago, Macrobrachium is probably a very recent genus which is in the act of immigrating into fresh water, and has yet to complete the process. It would appear, to judge from its widespread distribution in the lower and middle Mississippi drainage, that M. obione is the oldest species of the four in North America, and that M. carcinus and M. acanthurus are of about equal age. Because of its widespread occurrence in Texas rivers, M. carcinus is evidently less dependent on salt water to complete its breeding cycle than M. acanthurus. A curious anomaly in the known distribution of M. carcinus is its absence from the Mississippi River and the area between Florida and Louisiana. This may be due primarily to inadequate records, but it is possible that the species may not be able to compete with M. obione in the heart of the latter's range. The two large species, M. carcinus and M. acanthurus, overlap on the Texas coast and do not appear to be strong competitors, to judge from their common occurrence in the Alcazar Pool at St. Augustine. The sporadic distribution of M. olfersii is clearly a special case, inexplicable except as a result of human intervention, on the basis of our present information.
Figure 5. Distribution map indicating the occurrence of *Macrobrachium* in the United States.

An interesting feature of the distribution of *M. ohione* is its apparent restriction to a narrow portion of the South Atlantic seaboard in contrast to its widespread occurrence in the Mississippi below St. Louis, and in the Ohio River as far north as Washington County, far from the influence of salt water (see the distribution map, Fig. 5). It also seems to be absent from Florida. Insofar as tidewaters are concerned, this distribution is much the same as that coastal marine fauna which skips southern Florida and is found on the temperate northern shore of the Gulf of Mexico and the southeast Atlantic coast below Cape Hatteras. This distribution pattern is well indicated in Hutchins' (1947) recent paper on temperature zonation and geographical distribution. The northern distribution of *M. ohione* along the Atlantic coast agrees substantially with the surface isotherm of the minimum monthly mean of 45° F. It may be, in regions where this shrimp is a comparatively recent immigrant, that it is still dependent on bay waters to complete its breeding cycle and is accordingly dependent on these temperature ranges as well as upon salinity. There is opportunity here for investigations on the rate of dispersal of this shrimp in watersheds of the southern Atlantic states which might produce interesting information bearing on the general problem of geographical distribution and dispersal. It is interesting to note that Traubman's records for the occurrence of *M. ohione* in the Ohio River at the northern limit of its range indicate that this species occurs there only during the spring and summer months and that it was taken abundantly only in extreme southwestern Ohio in late May and early June.

Experiments conducted by Pora (1938) on the salinity tolerance of *Palaemon squilla*, a palaemonid of the Black Sea which is found in salinities from 8 to 20 0/00, and also in fresh water, indicated that his material was
stenohalin in reaction although the species has a euryhalin distribution pattern. When specimens were exposed to higher salinities, mortality was higher during the early hours of the experiment, but mortality decreased after prolonged exposure to high salinities. The reaction to decreased salinity was the reverse, i.e., low mortality at the onset of the experiment, followed by increasing mortality with prolonged exposure to lesser salinities than the "normal" salinity from which the experimental specimens were collected. The results of this experiment suggest, according to Pora, the existence of physiological species. It would be interesting to conduct similar experiments on *M. obione*, for it is quite possible that this species, in view of its distribution pattern, has two or more physiological races.

It was formerly believed that *M. acanthurus* and *M. carcinus* occurred on both Atlantic and Pacific sides of Central America, but more critical examination of the material by Dr. Holthuis has failed to substantiate this. Instead, we have pairs of closely related, comparable species:

**Atlantic**
- *M. acanthurus* (Wiegmann)
- *M. carcinus* (Linnaeus)
- *M. olfersii* (Wiegmann)

**Pacific**
- *tenellum* (Smith)
- *americanus* Bate
- *digueti* (Bouvier)

There appears to be no Pacific counterpart of *M. obione*.

Some interest has been expressed in the possibility of artificial propagation of these shrimp. It seems probable that small numbers could be maintained in lakes and spring fed ponds, but as yet our knowledge of the life history of any species is too fragmentary to be of help to fish-culturists. According to Gunter (1937) many apparently mature females of *M. obione* were not ovigerous during the breeding season, while McCormick (1934) found that ovigerous females also had immature eggs in their ovaries. Evidently the breeding season of *M. obione* is long, and this information indicates that either some of the shrimp may not spawn until the second year, or that two year old shrimp do not spawn. Further study is necessary to clarify this point, but the small size of many ovigerous females indicates that the second alternative is more probable. The occurrence of *M. acanthurus* in September and October indicates that this species has a later breeding season than *M. obione*.

Little is known of the food preferences of any other species than *M. obione*. McCormick (op. cit.) suggested that this species is omniverous and that it has been caught on green willow and cottonwood branches because of its habit of "chewing the green leaves." In Louisiana its food habits are those of the typical shrimp—old meat and dead fish. It will also attack live fish held in live boxes, sometimes "skinning catfish alive" according to Gunter. Probably all of the species are predominantly meat eaters, taking their food as they find it, alive or dead.

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