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DISTRIBUTIONAL RECORDS FOR FRESHWATER MUSSELS (BIVALVIA: UNIONIDAE) IN FLORIDA AND SOUTH ALABAMA, WITH ZOOGEOGRAPHIC AND TAXONOMIC NOTES

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ABSTRACT - New distributional records are presented for Florida and south Alabama unionids. The data represent recent collections, unpublished museum records and corrected literature records. The first substantiated records of *Ptychobranchus jonesi* in Florida, from specimens collected over 50 years ago in the Choctawhatchee River system, are given. *Anodonta suborbiculata*, not collected in Florida for 70 years, has recently been rediscovered in the Escambia River. The type locality for *Lampsilis haddletoni*, known only from the two specimens of the type series, is corrected to read Choctawhatchee River, West Fork, seven miles southeast of Ozark, Dale County, Alabama. Earlier reports of *Amblema perplicata* from the Yellow River are in error; the published locality data actually represent a Choctawhatchee River system record. In addition to *A. perplicata*, *Villosa villosa* also occurs in the Choctawhatchee River system, thus representing eastward and westward, respectively, range extensions for these two species. The ranges of *Anodonta grandis* and *A. peggyae* are extended westward to the Escambia River system. *Lampsilis teres* has been found in the Hillsborough River, thus extending its range southward. No longer considered an endemic of the Choctawhatchee River system, *V. choctawensis* also occurs in the Yellow and Escambia river systems. New drainage records for *Elliptio icterina* (Aucilla River), *Glebula rotundata* (Choctawhatchee River), *Medionidus penicillatus* (Choctawhatchee River), *Toxolasma paulus* (Alafia River), *Uniomerus caroliniana* (Waccasassa River), *V. vibex* (Alafia and St. Marys rivers) and *V. villosa* (Alafia, St. Marks and Waccasassa rivers) are herein reported. *Elliptio icterina* represents the only unionid record known from the Aucilla River system. These records add from one to four species to the known unionid fauna of nine drainages in the Apalachicolan Region of Florida and south Alabama and Peninsular Florida.

One genus (*Elliptoideus*) and at least 32 species are endemic to the Apalachicolan Region and Peninsular Florida, an important area for speciation and endemism, where endemics comprise 56% of the unionid fauna. The Apalachicola River system and secondarily the Escambia and Choctawhatchee rivers are thought to have been major centers of species origin. Lowland species and species generally found in small streams draining into the Gulf of Mexico may have extended their ranges via lowland dispersal routes created by broadscale flood events, possibly during sea level recessions. Mainstem convergences during sea level regressions of the Late Miocene and Late Pliocene have possibly facilitated dispersal of several species characteristic of larger rivers.

Stream captures are also thought to have played a substantial role in the dispersal of unionids characteristic of headwater tributaries, especially in the Apalachicolan Region. Evidence suggests two major centers of dispersal in the Apalachicolan Region; from the Escambia east towards the Choctawhatchee River, and from the Apalachicola River eastward. An Early Pliocene marine terrace, the Cody Scarp has apparently influenced the distributions of *Amblema perplicata, Fusconaia rotulata* and *Glebula rotundata;* the Apalachicolan Region distribution of all three species is restricted to localities downstream of the Cody Scarp. The possibility of valid but presently synonomized species is discussed. The current state of taxonomic confusion hinders attempts to clarify unionid zoogeography.

Key words: freshwater Bivalvia, distribution, zoogeography, taxonomy, Florida, Alabama.

INTRODUCTION

Florida and south Alabama unionid clams have been of considerable interest to malacologists. During the 1800's studies consisted primarily of descriptions of new species. Walker (1905) reported on collections of shells from the Chipola River and a tributary of Econfina Creek in northwest Florida. Based on extensive collections made primarily by C. A. and J.A. Burke between 1915 and 1918, van der Schalie (1940) discussed unionid distributions in the Chipola River, an Apalachicola River tributary.

In the early 1950's, Clench & Turner (1956) made numerous collections in drainages from the Escambia to the Suwannee rivers. Combined with earlier records, their work remains the benchmark treatise of the region's unionid fauna. Athearn (1964) described two new species from the Choctawhatchee River and presented conchological evidence for separating *Villosa australis* (Simpson 1900) from *Ptychobranchus jonesi* (van der Schalie 1934), two species which Clench & Turner (1956) considered to be synonyms.

Johnson (1965, 1967a, 1968, 1969, 1970) reported on unionid distributions and systematics in eastern Gulf of Mexico drainages and the St. Marys River of the Atlantic Slope while adding to the fauna a new species, *Anodonta peggyae* Johnson 1965, and several species overlooked by previous investigators. Johnson (1972) also published on the unionids of Peninsular Florida, covering drainages south of the Suwannee and St. Marys rivers.

Fuller & Bereza (1973) and Burch (1975) further refined the ranges of some eastern Gulf drainage endemics. The genus *Medionidus* was monographed by Johnson (1977), and included the known distributions of the three Gulf drainage species. The only comprehensive work encompassing the unionid fauna of Florida was Heard's (1979) identification manual, which included species lists for most of the state's major drainage systems.

Despite the number of studies that have considered unionid distributions in Florida and south Alabama, large sections of numerous rivers and their tributaries remain inadequately, or sometimes totally, unsampled. Athearn (1964) made note of the fact that streams in west Florida were poorly collected. Because of the dearth of records from the Yellow River and other small streams entering the Gulf of Mexico, Clench & Turner (1956: 105) omitted them completely in a table summarizing unionid occurrences in eastern Gulf drainages. The Florida portions of the Escambia, Yellow, Apalachicola, Ochlockonee (below Talquin Reservoir) and Aucilla river mainstems are virtually unsurveyed. Although numerous lots of material from sites along the mainstem Choctawhatchee River are housed at the Florida Museum of Natural History, most of the collections were made over half a century ago.

The intent of this study is to augment and further clarify unionid distributions in this region. Miscellaneous notes concerning zoogeography and taxonomy of study area unionids are also included.

METHODS

The distributional records presented herein were obtained from recent collections (personal or otherwise), unpublished museum records and corrected literature records. The author is understood to be the collector unless otherwise stated. Museum records were gathered from Florida Museum of Natural History (UF), Ohio State University Museum of Zoology (OSUM) and The University of Michigan Museum of Zoology (UMMZ). The number of specimens in a lot appears in parentheses after the museum designation and catalog number. Voucher specimens for new records collected by the author are deposited in the Florida Museum of Natural History. Scientific and common names generally follow Turgeon *et al.* (1988).

The Apalachicolan Region as defined by Clench & Turner (1956) is used in this study (Gulf of Mexico drainages from the Escambia to the Suwannee

rivers). Peninsular Florida is considered to include the remaining drainages of Florida inclusive of the Waccasassa and St. Johns rivers south (Johnson, 1972), in addition to the St. Marys River, which has a lowland unionid fauna very similar to that of the St. Johns. These two regions are collectively referred to as the study area. The Panhandle comprises Florida portions of drainages from the Escambia to the Ochlockonee rivers, while the Big Bend region encompasses small, lowland drainages between, but not including, the Ochlockonee and Suwannee rivers. Species ranges generally consider only that portion occurring in the study area (for complete range information, see Burch, 1975). Fig. 1 identifies river systems for which new drainage records are presented as well as drainages mentioned in the discussion. Econfina Creek of the Florida Panhandle should not be confused with Econfina River, located to the east in the Big Bend region. Standard state and directional (compass) abbreviations are used in locality information. Distances appearing in locality data of personal collections are expressed in kilometers (km) while distances for many museum records may be expressed in miles (mi). Where measurements (in millimeters) appear in the text, L = length (anterior to posterior extremities), H = height (dorsal to ventral extremities) and W = width (obesity).

SPECIES ACCOUNTS

Amblema perplicata (Conrad 1841) (Roundlake)

Amblema perplicata is reported from the Escambia and Yellow rivers in Alabama and Florida (Johnson, 1970; Burch, 1975). The Yellow River record was based on Johnson's (1970: 270) assumption that Picket Wretch Lake, Walton County, Florida, is in that system, when actually it is in the Choctawhatchee River system. Specimens from this site collected in August 1934 by L. M. Rushing are cataloged UF 1481 (3) and UF 3231 (1). The following additional collections are from the Choctawhatchee River, Walton County, Florida: Cowford Ferry, August 1934, L. M. Rushing, UF 3237 (2); Yellow Bluff, UF 3236 (2); and Oakey Bend, UF 3233 (1); the latter two collections made presumably in October 1933 by D. B. Gillis.

Anodonta grandis Say 1829 (Giant floater)

Johnson (1970) listed the range of *Anodonta grandis* in the Apalachicolan Region as the Choctawhatchee, Apalachicola

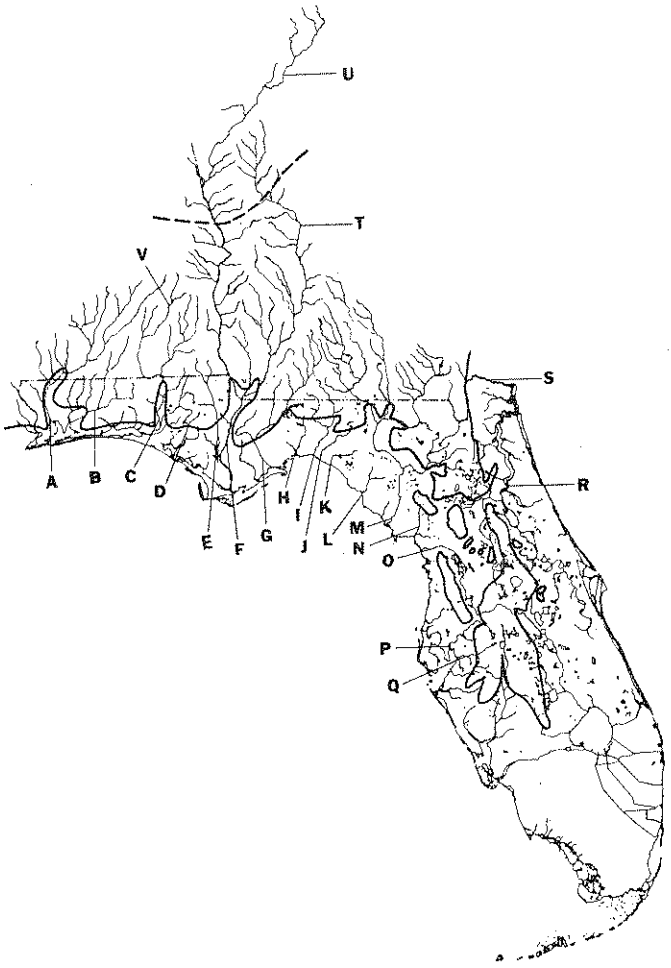

FIG 1. Drainage map (modified from Heard, 1979) of river systems comprising the Apalachicolan Region and Peninsular Florida. Drainages with new unionid records and other drainages mentioned in the discussion are identified: A) Escambia; B) Yellow; C) Choctawhatchee; D) Econfina Creek; E) Chipola; F) Apalachicola; G) Ochlockonee; H) St. Marks; I) Aucilla; J) Econfina River; K) Fenholloway; L) Steinhatchee; M) Suwannee; N) Waccasassa; O) Withlacoochee; P) Hillsborough; Q) Alafia; R) St. Johns; S) St. Marys; T) Flint; U) Chattahoochee; V) Pea. The bold solid line depicts the approximate location of the Cody Scarp, an Early Pliocene high-sea stand about 30 m above present mean sea level. The bold dashed line depicts the approximate location of the Fall Line, the divide between the Piedmont and Coastal Plain physiographic provinces.

and Ochlockonee river drainages. Johnson (1970) also stated that Clench & Turner's (1956) records for *Anodonta gibbosa* Say, 1824 in this area were apparently *A. grandis*. *Anodonta grandis* also occurs in the Escambia River system, Conecuh River, Alabama, author and W.H. McCullagh: US hwy. 231 crossing, Pike County, 27 August 1988, UF 134931 (1); and US hwy. 29 crossing, below Gantt Dam, Covington County, 28 August 1988, UF 134932 (1). An additional collection is representative of the Escambia River system, Florida: Chumuckla Springs, Santa Rosa County, 3 June 1988, author, R. S. Howard and D. Nowling, UF 134929 (2).

Anodonta peggyae Johnson 1965
(Florida floater)

In his description, Johnson (1965) reported that *Anodonta peggyae* ranged from the Choctawhatchee to Hillsborough rivers. Heard (1979) also included the Yellow River in Florida as being within the species range. The range of *A. peggyae* is extended to the Escambia River system based on the following collections from Santa Rosa County, Florida, May 1917, C. A. Burke: Chumuckla Springs, UMMZ 163896 (24); and Escambia River, near McDavis, UMMZ 163571 (1).

Anodonta suborbiculata Say 1831
(Flat floater)

In 1917, C. A. Burke collected a specimen of *Anodonta suborbiculata* from Chumuckla Springs, Escambia (actually Santa Rosa) County, Florida, UMMZ 101375 (1). W. H. Heard (pers. comm.) considered this the only known record for Florida. Recent efforts to secure additional specimens at Chumuckla Springs proved unsuccessful. However, the species was rediscovered in the Escambia River, Florida hwy. 4 crossing, Escambia-Santa Rosa counties, Florida, 3 June 1988, UF 134930 (1). The small specimen was estimated to be about four years old and found in riverine habitat, generally non-typical for *Anodonta suborbiculata* (Johnson, 1980; Gordon, 1984), at a well

collected site. The occurrence of *A. suborbiculata* in Florida should be considered sporadic at best.

Elliptio icterina (Conrad 1834)
(Variable spike)

Elliptio icterina is a highly variable form with numerous synonyms (Johnson, 1970, 1972) and is most likely a species complex. Since the type locality is in the Savannah River, it is possible that *E . icterina sensu stricto* does not occur in the study area. However, due to the fact that the specific epithet has been widely used in the literature in referring to Florida region forms (Johnson, 1970, 1972; Burch, 1975; Heard, 1979), *icterina* is used here simply for the purpose of reducing confusion.

Although *Elliptio icterina* has been reported from most drainages in the study area (Johnson, 1970, 1972; Heard, 1979), records were, up to now, not available for the Aucilla River. Specimens of *E. icterina,* collected at the US hwy. 27 crossing of the Aucilla River, Taylor-Jefferson counties, Florida, 28 September 1986, H. G. Lee and W. H. McCullagh, UF 134938 (2), represent the only record for unionids in the Aucilla River system.

Glebula rotundata (Lamarck 1819)
(Round pearlshell)

The Apalachicolan Region distribution of *Glebula rotundata* was reported to be the Escambia and Apalachicola rivers (Clench & Turner, 1956; Johnson, 1970; Heard, 1979). The following represent new drainage records for the Choctawhatchee River system, Walton County, Florida: Oakey Bend Lake, October 1933, D. B. Gillis, UF 3878 (3); and Bushy Point Lake, 1933, D. B. Gillis, UF 3877 (2); both Choctawhatchee River; and Dainley Fish Lake, August 1934, L. M. Rushing, UF 3876 (12) and UF 8401 (1). The present status of *Glebula rotundata* in this system is unknown.

Clench & Turner (1956: 192) considered *Glebula rotundata* to be "exceedingly rare" in the Apalachicolan Region. *Glebula*

rotundata, however, is actually one of the most commonly encountered unionids in Dead Lake (Chipola River) and the lower Apalachicola River. *Glebula rotundata* should be looked for in the lower mainstems of the Yellow and Ochlockonee rivers.

Lampsilis haddletoni Athearn 1964
(Haddleton lampmussel)

Lampsilis haddletoni is known only from the type locality: Choctawhatchee River, West Fork, seven miles southwest of Ozark, Dale County, Alabama (Athearn, 1964; Johnson, 1967a). The West Fork, however, flows east of Ozark, thus making the locality erroneous. The type locality is corrected to read: Choctawhatchee River, West Fork, 7 mi. southeast of Ozark, Dale County, Alabama. This locality is mentioned elsewhere in the publication of the original description (Athearn, 1964: 138)

Lampsilis teres (Rafinesque 1820)
(Yellow sandshell)

In the study area, *Lampsilis teres* was reported in Gulf drainages from the Escambia to the Withlacoochee rivers (Heard, 1979). The range of *Lampsilis teres* is extended south to the Hillsborough River, Hillsborough County, Florida: Florida hwy. 582 crossing, 19 April 1974, H. G. Lee, UF 47282 (17); and Florida hwy. 579 crossing, 4.4 km SSW of Branchton, 7 April 1988, UF 134939 (2).

Medionidus penicillatus (Lea 1857)
(Gulf moccasinshell)

An Apalachicolan endemic, *Medionidus penicillatus* has been collected in Econfina Creek, Chipola and Apalachicola rivers

and disjunctly in the Yellow River, Alabama (Johnson, 1977). Museum lots from several sites in the Choctawhatchee River system, Walton County, Florida, were examined: Choctawhatchee River, east of Red Bay, October 1933, D. B. Gillis, UF 4139 (2); Limestone Creek, August 1933, D. B. Gillis, UF 4151 (8); Sandy Creek, September 1933, D. B. Gillis, UF 4147 (1); and Bruce Creek, July 1933, D. B. Gillis, UF 4157 (1). The current status of *Medionidus penicillatus* in the Choctawhatchee River system is uncertain.

Ptychobranchus jonesi (van der Schalie 1934)
(Southern kidneyshell)

Burch (1975) stated that the distribution of *Ptychobranchus jonesi* was the Choctawhatchee River system of Alabama and Florida and the Escambia River system in Florida. However, there was no mention of specific Florida records for *Ptychobranchus jonesi* by van der Schalie (1934), Athearn (1964), Johnson (1967a), Fuller & Bereza (1973) nor Heard (1979). The first substantiated Florida records are from the Choctawhatchee River system, Walton County: Sam Stacey's Landing, Choctawhatchee River, (presumably 1933), D. B. Gillis, UF 8429 (1); and Sandy Creek, September 1933, D. B. Gillis, UF 8430 (1). The present status of *P. jonesi* in Florida is unknown.

Toxolasma paulus (Lea 1840)
(Iridescent lilliput)

Toxolasma paulus, as *T. parvus* (Barnes, 1823), has been collected in most of the major drainages of the study area from the Hillsborough and Kissimmee rivers north (Johnson, 1972; Heard, 1979). A small Peninsular Gulf drainage south of the Hillsborough River, the Alafia River system also contains *T. paulus*: Fish Hawk Creek, 3.8 km southwest of Lithia, Hillsborough County, Florida, 2 March 1988, UF 134933 (26).

Uniomerus caroliniana (Bosc 1801)
(Florida pondhorn)

Heard (1979) reported *Uniomerus caroliniana* from most of the major drainages of Florida. A population also exists in Waccasassa River, Alternate US hwy. 27 crossing, Levy County, Florida, 6 July 1988, UF 134928 (9). Other small, poorly surveyed rivers draining Florida's Gulf coast may harbor additional populations of *Uniomerus caroliniana.*

Villosa choctawensis Athearn 1964
(Choctaw bean)

Villosa choctawensis was thought to be endemic to the Choctawhatchee River system (Athearn, 1964; Johnson, 1967a, 1970; Burch, 1975; Heard, 1979), recent collections extend the range of *Villosa choctawensis* into the Yellow River in Alabama and Florida and the Escambia River system in Alabama. Yellow River mainstem localities include: 12.3 mi south southeast of Andalusia, Covington County, Alabama, 16 September 1973, B. Wall and H. Harima, OSUM 34713 (2); and Florida hwy. 2 crossing, 7.2 km east of Blackman, Okaloosa Co., Florida, 2 June 1988, UF 135794 (2). The following represent records for the Escambia River system, Alabama: Pigeon Creek, 7.7 mi east southeast of Greenville, Butler County, 9 October 1986, F. G. Thompson, UF 123279 (1); Patsaliga River, at Horton's Lake, 10 mi N of Searight, Crenshaw County, July 1915, C. A. Burke, UF 134937 (1); and Little Patsaliga Creek, Alabama hwy. 50 crossing, at Potsburg, Crenshaw County, 1 October 1967, H. G. Lee, OSUM 23432 (1). Although no specimens are known from the Florida portion of the Escambia River system, *Uniomerus caroliniana* may also occur there.

Villosa vibex (Conrad 1834)
(Southern rainbow)

Villosa vibex is generally distributed throughout most of the study area (Johnson, 1970, 1972; Burch, 1975; Heard, 1979).

However, published records for the St. Marys River system were, up to now, lacking. Specimens from the St. Marys drainage were collected from the following tributary: Brandy Branch, US hwy. 301 crossing, Nassau County, Florida, 19 June 1988, author and J. D. Williams, UF 134934 (1).

Although Johnson (1972: 189) failed to note *Villosa vibex* in the Alafia River, his list of specimens examined (Johnson, 1972: 238) included a record (under Hillsborough River System) for Fish Hawk Creek, near Lithia, Hillsborough County, Florida. The presence of *Villosa vibex* in the Alafia River system has been substantiated by a recent collection from Fish Hawk Creek, 3.8 km southwest of Lithia, Hillsborough County, Florida, 2 March 1988, UF 134935 (16).

Villosa villosa (Wright 1898)
(Downy rainbow)

Villosa villosa has been recorded from most of the major rivers from the Chipola River eastward to the St. Marys River and southward to the St. Johns and Myakka rivers (Johnson, 1972; Heard, 1979), but has not been reported from several of the smaller drainages within this range. The range of *V. villosa* is extended westward to the Choctawhatchee River system, Florida: Horseshoe Lake, 1933, D. B. Gillis, UF 3159 (42) and September 1934, L. M. Rushing, UF 3161 (5); both Washington County; Bushy Point, UF 3168 (26) and UF 8456 (1); Oakey Bend, UF 3160 (9); and Inlet Lakes, UF 3156 (13); all Walton County, October 1933, D. B. Gillis. Although specimens from these localities are somewhat shinier with more prominent green rays than typical *V. villosa*, they are very similar in most other shell characters. Other Florida drainage records are: St. Marks River, US hwy. 27 Bridge, 1 mi. east of Chaires Crossroads, Leon County, 10 November 1983, G.H. Burgess *et al.*, UF 42670 (2); Waccasassa River, US hwy. 27A crossing, Levy County, 6 July 1988, UF 134936 (10); and Alafia River system, branch of Howell's Creek, 3 mi. south of Plant City, Hillsborough County, 8 November 1934, A. O. Baynard, UF 3638 (5).

Reported to be a rare inhabitant of spring-fed streams and clear rivers (Clench & Turner, 1956), *Villosa villosa* was noted by Johnson (1972: 235) as occurring also in "the rather acidic and muddy St. Marys River." *Villosa villosa* may actually occur abundantly in habitats with slack current, murky water and muddy substrate such as Talquin (Ochlockonee River) and Mosquito Creek (Apalachicola River drainage) reservoirs and Dead Lake of the Chipola River. In such lacustrine habitats specimens may reach great size. The largest of 48 specimens examined from Mosquito Creek Reservoir measured L=85, H=40, W=30. Peninsular riverine populations (*e.g.*, Hillsborough, Withlacoochee and Waccasassa rivers), where the species may also occur commonly, are diminutive in size. Of 29 specimens collected from the Hillsborough River the largest measured only L=42, H=25, W=15.5. Heard (1979) hypothesized that *V. villosa* populations displayed differential life spans; specimens achieve great size (*e.g.*, Mosquito Creek Reservoir) simply because they live longer. Further studies are needed to determine the effects of genetic and environmental factors on growth in *V. villosa.*

DISCUSSION

New Drainage Records

The newly reported drainage records add from one to four species to the previously known unionid faunas of nine streams in the Apalachicolan Region and Peninsular Florida. The addition of *Amblema perplicata, Glebula rotundata, Medionidus penicillatus* and *Villosa villosa* to the Choctawhatchee River fauna brings the total number of species reported there to 24. The presence of *Anodonta grandis, A. peggyae* and *V. choctawensis* in the Escambia River makes 29 species known for the drainage. Six species are recorded from the Alafia River system with the addition of *Toxolasma paulus, V . vibex* and *V. villosa. Villosa villosa* in both the St. Marks and Waccasassa rivers, as well as *Uniomerus caroliniana* in the latter river system, bring the total number of species in these two small drainages to five and four, respectively. The Aucilla River

Elliptio icterina record reported here is the first unionid record known for the Aucilla River system. *Lampsilis teres* in the Hillsborough River, *V. vibex* in the St. Marys River and *V. choctawensis* in the Yellow River increase the totals to nine, five and 14 species, respectively, for these three river drainages.

Not surprisingly, the lack of reported drainage records in much of the study area can generally be attributed to artifacts of sampling. The St. Marys, Alafia and other small river systems with depauperate faunas generally have not been given the collecting effortequivalent to that given larger drainages. Several species may be added to these faunas with more adequate sampling.

Inaccessability is the primary reason for the lack of unionid collections from Panhandle rivers. Few highways have bridged the wide bottomland swamps commonly associated with them. Like large rivers elsewhere in southeastern United States, low water conditions are imperative for adequate sampling. The larger rivers should be floated to ensure better access to mussel beds. In addition, SCUBA is necessary to determine the presence of unionids in deeper river channels.

Speciation and Endemism

Prolonged marine isolation of large river systems has promoted a high degree of speciation and endemism in the study area, especially in the Apalachicolan Region. Portions of the upper Apalachicola River system (Chattahoochee and Flint rivers) occur above the Fall Line, the topographic boundary between the Piedmont and Coastal Plain physiographic provinces (Fig. 1). Drainages of the upper Apalachicola River system have existed since at least Late Mesozoic (Swift *et al.*, 1986) and persisted during subsequent high sea level stands (*e.g.*, Middle Miocene and Early Pliocene) that obliterated several of the adjacent drainages. The age and isolation of the upper Apalachicola River system have made the area an important center of speciation.

The Escambia and Choctawhatchee river drainages have apparently served as important centers of origin as well. The

size of their drainage basins, intermediate location between the faunistically rich Mobile Bay and Apalachicola River systems and presence of several species endemic to one or both rivers (and in many cases the intermediate Yellow River) are evidence for this assertion. The origin and dispersal of the unionid fauna of these rivers will be discussed at length in the following section. The Chipola, Ochlockonee and Suwannee rivers may have fostered speciation also; each system contains at least one endemic species (Johnson, 1970; Heard, 1979). Occurrence of endemics possibly indicates either relatively recent evolution or inability of these species to disperse, possibly due to ecological restrictions of the mussels themselves or their host fishes. One endemic genus (*Elliptoideus*) and at least 32 endemic species presently comprise the fauna of the Apalachicolan Region and Peninsular Florida. Endemic species comprise 56% of the unionid fauna in these areas.

Methods and Routes of Dispersal

Considering the lowland nature of much of the Big Bend portion of eastern Gulf coastal Florida, some species should be more generally distributed than past studies have indicated. Dispersal of lowland or small stream species via low, swampy regions could be facilitated during unusually high fresh water conditions that have occurred periodically in Recent as well as over geologic time. Furthermore, drainage divides between many systems in the Big Bend region are ill-defined. Many of the new distribution records presented herein may conceivably be explained via such a dispersal method.

According to Swift *et al.* (1986), the freshwater fish fauna of Big Bend drainages are nearly identical. The fish family Centrarchidae, with several species generally distributed in this area, has been very successful at invading new drainages via swampy, lowland routes (Swift *et al.*, 1977; Bermingham & Avise, 1986), particularly during sea level regressions. It is interesting to note that as a family, centrarchids serve as glochidial host for 35% of the North American unionids for which fish host species are known (Fuller, 1974). Fish hosts for study area unionids are virtually unknown. Centrarchids are

excellent candidates, however, due to their widespread distribution, abundant populations and the relatively high percentage of species composing the fish fauna.

With these considerations in mind, rivers such as the St. Marks, Aucilla, Econfina, Fenholloway and Steinhatchee (Fig. 1) would be expected to have very similar unionid faunas. Although Swift *et al.* (1986) showed that the Waccasassa River freshwater fish fauna clustered with rivers to the south (and not Big Bend drainages), its unionid fauna is probably similar to other small, lowland Big Bend streams. However, it should be kept in mind that poorly understood ecological factors may preclude occurrence of certain species from specific drainages, thus accounting for actual gaps in species distributional patterns in the absence of sampling bias. Most of these systems probably contain at least species of the *Elliptio icterina* complex, *Uniomerus carolinana, Villosa vibex* and *V. villosa*. Prior to this study, from zero to three species were reported from Big Bend streams (Heard, 1979).

Distributions of many large river forms may best be attributed to mainstem convergence, *i.e.*, presently marine-flooded mainstems that were common to two or more existing drainages. Vail & Hardenbol (1979) have traced several sea level regressions of approximately 100 meters since the Late Oligocene. The last major drops occurred during the Late Miocene and Late Pliocene (other lesser sea level regressions took place during the Pleistocene). At these intervals, which lasted up to 1-2 million years for the Late Miocene event, Peninsular Florida was nearly double in size. The area was thought to resemble present-day Florida with low gradient streams and sinkholes (Swift *et al.*, 1986). The occurrence of *Lampsilis teres* in the Hillsborough River could possibly be attributed to mainstem convergence between it and the Withlacoochee River to the north.

Although the Panhandle landmass did not expand to the degree of Peninsular Florida during major sea level regressions, Panhandle mainstems lengthened substantially nonetheless, particularly drainages from the Apalachicola River east. Convergence of river mainstems may account for the limited distribution of *Elliptoideus sloatianus* (Lea, 1840) and *Villosa subangulata* (Lea, 1840) to the Apalachicola and Ochlockonee

river systems. A sea level drop of only a few meters could have allowed a union of the Escambia and Yellow rivers (both rivers presently flow into Pensacola Bay) and conceivably resulted in the passage of *Fusconaia escambia* Clench & Turner, 1956 and possibly other species.

Previously known in extreme west Florida from the Escambia River only, the presence of *Amblema perplicata* and *Glebula rotundata* in the Choctawhatchee River may be attributed to a past mainstem confluence between these two drainages. Deviating from its southerly course, the lower Choctawhatchee River (including Choctawhatchee Bay) turns abruptly west for 65 km before emptying into the Gulf of Mexico. The mouth of Choctawhatchee Bay is 55 km east of the mouth of the Escambia River (Pensacola Bay). A number of Apalachicolan Region endemics are shared exclusively by the Escambia and Choctawhatchee rivers, and in most instances the intermediate Yellow River (*e.g., Fusconaia succissa* (Lea, 1852), *Pleurobema strodeanum* (Wright, 1898), *Ptychobranchus jonesi, Villosa australis* and *V. choctawensis*, not to mention several more widely distributed species). Furthermore, the freshwater fish fauna of the Escambia and Choctawhatchee rivers is essentially the same (Bailey *et al.*, 1954). Although one or both species may eventually be found in the lower Yellow River, an absence of *Amblema perplicata* and *Glebula rotundata* from the Yellow could possibly be attributed to the smaller size of the drainage and lack of necessary large river habitat.

The occurrence of *Glebula rotundata* in the Apalachicola River system, the easternmost drainage within its range (Burch, 1975), suggests a lowland dispersal route, possibly during lowered sea levels. The endemic *Amblema neislerii* (Lea, 1858) replaces *A. perplicata* in the Apalachicola River system.

Headwater stream captures have probably facilitated dispersal of several unionid species. It is unrealistic to assume that the distributions of the Apalachicolan Region endemics mutually shared by the Escambia, Yellow and Choctawhatchee rivers (see above) is solely attributable to lowland or convergent mainstem dispersal methods. The present configuration of the Pea River, the major western tributary of the Choctawhatchee River (Fig. 1), suggests that it may have once flowed westward into the Yellow River. If this hypothetical

capture took place subsequent to a drop in sea level, a passageway would have conceivably been created for westward species (*i.e,* those originating in the Escambia River) to reach the Choctawhatchee River.

An eastward transfer of species is favored over a westward transfer in the western portion of the Apalachicolan Region for other reasons as well. For instance, the Escambia has more species (29) than does the Choctawhatchee (24). The discrepancy in number of species is probably a result of the proximity of the Escambia to the Mobile Bay basin, faunistically the most speciose system among eastern Gulf drainages (Johnson, 1970). Secondly, a major faunal break occurs between the Choctawhatchee and Apalachicola rivers. Of the 17 Apalachicolan Region endemics found in either the Choctawhatchee or Apalachicola river systems, only *Medionidus penicillatus* is reported from both drainages. Several Apalachicolan Region endemics that probably originated in the Apalachicola River system (*e.g., Elliptoideus sloatianus, Pleurobema pyriforme* (Lea, 1857), *Quincuncina infucata* (Conrad, 1834) and *Villosa subangulata*) have apparently dispersed only eastward into the Ochlockonee and in some cases the Suwannee River system. Eastward dispersal of some unionids may have been hastened by stream capture. The channel of Telogia Creek, a major western tributary of the Ochlockonee River that flows southwesterly before completely reversing its course to the northeast, suggests that it may have been captured from the Apalachicola River (Gilbert, 1987). A westward dispersal of species originating in the Apalachicola River system, therefore, appears unlikely in most instances. The presence in the Escambia River of *Fusconaia* (represented by three species, *F. escambia, F. rotulata* (Wright, 1899) and *F. succissa*) and *Ptychobranchus,* genera present in the Mobile Bay basin but not the Apalachicola River system, is further basis for a western origin of the fauna. Therefore, it is probable that at least these three *Fusconaia* species and *P. jonesi* evolved in the Escambia River system from stock originating in the Mobile Bay basin. The three species endemic to the Choctawhatchee River (*Elliptio macmichaeli* Clench & Turner, 1956, *Lampsilis haddletoni* and *Q. burkei* Walker, 1922) possibly indicate recent evolution.

The well known interregional capture of the upper Chattahoochee River by the Savannah River may have allowed transfer of certain fishes (Swift *et al.*, 1986; Bermingham & Avise, 1986) and unionids (Johnson, 1969, 1970). Transfer of faunal elements by this capture, however, more likely resulted in species dispersing from the Chattahoochee into the Savannah River system. Johnson (1969) assumed that the occurrence of *Anodonta couperiana* Lea, 1840 in the Apalachicola and Ochlockonee river systems of Florida could be attributed to the Chattahoochee/Savannah stream capture. However, *A. couperiana* is restricted in distribution to the Coastal Plain. A much more likely scenario might be dispersal via lowland routes, possibly during sea level regressions. The present disjunct distribution of *A. couperiana* may be attributed to local extinctions in intervening drainages, especially in north Florida where only the Aucilla and Suwannee rivers separate extant lowland populations in the St. Johns River system from populations in the Panhandle. Interregional headwater captures for species primarily restricted to the Coastal Plain (as are most study area unionids) are not considered to be an important means of fish dispersal (Bermingham & Avise, 1986).

Sepkoski & Rex (1974) suggested that inter-drainage unionid transfers between streams within both the Gulf and Atlantic slopes may have taken place via salt-tolerant, secondary fishes. Seawater, however, is generally considered an absolute barrier for the dispersal of organisms restricted to freshwater. Furthermore, the passage of viable glochidia on secondary fishes through saline waters has not been proven. Until studies determine that it is possible for unionids to be transferred between marine isolated drainages by salt-tolerant fishes, this means of dispersal should be considered questionable.

Influence of Cody Scarp on Zoogeography

Physiography, as affected by sea level transgressions, has undoubtably influenced unionid zoogeography in the study area. The Cody Scarp is a conspicuous marine terrace formed during the Early Pliocene (Puri & Vernon, 1964) that has

produced a physiographic break in topography approximately 30 m above present mean sea level (Fig. 1). Previous studies have shown the scarp to be of considerable zoogeographic importance, at least for certain fishes (Swift *et al.*, 1977; Swift *et al.*, 1986; Gilbert, 1987). Streams below the scarp are typically lowland (sluggish or swampy) in nature, while streams of the rolling Northern Highlands above the scarp have flowing, meandering channels (Gilbert, 1987).

The known distributions of *Amblema perplicata* and *Glebula rotundata* in the study area are in lowland rivers exclusively below the Cody Scarp. The Escambia River endemic *Fusconaia rotulata* also appears to be limited to the portion of the mainstem from the Cody Scarp downstream. However, the distributions of other large river species in the Apalachicolan Region, such as *Amblema neislerii, Elliptoideus sloatianus, Megalonaias boykiniana* (Lea, 1840) and *Elliptio crassidens* (Lamarck, 1819), seem to be uninfluenced by this physiographic feature and these species are generally found both above and below the scarp. Biological or ecological factors have probably played major roles in the zoogeography of these species.

Taxonomic Considerations

In addition to the obvious need for further, more thorough collections, future taxonomic work is required to determine the possible validity of other forms. At present, practically nothing is known concerning the anatomy and genetics of study area species. Detailed internal and external soft anatomy studies, as well as molecular or biochemical investigations, are necessary to elucidate unionid taxonomy.

Dozens of nominal species have been described from the Apalachicolan Region and Peninsular Florida. Numerous forms were described by S. H. and B. H. Wright between 1883 and 1934 (Johnson, 1967b). Many of the Wright's *Unio's* have been synonomized under various *Elliptio* species, primarily in the work of Johnson (1972).

Similar to *Elliptio icterina* (see Species Accounts), the Peninsular endemic *E. buckleyi* (Lea, 1843) is also most likely a species complex. Nominal forms described from upland lakes and streams may have been isolated for long enough periods

during high sea level stands of the Miocene and Pliocene to differentiate from ancestral stock. A good example may be *E. subluridus* (Simpson, 1900), described from Orange Creek of the St. Johns River system. The type locality is from an area known for disjunct populations of several fish species (Burgess *et al.*, 1977; Burgess & Franz, 1978; Swift *et al.*, 1986; Gilbert, 1987). Species occupying the upland-most portion of the St. Johns River basin, Orange Creek and a few other adjacent streams (Burgess & Franz, 1978: fig. 2) were isolated during at least the Middle Miocene and Early Pliocene (Vail & Hardenbol, 1979). The duration of isolation was sufficient to allow for the evolution of several unrelated invertebrate taxa which are now endemic to the area (Burgess & Franz, 1978). Previously more widely distributed fishes survived in these upland refugia with rising sea levels (Gilbert, 1987). Ecological barriers may then have prevented certain fish species from reestablishing marine extirpated populations when sea levels dropped, thus accounting for the present disjunct distributions.

Considered a synonym of *Elliptio buckleyi* by Johnson (1972), *E. subluridus* completely lacks the sharp posterior ridge of *E. buckleyi*, and also displays an oval outline uncharacteristic of typical specimens of *E. buckleyi*. The habitat of Orange Creek is unsuitable for *E. buckleyi*. Furthermore, no records exist for *E. buckleyi* in other streams (*e.g.*, Black, Rice and Deep creeks) draining uplands in this area (Johnson, 1972). Taxonomic studies are needed to unequivocally verify the validity of *E. subluridus*.

Other nominal species of *Elliptio* described from the St. Johns River include forms considered synonyms of *E. dariensis* (Lea, 1842) by Johnson (1972). *Elliptio dariensis* is found elsewhere only in the Altamaha River (Johnson, 1970). *Elliptio monroensis* (Lea, 1843) was recognized by Morrison (1973); considerably smaller and thinner shelled than *E. dariensis*, *E. monroensis* is very possibly a distinct taxon. This and other nominal *Elliptio* species from the St. Johns River may have specifically recognized counterparts in other Atlantic Slope drainages (J. D. Williams, pers. comm.). The presence of *E. crassidens* in the St. Marys River led Johnson (1970, 1972) to believe that the unionid fauna of this drainage was more closely linked with unionids of the Apalachicolan Region (as defined by Clench &

Turner, 1956) and not other Atlantic Slope drainages. It is possible that the species called *E. crassidens* in the St. Marys is another species with affinities to more northern *Elliptio* species.

Beyond the *Elliptio* confusion, southeastern species of *Anodonta, Lampsilis, Pleurobema, Toxolasma, Uniomerus* and *Villosa* require thorough systematic investigations to delineate species boundaries. Once accomplished, distributional data may provide information towards a better understanding of unionid zoogeography in the Appalachicolan Region and Peninsular Florida.

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