

Zoogeography of the Aquatic Fauna of the St. Johns River System with Comments on Adjacent Peninsular Faunas

GEORGE H. BURGESS

Florida State Museum and Department of Zoology, University of Florida, Gainesville, 32611

and

RICHARD FRANZ

Florida State Museum, University of Florida, Gainesville 32611

ABSTRACT: The Florida peninsula has been subjected to periodic marine inundations and regressions since the Oligocene. Freshwater organisms presently found in the St. Johns River system were derived from stocks that remained on offshore islands during the "Wicomico" (+100 ft) high stand, or from immigrants that subsequently entered the Oklawaha River from a Santa Fe River region refugium as sea levels dropped. Elements of the latter fauna have relict distribution in some of the streams in the intervening area between these rivers; ensuing geological activity led to the isolation (and endemism) of additional forms in the Black Creek drainage. A number of marine-derived organisms, presumably of peninsular origin, apparently survived on or invaded offshore islands during high sea levels.

INTRODUCTION

During recent surveys of the freshwaters of northeastern Florida we have become impressed with the large numbers of lotic species in the St. Johns River system that have their closest affinities with organisms distributed outside the Florida peninsula or with Santa Fe-Suwanee river organisms (Table 1). Some of these taxa are dif-

TABLE 1.—Distributional patterns and relationships of selected elements of the St. Johns River system lotic fauna. Relationships are enclosed in brackets

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- I. Endemic to Black Creek
(Decapoda: Cambaridae)
Procambarus pictus: Headwaters, tributaries. [*Procambarus lucifugus* in caves in Suwannee and Withlacoochee river basins; *P. youngi* is closest Florida surface relative (in Apalachicola River drainage). (Hobbs, 1958)]
(Insecta: Chironomidae)
Conchapelopia gigas: Tributaries (Peters Creek). [Affinities with northern forms; two other species also occur in Florida. (W. Beck, pers. comm.)]
Nilotanytus americanus: Tributaries (Peters Creek). [One other species occurs from Coosa River drainage in Georgia northward. (W. Beck, pers. comm.)]
Paramerina anomala: Tributaries (Peters Creek). [Four other species in Texas, Virginia, and northwestern United States. (W. Beck, pers. comm.)]
- II. Endemic to St. Johns-Oklawaha rivers
(Gastropoda: Hydrobiidae)
Spilochlamys gravis: Middle St. Johns and Oklawaha rivers. [*Spilochlamys turgida* in S-central Georgia. (Thompson, 1969)]
Aphaestracon rhadinus: Tributaries of lower St. Johns River. [*Aphaestracon hypophyllina* in Santa Fe-Suwanee and Waccasassa rivers. (Thompson, 1968)]
A. monas: Wekiva River, Orange Co. [*Aphaestracon hypophyllina* in Santa Fe-Suwanee and Waccasassa rivers. (Thompson, 1968)]
A. asthenes: Blue Springs, Volusia Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
A. pycnus: Alexander Springs, Lake Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
A. theiocrenetus: Clifton Springs, Seminole Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
A. chalarogyrus: Magnesia Springs, Alachua Co. [*A. rhadinus* species group. (Thompson, 1968)]

TABLE 1.—(continued)

- Cincinnatia fraterna*: Tributaries of lower St. Johns River. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
- C. parva*: Blue Springs, Volusia Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
- C. petrifons*: Rock Springs, Orange Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
- C. ponderosa*: Sanlando Springs, Seminole Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
- C. vanhyningi*: Seminole Springs, Lake Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
- C. wekiwae*: Wekiva Springs, Seminole Co. [Unique to the St. Johns River system with close relationships outside the basin. (Thompson, 1968)]
- Ammicola rhombostoma*: Tributaries to lower St. Johns River in Clay and Putnam counties. [Unique to St. Johns River system. (Thompson, 1968)]
- (Decapoda:Cambaridae)
- Procambarus geodytes*: Sulfur springs along Oklawaha and middle St. Johns River. [Procambarus advena in flatwoods of Okefenokee basin. (Hobbs, 1942)]
- (Osteichthyes:Centrarchidae)
- Micropterus salmoides floridanus*: Oklawaha-St. Johns rivers and smaller peninsular rivers. [Micropterus salmoides salmoides in drainages north of Savannah River and west of Choctawhatchee Bay; intergrades occur in Suwannee drainage and other intervening areas. (Bailey and Hubbs, 1949)]
- (Osteichthyes:Cyprinidae)
- Notropis emiliae peninsularis*: Oklawaha-St. Johns rivers and smaller peninsular rivers. [Notropis emiliae emiliae in drainages N of Nassau and W of Ochlocknee river systems; intergrades occur in Suwannee drainage and other intervening areas. (Gilbert and Bailey, 1972)]
- III. Endemic to St. Johns and Suwannee systems
- (Gastropoda:Pleuroceridae)
- Goniobasis floridensis*: 4 allopatric populations: (1) Oklawaha River. [Goniobasis floridensis in Santa Fe-Suwannee rivers.] (2) Lake George area in St. Johns River. [Populations in Oklawaha River.] (3) Springs in Orange and Lake counties. [Populations in Lake George and possibly in Waccasassa River.] (4) Santa Fe-Suwannee rivers. [Goniobasis floridensis in Oklawaha River. (R. Franz, pers. observ.)]
- (Gastropoda:Hydrobiidae)
- Ammicola retromargo*: Black and Clark creeks (St. Johns drainage), Santa Fe River and creek in Dixie Co. (Suwannee drainage). [Subgenus Lyogyrys widely distributed in eastern North America. (Thompson, 1968)]
- (Gastropoda:Viviparidae)
- Campeloma floridense*: Black Creek, springs along Oklawaha River, and middle St. Johns River. [Unknown. (F. G. Thompson, pers. comm.)]
- (Amphipoda:Gammaridae)
- Gammarus* new sp.: Undescribed species from Silver River, a tributary of Black Creek, and a spring along Santa Fe River. [G. tigrinus-fasciatus complex known from Georgia northwards. (J. R. Holsinger, pers. comm.)]
- IV. Disjunct populations in the St. Johns, or Santa Fe-St. Johns systems
- (Gastropoda:Hydrobiidae)
- Notogillia wetherbyi*: St. Johns River system, Waccasassa, Withlacoochee, and lower Suwannee rivers. [Chipola River in Florida and Georgia. (Thompson, 1968)]
- (Insecta:Baetiscidae)
- Baetisca gibbera*: Black Creek. [Escambia River and upper Suwannee drainage in Georgia. (Berner, 1955)]
- (Insecta:Chironomidae)
- Potthastia* new sp.: Undescribed species from tributary of Black Creek. [Northern Georgia. (W. Beck, pers. comm.)]
- (Insecta:Plecoptera)
- Acroneuria* sp.: Black Creek. [Florida panhandle. (Berner, 1955)]
- Neophasganophora capitata*: Black Creek. [Apalachicola River. (Berner, 1955)]
- (Osteichthyes:Cyprinidae)
- Notropis welaka*: Oklawaha-St. Johns rivers. [Apalachicola River westward. (Burgess et al., 1977)]

TABLE 1.—(continued)

<i>Notropis cummingsae</i> :	Oklawaha River and three tributaries, Clark and Rice creeks. [Aucilla River westward to Choctawhatchee River system. (Burgess <i>et al.</i> , 1977)]
(Osteichthyes: Ictaluridae)	
<i>Ictalurus brunneus</i> :	Entire St. Johns River system. [Apalachicola and Altamaha rivers. (Burgess <i>et al.</i> , 1977)]
(Osteichthyes: Percidae)	
<i>Etheostoma olmstedi</i> :	Two tributaries of Oklawaha River. [Altamaha River. (Burgess <i>et al.</i> , 1977)]
(Amphibia: Ranidae)	
<i>Rana hecksheri</i> :	Santa Fe River and lower St. Johns River system. [Ochlocknee River westward. (Florida State Museum records)]
(Amphibia: Plethodontidae)	
<i>Pseudotriton montanus floridanus</i> :	Upper Santa Fe River, tributaries to lower Oklawaha River, and Duval Upland creeks. [Ochlocknee River westward. (Florida State Museum records)]

ferentiated at the species, subspecies or racial levels, while others are taxonomically indistinguishable from their nearest geographical relatives. Several investigators (Hobbs, 1942; Hubbs and Raney, 1951; Berner, 1955; Thompson, 1968; Yerger and Relyea, 1968; Johnson, 1972; Burgess *et al.*, 1977) have independently noted distributional anomalies within specific aquatic taxa but did not recognize them as members of a larger lotic community. Although attempts were often made to explain these distributions based on sea level fluctuations, none adequately explained the dispersal of the organisms into the St. Johns River system.

GEOLOGICAL HISTORY AND FAUNAL COLONIZATION

Since its formation, the Florida peninsula has been subjected to periodic marine inundations alternating with re-emergences of dry land. Marine terraces and deposits formed during high stands of sea level, as well as extensive terrestrial fossil deposits from old sinkholes and stream channels, document this alternation of marine and nonmarine environments since the Oligocene (Webb and Tessman, 1968; Patton, 1969; Webb, 1974). The peninsular land mass shrank during transgressions of the sea and enlarged during regressions. The earliest (and highest) stands are thought to have occurred during the late Miocene and Pliocene (Alt, 1968); these transgressions submerged most of the peninsula as we now know it and eliminated much of the freshwater fauna and flora that had become established prior to the rises.

The first major invasion of modern peninsular Florida by stocks of the present-day stream fauna probably occurred sometime after sea levels stood at 28-30 m (90-100 ft) above present sea level. This high stand is referred to as the "Wicomico Shoreline" by Cooke (1945) and Hoyt and Hails (1967) and corresponds to Alt's (1968) "Surry Scarp." For the sake of convenience in the ensuing discussion we will use the former terminology. The absolute timing of this transgression continues to be a topic of debate; Cooke (1945), MacNeil (1950) and Hoyt and Hails (1967) considered it to have occurred in the Pleistocene, but other authors (Alt and Brooks, 1965; Alt, 1968) place it in the Pliocene. Robertson (1976) more recently showed that the sea stood near Haile (Alachua Co.) in the latest Pliocene. During the "Wicomico" high stand Florida was reduced to a short stubby peninsula (the present Northern Highlands) extending southward to approximately the present-day Oklawaha River, with more southerly high areas such as Brooksville, Lakeland and Lake Wales ridges existing as offshore islands (Fig. 1). Parts of the ancestral Suwannee and Santa Fe rivers made up the principal peninsular drainage. Sufficient elevations probably existed in the "Wicomico" peninsula to allow for the presence of flowing, highly oxygenated streams. Numerous streams apparently drained the periphery of

the peninsula, since fossil stream sites are abundant in western Alachua County (S.D. Webb, pers. comm.). We believe that streams in this area acted as refugia for stream communities, some of which eventually became established in the St. Johns River system.

Several major topographic features were formed on the margins of the "Wicomico" peninsula, including Trail Ridge, Duval Upland and Baywood Promontory (Fig. 2). According to Pirkle *et al.* (1974), Trail Ridge was formed as a beach ridge at the height of the "Wicomico" high stand, and the Duval Upland and Baywood Promontory developed as regressional plains as sea levels dropped. Following the formation of these features, stream systems developed draining the area S and E of Trail Ridge. Among these were Orange, Little Orange, Deep, Rice and Black creeks, or their precursors (Fig. 2). The latter two creeks drained eastward, the others to the S. Through headwater stream capture, organisms were presumably able to move from the upper Santa Fe River drainage and nearby streams into the newly developing, southerly flowing streams and eventually into the Oklawaha River, which also was



Fig. 1.—Shoreline of the "Wicomico" sea superimposed on present-day Florida and its drainages. After Cooke (1945)

beginning to form at this time. Fauna moving into the easterly flowing streams probably did not achieve interchange with the St. Johns River for a considerable period of time, since these streams probably drained directly to the sea until at least as late as the Pamlico (Cooke, 1945: Fig. 47).

Sometime after colonization of the new stream systems, connections between adjoining drainages were lost. In the area S of Trail Ridge (in present-day Putnam County) extensive solution erosion of both the Hawthorne sediments and the Ocala limestone resulted in increased downward movements of water into the aquifer (Pirkle and Brooks, 1959). Solution draining did not occur on the Duval Upland, however, because of the nearly impermeable Hawthorne Formation and deep lime-

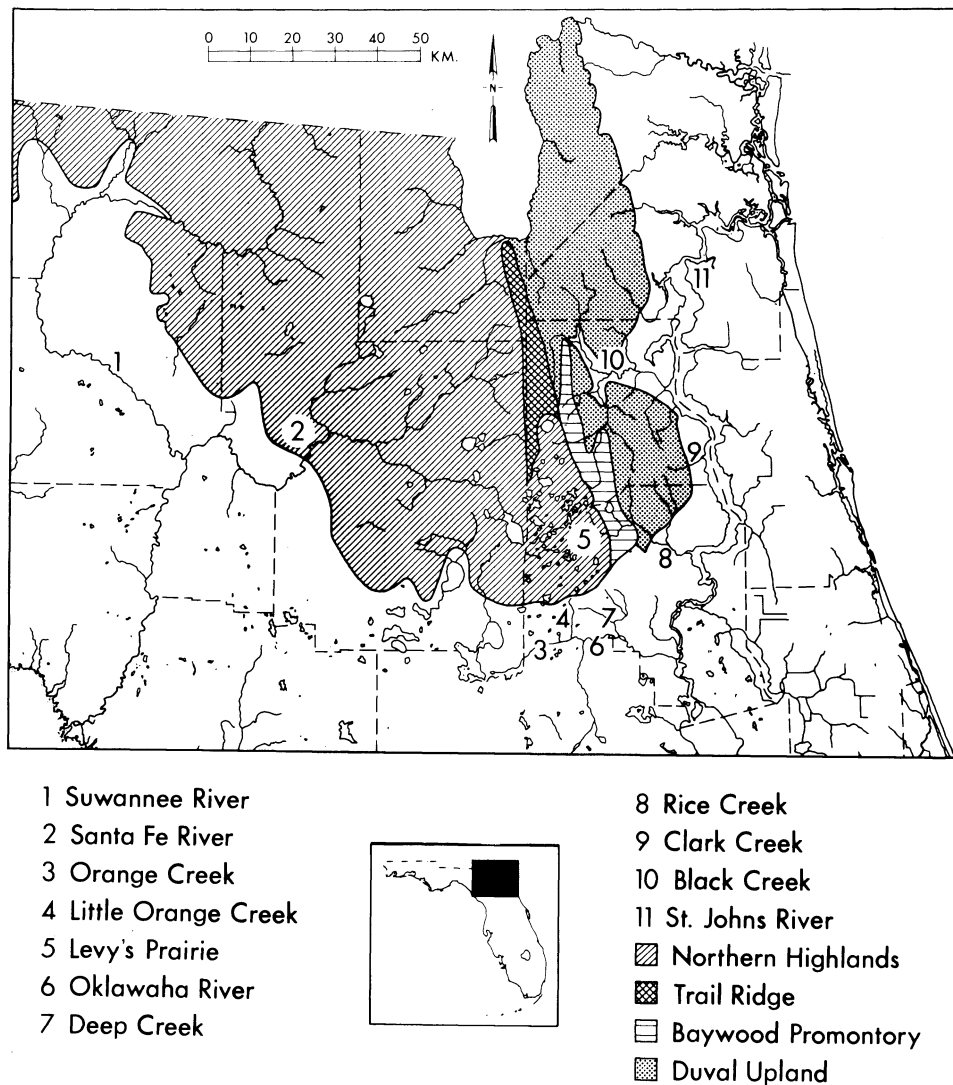


Fig. 2.—Northeastern Florida, showing major features discussed in text.

Modified from Puri and Vernon (1964) and Pirkle *et al.* (1974)

stone acting as an aquiclude. This erosion must have occurred during one or more glacial intervals, when sea levels were lowered and solution processes would have been accelerated. Faunal exchange between the Santa Fe region and the newly developed streams was therefore effectively cut during the Pleistocene, when the intervening area (partly now Levys Prairie) evolved into a series of solution lakes and sinkholes.

Later Pleistocene sea levels never attained the heights of earlier ones, including the "Wicomico" (Hoyt and Hails, 1967). They did, however, flood large areas of the St. Johns River basin and no doubt caused the extirpation of stream communities over large areas. One portion of the St. Johns system consistently escaped post-"Wicomico" flooding and may have acted as an isolated refugium for elements of the colonizing lotic community. Today, this region includes the streams draining the Duval Upland and Baywood Promontory and the area forming the northern shore of the lower Oklawaha River. Two streams, Black Creek and, to a lesser extent, Rice Creek, apparently figured prominently in the zoogeography of the area. Both creeks emanate along Trail Ridge at elevations of over 60 m and flow eastward into the St. Johns River. They are cool, tannin-stained and swift-flowing, with a gradient of 0.9-6.0 m per km (Clarke *et al.*, 1964). They originate from seepage areas in pine flatwoods, with feeder streams converging to form increasingly larger tributaries. Both have been able to maintain their integrity, even during glacial periods when sea levels were lowered possibly as much as 100 m below present m.s.l. (Emery, 1967; Webb, 1974), because of the lack of solution draining in this area. Tidal scouring, which presumably occurred during the Yarmouth interglacial when an arm of the St. Johns River embayment extended into the area, may have been responsible for the deepening (up to 28 m) of the lower reaches of Black Creek (McLane, 1955). This deepening, and its accompanying tranquil waters, have acted to ecologically limit the downstream movements of certain endemic sedentary, rheophilic, shallow-water organisms (*e.g.*, a crayfish, *Procambarus pictus*, and three chironomid flies). Additionally, the marine or estuarine nature of the mouths of these creeks probably served to isolate their lotic faunas (Johnson, 1972) for extensive periods of time. Black Creek may still be so affected, since the creek contains four endemic species (Table 1); Rice Creek apparently is not so restricted and harbors no known endemics.

DISTRIBUTIONAL EVIDENCE

The present-day distributions of two fishes (*Notropis cummingsae* and *Etheostoma olmstedi*), a salamander (*Pseudotriton montanus floridanus*), a crayfish (*Procambarus pictus*), certain snails (*Goniobasis floridense*-Oklawaha River form and *Amnicola retromargo*) and an amphipod (*Gammarus* new sp.) support the proposed connection between the upper Santa Fe region and the Oklawaha River. In the St. Johns River system all of these animals are restricted to the Oklawaha River (and its tributaries) and creeks of the Duval Upland. Other species, such as the fishes *Notropis welaka* and *Ictalurus brunneus*, apparently were able to move into other parts of the St. Johns system, including the St. Johns River proper, because of their affinities for deeper water (Burgess *et al.*, 1977). Some of these forms are now lacking in the Santa Fe River; presumably they were extirpated as a result of competition with later arriving forms (*see below*) and/or changing ecological conditions. Iverson (1977) has previously suggested a Santa Fe River refugium in discussing the zoogeography of the turtle *Sternotherus minor*.

A substantial number of species have widely disjunct populations in the St. Johns River, or in the Santa Fe and St. Johns rivers (Table 1). We think that the absence of these forms in the intervening systems is explainable on the basis of: (1) inundation of both the small rivers between the Ochlocknee and Suwannee rivers and the lower reaches of the larger rivers, including the major panhandle rivers and the Suwannee and Santa Fe rivers, during high stands in sea level; (2) partial or com-

plete drying up of many streams through solution draining during glacial intervals, and (3) competition.

Competition would have increased as species became more compressed in a Santa Fe refugium during the "Wicomico" high stand, and almost certainly would have been keen for available resources, particularly since some forms were in marginal habitats. Following sea level regression, organisms moving out of the Santa Fe River into the lower Suwannee and other coastal rivers would possibly have found alien habitats, along with other lowland species moving in from the W and N. Competition occurring at this time may have resulted in additional extinctions. Many species (e.g., the fishes *Notropis cummingsae*, *N. welaka*, *Ictalurus brunneus*, *Etheostoma olmstedii*; Burgess *et al.*, 1977) are at the periphery of their natural ranges in northern Florida. Survival and the ability to compete with other species are usually reduced in such areas when compared to the more central parts of a species range. It is not difficult, for example, to envision a predominantly northern form (*Etheostoma olmstedii*) being outcompeted in the Suwannee River system by a southern species (*Percina nigrofasciata*) occupying a similar habitat.

The St. Johns populations of *Notropis cummingsae* (Hubbs and Raney, 1951), *Ictalurus brunneus* (Yerger and Relyea, 1968), *Etheostoma olmstedii* (Burgess, unpubl. ms.) and the darter *Percina nigrofasciata* (Crawford, 1956) are considered to have differentiated at the racial level, indicating at least a moderate time of isolation. The disjunct distributions of the insects *Acroneuria* sp. and *Neophasganophora capitata* (Black Creek and Florida panhandle streams), *Baetisca gibbera* (Black Creek, Florida panhandle streams and upper Suwannee River in Georgia; Berner, 1955) and *Potthastia* new sp. (Black Creek and northern Georgia; W. Beck, pers. comm.); the pelecypod *Elliptio dariensis* (St. Johns River system and Altamaha River; Johnson, 1972); and the frog *Rana hecksheri* (lower St. Johns River system, Santa Fe River and Florida panhandle; Florida State Museum records) may be similarly explained.

The presence of both shared endemic forms (*Campeloma floridensis*, *Gammarus* new sp. and *Amnicola retromargo*) and of closely related species (of the genera *Spilochlamys*, *Goniobasis* and *Aphaostracon*) in the St. Johns and Santa Fe river drainages (Table 1) also suggests movement of lotic species between these systems. The snail *Campeloma floridensis* provides one of the most suggestive pieces of distributional evidence, being found in a few isolated springs along the upper Santa Fe River and throughout the St. Johns River (F.G. Thompson, pers. comm.). Its limited presence in the Santa Fe may imply relict distribution. The cause of its almost total demise in this river may involve competitive exclusion by the later-arriving *Campeloma geniculum*. In the area of sympatry the more robust *C. geniculum* inhabits the larger streams and the main river itself. The form of *Goniobasis floridense* that occurs in the Oklawaha River appears intermediate between those in the Santa Fe and those in the Lake George areas of the St. Johns River, further supporting this view.

Intergrades of both the pugnose minnow (*Notropis emiliae*) and largemouth bass (*Micropterus salmoides*) occur in the Santa Fe-lower Suwannee system, indicating that this area at one time also lacked representatives of these species. Apparently subsequent recolonization of the system by distinct subspecies from the N (the upper Suwannee was not inundated) and from the S (Gilbert and Bailey, 1972) brought about the present situation. This explanation would require a longer period of peninsular isolation (pre-"Wicomico") for these species, as implied by Gilbert and Bailey (1972) and Burgess *et al.* (1977), and survival on a "Wicomico" island during the +28-30 m high stand of sea level. Clench and Turner (1956), in discussing distributions of freshwater mollusks, suggested that a "Wicomico" island must have been large enough to have had a freshwater drainage system with some lakes and

streams. Neill (1957) noted the importance of the central Florida uplands as a refugium for a large number of organisms during high stands of sea level in the Plio-Pleistocene and suggested that springs, seepage areas, lakes, ponds and swampy depressions may have provided suitable habitats for survival of certain aquatic species during that time. Johnson (1972) subsequently postulated that the bivalves *Elliptio buckleyi* and *Villosa amygdala* had survived on island refugia during higher sea levels. This central Florida area has long been recognized as an area important in the derivation of many endemic peninsular taxa, including the Florida scrub jay [*Aphelocoma c. coerulescens* (Pitelka, 1951)], several reptiles [*Tantilla relicta* (Telford, 1966), *Stilosoma extenuatum* (Highton, 1956), *Neoseps reynoldsi* (Telford, 1959, 1962), *Eumeces egregius* (Mount, 1965), *Sceloporus woodi* (Jackson, 1973) and *Rhineura floridana* (Zug, 1968)], the beetle genera *Mycotrupes* and *Peltotrupes* (Hubbell, 1954; Woodruff, 1973) and the spiders *Geolycosa patellonigra* and *G. xera* (McCrone, 1963).

Thompson (1968) stated that the large number of hydrobiid snail species (of the genera *Cincinnatia*, *Hyalopyrgus*, *Aphaostracon*, *Spilochlamys* and *Notogillia*; Table 1) endemic to the Florida peninsula necessitated their existence in the area for a prolonged period of time (since the end of the Miocene or early Pliocene). He proposed that they most likely endured on a peninsula that persisted throughout this time rather than on offshore islands. Johnson (1973) disagreed, arguing that most of these forms (all but the two species of *Hyalopyrgus*) had invaded the area in the more recent Pleistocene via coastal routes made available by lowered sea levels. He further suggested that *H. brevissimus*, *H. aequicostatus* and possibly *Amnicola dalli johnsoni* may have survived on islands during the "Wicomico" flooding. We think these three species, as well as *Spilochlamys gravis* and the St. Johns endemics of the genera *Cincinnatia* and *Aphaostracon* existed on offshore islands during the "Wicomico" high stand.

The phylogenetically closest relative of *Spilochlamys gravis* (a St. Johns endemic) is *S. turgida*, found in the Ocmulgee River in S-central Georgia (Thompson, 1969). The immediate ancestor of these two species may have been outcompeted in the Santa Fe-Suwannee rivers by *S. conica*, which is presently distributed from the Santa Fe-Suwannee and Waccasassa rivers westward (Thompson, 1968). Two species groups within the genus *Cincinnatia* were defined by Thompson (1968). The *vanhyningi* group apparently arose from stocks left stranded on offshore "Wicomico" islands, whereas the *floridanus* assemblage evolved from stocks in a Santa Fe refugium. As sea levels dropped, the latter group reinvaded the lower Suwannee River and other west coast rivers, and also entered the St. Johns system through Oklawaha River connections mentioned earlier. The genus *Notogillia* is probably a more recent immigrant to the St. Johns system, since all Florida records are of the single species *N. wetherbyi*. Following sea level regression this species may have followed the same reinvasion paths as did the *C. floridanus* species group.

Hobbs (1942) suggested that Black Creek and the St. Johns River system were colonized by organisms moving S from Georgia along Trail Ridge. Although this may be true for certain lentic or burrowing forms, such as crayfishes (*Procambarus advena*, *P. pubischelae*, *P. seminolae* and *P. geodytes*), it does not seem to be the case for stream-dwellers. The distribution patterns of two highly motile fish species and their subspecies and intergrades support a Santa Fe-Oklawaha connection rather than a Georgia-St. Johns exchange. Black Creek forms the northern limit for the peninsular endemic *Micropterus salmoides floridanus* (Bailey and Hubbs, 1949) and the intergrade pickerel *Esox a. americanus* x *E. a. vermiculatus* (Crossman, 1966), whose distribution is to the S and W. Populations in the St. Marys River, the first major drainage immediately north of Black Creek, are of *M. s. salmoides* x *M. s. floridanus*, found to the N and W, and *E. a. americanus*, the typical northern form.

Although the minnow, *Notropis emiliae* has not yet been taken in Black Creek, we predict that any collected from this area will be the peninsular endemic *N. e. peninsularis* rather than the intergrade *N. e. emiliae* x *N. e. peninsularis*, which occurs in the St. Marys River and to the N and W (Gilbert and Bailey, 1972).

One portion of the aquatic fauna of the St. Johns system that deserves mention is the marine-derived component. The present-day St. Johns River system is unique in the extent to which marine organisms (especially fishes) penetrate the upper, strictly freshwater reaches of the rivers (Tagatz, 1968). Odum (1953) explained this on the basis of the abundance of calcium chloride in the water and the presence of salt springs in certain areas of the river system.

Seven cyprinodontid fishes, *Cyprinodon variegatus hubbsi*, *Fundulus cingulatus*, *F. confluentus confluentus*, *F. seminolis*, *Jordanella floridae*, *Leptolucania ommata* and *Lucania goodei*, apparently originated on peninsular Florida. All are secondary or peripheral freshwater forms (Divisions II, IV and VI of Myers, 1938, 1951) whose origin as a group may lie in salt or brackish water. Presumably these forms were derived from stocks that persisted on, or invaded a "Wicomico" island.

SUMMARY

The lotic fauna of the St. Johns River system has been derived from at least two major invasions of freshwater organisms. The first occurred prior to the +100 ft ("Wicomico") sea level inundation and the second subsequent to this high stand. Organisms that existed on the Southern Florida peninsula before the "Wicomico" inundation were either entirely extirpated by the rising sea or survived on island refugia. The second invasion occurred as the seas regressed following the "Wicomico" high stand. At that time lotic organisms were able to colonize the re-emerging peninsula, entering the Oklawaha River via southerly flowing streams from a refugium in the Santa Fe River region. Later rises (and falls) in sea level eliminated portions of the fauna, but certain streams on the Duval Upland (especially Black Creek) escaped flooding (and draining) and, through isolation, maintained distinctive elements of the Plio-Pleistocene colonizing fauna. Distributional patterns of aquatic organisms support a Santa Fe-Oklawaha exchange rather than a Georgia-St. Johns connection. Additional elements of the St. Johns River system's present-day fauna are derived from marine organisms that persisted on, or invaded a "Wicomico" island.

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