The Edwards Aquifer is home to a very diverse assemblage of forty, highly adapted, aquatic, subterranean described species. Several additional invertebrate species have been discovered, but have not yet been described. The most unusual of the species are blind catfish existing more than 600 m beneath the land surface. Possible explanations regarding the existence of this community include marine organisms adapting to the aquifer from a time when paleokarstification occurred and the caves were then inundated in a marine situation similar to that today in Bermuda. Some organisms may have entered the aquifer during the Miocene when extensive faulting occurred along the present Balcones Escarpment. Finally, some organisms may have entered the aquifer through spring openings to escape the colder surface temperatures during the ice ages. The paleogeographic implications of the diverse fauna are astounding.

Table 1: Described biota of the Edwards Aquifer.

Figure 1: Balcones Fault Zone Edwards Aquifer. larger legend

INTRODUCTION

The unusually diverse subterranean aquatic community of the Edwards Aquifer poses some interesting questions regarding its origin. There have been a total of 40 species described from the aquifer: Table 1 (Hershler and Longley, 1986). The two most diverse groups in the faunal assemblage are the crustacean, gammarid amphipods and the gastropod, hydrobid snails. In both groups there are species apparently derived from both marine and freshwater ancestors. This diversification would have logically occurred since the Cretaceous period. The major question posed by these species occurrence in the deep confined aquifer is how did they get there. The zoogeographic and ecological implications are considerable.

The Edwards (Balcones Fault Zone) aquifer extends for 282 km from Brackettville to Salado (Fig. 1). Within the aquifer, areas below the Balcones Escarpment are confined (artesian) and those above are typically unconfined (water table). The large size and the amount of cavernous porosity in the confined region of the aquifer makes this aquifer one of the world's most unique karst aquifers. The deposition of the Edwards Formation began almost 100 million years ago. The deposition occurred in a shallow sea with a variety of environments from tidal flats to coral reefs. The area may have been similar to shallow areas in the Bahaman islands today. The early limestones were alternately submerged and then exposed, allowing early formation of cavernous porosity. It is possible that caverns similar to those in Bermuda that connect Blue Holes to caverns inland may have formed. In time, all of Central Texas was covered by a deep Cretaceous sea. Many hundreds
of feet of sediments were deposited over this early aquifer. As the North American continent was slowly uplifted, the Cretaceous seas receded. Rivers formed that cut across the overlying sediments, again gradually exposing the underlying Edwards with its cavernous porosity.

By the Miocene another major event in the history of the Edwards Formation occurred (12 to 17 million years ago). This was a period of extensive faulting resulting in the Balcones Fault Zone, concurrent with subsidence in the Gulf of Mexico area. The formations dipped toward the present day Gulf coast. The faults allowed new movement of groundwater in the Edwards, in some areas acting as recharge points and in others as resurgence points (springs). Further solutioning continued with enlargement of the cavernous porosity along the fault zone. The major geologic event that may have ultimately influenced the biological composition of the aquifer began with the onset of the ice ages some three million years ago. This brief synopsis of the history of the Edwards will relate to when organisms of the various groups represented there may have first colonized the Edwards Aquifer.

DISCUSSION

The two most diverse groups represented in the aquifer are amphipod crustaceans and prosobranch gastropods. Most of the discussion will center on these two groups. The vertebrate fauna is also very interesting.

Amphipods

Information obtained from samples of an artesian well on the Southwest Texas State University campus indicates that both in numbers of genera and species the subterranean amphipod diversity far exceeds any other groundwater community studied in North America.

The family Crangonyctidae is restricted to the Holarctic region and is believed to have originated on the old Laurasian landmass prior to the separation of North America and Eurasia in the Jurassic (Holsinger, 1978). The crangonyctids are allied morphologically at the superfamilial level with several families living on landmass remnants of Gondwanaland in the Notogaean region. The crangonyctids are therefore believed to be an ancient group that was probably present in North American freshwaters prior to the Cretaceous. Since the Edwards Aquifer is developed in Cretaceous-age limestones, the presence of Stygobromus there would imply that members of this genus have invaded and colonized subterranean water in this part of North America since the Cretaceous. It is presumed that the invasions were by ancestral immigrants from a part of the continent that remained above the marine waters during late Mesozoic times.

The family Hadziidae is part of a group composed of species that inhabit marine, brackish or freshwater habitats, largely in temperate or tropical regions. Many are found in the old Tethys Sea region (i.e., the greater Caribbean and Mediterranean regions in particular). All freshwater species are troglobites or phreatobites. Closely related subterranean hadziid genera also occur in brackish and freshwater habitats in the Mediterranean region, and in shallow marine and anchialine habitats at a few spots in other tropical oceans. The genera occurring in the Edwards were probably derived from marine and/or brackish-water ancestors at various times from the late Cretaceous to the late Tertiary (Holsinger, 1974). These forms were probably relict during the recession of marine waters in the late Cretaceous.

The family Bogidiellidae is part of a larger complex of the superfamily Bogidielloidea. The majority of species are recorded from the greater Caribbean and Mediterranean regions. Ruffo (1973) and Stock (1977, 1978) have made strong cases for the evolution of freshwater members of Bogidiellidae from marine ancestors, with freshwater invasion occurring at different places over a long period of time.

The family Artesiidae is known only from the Edwards Aquifer. Its probable affinity with Bogidiellidae makes it likely that this family had a marine origin, with ancestral forms relict in freshwater following the Cretaceous embayment of Central Texas.

The family Sebidae, which is predominately marine, consists of small, weakly pigmented, mostly eyeless species from benthic habitats. Due to their characteristics, this group would have been good candidates for colonization of interstitial freshwater habitats during marine transgressions. The presence of species in a land-locked, oligohaline-brackish water lake in the Renell Islands of the South Pacific, assumed to have been
isolated there since the Late Pliocene (Bousfield, 1970), may indicate the manner in which the ancestors of the Edwards Aquifer form became isolated in, and adapted to, the transitional aquatic environment of south-central Texas during recession of sea water in the late Cretaceous or early Tertiary.

Gastropods

The Hydrobiidae (Rissoacea) are a large family (over 100 genera and 1000 species; Davis, 1979) of dioecious, gill-breathing snails that have radiated into diverse fresh- and brackish-water habitats worldwide. Minute, unpigmented hydrobiids occupy groundwater habitats in numerous areas, with a large fauna occurring in karst regions of Europe, and fewer numbers occurring in North America, Mexico, Japan, and New Zealand (Hershler and Longley, 1986). Little is known of the zoogeography of these taxa, in large part due to their small size (often less than 2 mm) and the difficulties in sampling their habitat. The described species of the Edwards Aquifer have been found in 14 artesian wells and four springs. The wells that yielded snails ranged in depth from 59 to 582 m. All of these wells are cased and there is no doubt that the snails were expelled from the deep artesian zone. Their habitat probably includes fractures, joints and caverns in the Edwards formation. It is also possible, given their small size, that they even inhabit interstices.

Other Invertebrates

In samples of wells in the San Antonio area, some specimens of a Foraminiferan from the family Lagenidae were found. They appear to be fresh not fossil forms. They were tentatively identified as a species of Robulus. For identification Cushman, (1928) was used. Vandel, (1965) discusses a discovery by A.L. Brodsky of an abundant population of Foraminifera in some wells in the Kara-Kum desert in the Trans-Caspian Province. The wells were about 20 m deep and were fed by slightly brackish groundwater. Further work has not been done on the San Antonio forms, but will be completed in the future.

The only known North American Thermosbaenacean, Monodella texana, is found in the Edwards Aquifer. This representative of the family Monodellidae is most closely related to species that occur around the Mediterranean and West Indies (Stock and Longley, 1981). The species found in the Mediterranean region are all freshwater including groundwater forms. The absence of marine Thermosbaenacea in the Mediterranean may be explained by events in the late Miocene hydrographic history of that basin. The sea level dropped considerably and much of the remaining water was temporarily transformed into brine. Conceivably the marine ancestors became extinct in the Mediterranean during the late Miocene. In the West Indies, where no such drastic salinity change took place, marine Thermosbaenacea did survive. It is likely that ancestors of this species also entered the Edwards Aquifer during a time when Central Texas was a marine area.

Troglobitic isopods in the freshwater Asellidae and predominantly marine Cirolanidae show contrasting patterns of distribution and speciation. Asellids are derived from an ancient Holarctic group probably already established in freshwater prior to the breakup of Laurasia (Barr and Holsinger, 1985). Few cirolanid isopods live in fresh water; most of them are troglobites. Species from Bermuda, the Bahamas, and Aruba occur in anchialine waters; the remainder inhabit freshwater habitats in Texas, Virginia, Mexico, and several West Indian islands. Except for the species in the Bahamas, which were probably derived from marine ancestors by direct dispersal, most cirolanids appear to have originated by stranding during regression of marine embayments or through uplifting.

The shrimp of the family Palaemonidae were probably derived from ancestral forms that gave rise to the forms found in the Aquifer and Texas estuaries today.

Vertebrates

Longley (1978) discusses the status of two troglobitic salamanders occurring in the groundwaters of the San Marcos area. The species Typhlomolge rathbuni and Typhlomolge robusta are highly adapted neotenic species of the family Plethodontidae. They are considered the amphibians most adapted to cave existence in the world. They reproduce while retaining their gills, a larval characteristic. They have long legs with little musculature, an obvious adaptation to their total aquatic existence.

Two species of blind catfish of the family Ictaluridae occur in the groundwaters of the San Antonio area. They are highly adapted species having no airbladders, unlike their surface relatives. One species, the Toothless
Blindcat, Trogloglanis pattersoni has a suckerlike mouth on the underside of its head unlike any other member of the family. The fish are found in outflow from wells that penetrate the Edwards Formation between 402 m at the Artesia well and 582 m at the O.R. Mitchell (now S. Kleburg) well. These are flowing artesian wells having considerable artesian pressure (Longley and Karnei, 1979). Considering the amount of change in these species when compared to other species in their families, it seems logical to postulate that they found their way into the aquifer in prepleistocene times, perhaps as a means of escaping the colder temperatures on the surface. The temperatures of the groundwater tend to remain constant and would naturally dampen the effects of periods of extreme cold, an advantage to these fish. The same type of retreat into springs and then further down in caves was probable for all of the vertebrates in the aquifer.

SUMMARY
The unique community of aquatic subterranean forms inhabiting the Edwards Aquifer raises many questions regarding their origins. Additional study is needed to relate marine relict species occurrences in this system. When adequately sampled, other aquifer systems, such as the Floridean Aquifer, will possibly show similar relationships.

REFERENCES
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