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The occurrence of the troglobitic amphipod, Stygobromus tenuis tenuis (Smith) (Crangonyctidae) in the Taconic Mountains of southwestern Massachusetts (USA): a case for the existence of a subterranean refugium in a glaciated region

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SUMMARY

Stygobromus t. tenuis is one of only two species of troglobitic amphipods known to occur in the New England physiographic province. The rarity of subterranean organisms in New England is attributed to limited karst development and eradication of organisms from the region during glacial times. Traditionally it has been believed that those troglobitic species presently occurring north of the glacial terminus migrated there following glacial retreat from refugia south of the areas influenced by glacial conditions. However, a few recent studies favor the existence of subsurface refugia in glaciated regions during glacial times. *Stygobromus t. tenuis* is recorded from springs connected with deep, solution zone aquifers in the Taconic Mountains of western New England, an area well north of the glacial terminus. It is suggested that these aquifers served as a refugium for *S. t. tenuis* during the latter part of perhaps all of the Pleistocene Epoch.

INTRODUCTION

The New England physiographic province, relative to other provinces in eastern North America, is not known to contain a diverse or widespread troglobitic fauna. There are two reasons for this. First the region does not have the geological features conducive to the development of an extensive troglobitic fauna.

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The few areas within the New England province that are characterized by carbonate rocks are limited to a narrow north-south trending zone along the western margin of the region. Furthemore, these carbonate belts, together comprising the Taconic Mountains, were greatly metamorphosed in the mid Paleozoic Era and the presently existing rocks are somewhat solution resistant. The second reason is that the entire New England region, excepting portions of the then exposed continental shelf, was covered by ice during at least the last major (Woodfordian) glacial thrust of the Wisconsin ice age. The continued existence of subterranean animals in New England would be hampered by permafrost during the glacial peak and by excessive recharging and flushing of subsurface habitats by meltwater during glacial retreat.

Only two aquatic troglobitic (albinistic and eyeless) animal species have been recorded from the New England province. Both are members of the gammaridean amphipod family Crangonyctidae. One species, *Stygobromus borealis* Holsinger, is endemic to New England and has been collected from only two localities in the northern Taconic Mountains (Holsinger, 1978). The other species, *S. tenuis tenuis* (Smith), previously has been authentically documented in New England only from shallow wells and seeps in the Connecticut River valley in south-central Connecticut (Holsinger, 1967, 1978). Neither species has been found in abundance in New England and *S. t. tenuis* has not been reported from New England in this century.

This paper reports the occurrence of *S. t. tenuis* in the southern Taconic Mountain region of southwest Massachusetts, an area well north of the terminal moraine of the last Wisconsin glaciation. The presence of populations of *S. t. tenuis* well within a formerly glaciated region coupled with the nature of the geology of the area in which these amphipods dwell requires some consideration for the existence of a subterranean refugium for troglobitic animals in the Taconic Mountains during the Pleistocene Epoch.

RESULTS

In a partial survey of the peracaridans of Connecticut, Kunkel (1918) listed *S. t. tenuis* from Canaan, in northwestern Connecticut; however, no specimens presently exist to confirm the record (Holsinger, 1967). A search was therefore initiated in early 1982 of springs, cave outlet streams and springhouses in northwestern Connecticut and southwestern Massachusetts to

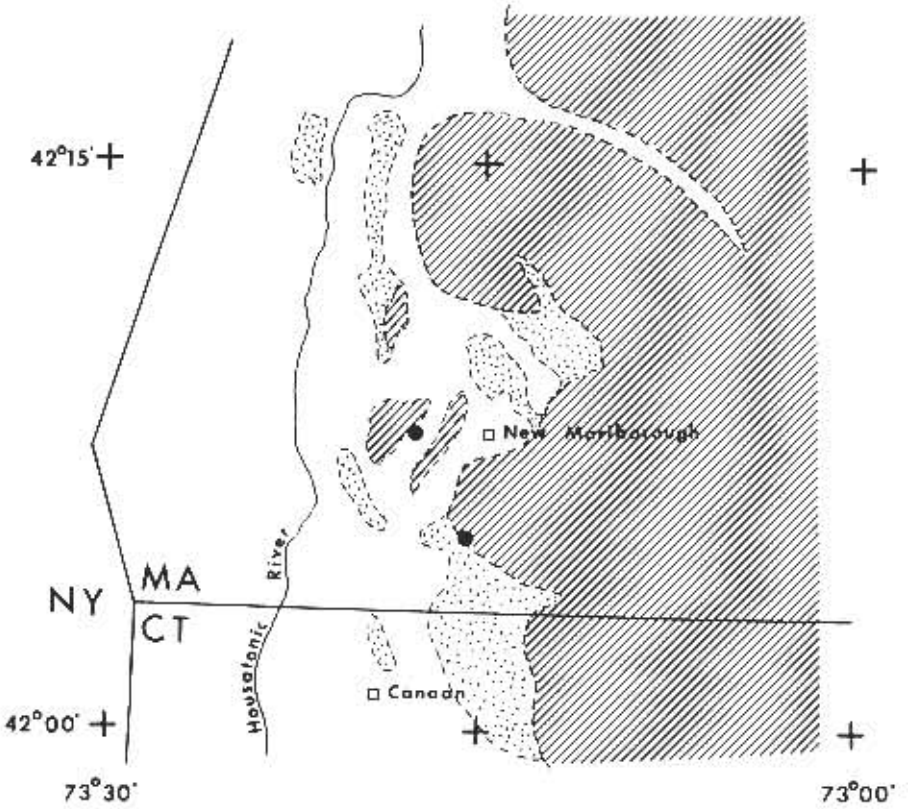

Fig. 1 - Map showing locations of recent collections of *S. t. tenuis* (solid circles). Physiographic features are generalized and follow Ratcliffe (1969, 1975a). Diagonal lines represent Precambrian gneissic rocks of the upland massif; clear areas are carbonate rocks overthrusted by the Precambrian gneissic rocks. Stippled areas are slices of the westward displaced carbonate rocks which form the Monument Mountain through slice. Dashed lines denote contact. Other formations west of the Housatonic River have been omitted. One centimeter equals three kilometers.

determine if *S. t. tenuis*, or perhaps some other species of subterranean amphipod, occurred in the region.

Over a three month period of investigation, only two sites in New Marlgerough, Berkshire County, Massachusetts, produced specimens of amphipods (fig. 1). Collections at the sites were repeatable, though, and a large enough series of specimens was collected to make a definite identification of the species.

A total of 59 specimens, including breeding adults, subadults, and immatures, were studied and all have been deposited in the Invertebrate Division of the Museum of Zoology, University of Massachusetts at Amherst, (UMA).

The distribution of specimens and pertinent collection data are as follows:

Massachusetts, Berkshire Co., New Marlborough, sprinhouse on Benton Hill (elevation 258 m), 12 May, 1982, five males and six females; 10 June, 1982, eleven males and three females, 30 June, 1982, seven males and three females (UMA Ar. 1297, 1-3); springhouse on Brush Hill (elevation 243 m), 10 June, 1982, seven females, 30 June, 1982, five males and twelve females (UMA Ar. 1298, 1-2).

No substantial differences were observed between these specimens and specimens described by Kunkel (1918) and Holsinger (1967), but, it was noted that the coxal gills of the seventh pereopod (fifth of some authors) of the nine largest males (6.5-8.5 mm in length) were somewhat reduced, vestigial, or absent (one individual). Additionally, in a sample of five large males it was found that the ratio of the length of the rami of the first uropod averaged 52-percent (vide Kunkel, 1918) whereas Holsinger (1967) reported the ratio to be from 75 to 80 percent.

DISCUSSION

The two collections extend the range of *S. t. tenus* 75 km further northwest of the subspecies' previously known northern range limit, well beyond the lowland valley region of southern New England, and into the southwestern extremity of the "High" Taconic Mountain system (Housatonic River drainage) of the western New England province. The collections also document the occurrence of *S. t. tenuis* some 140 km north of the terminal moraine of the Wisconsin glaciaton. Furthemore, although the subspecies was not collected in Canaan, Connecticut, during this study, I suggest that Kunkel's (1918) Canaan record is based on *S. t. tenuis*. These findings are significant in that the subspecies was previously known to occur only in shallow ground water environments near the coast in southern New England, New York, and Maryland (Holsinger, 1967, 1978). Little argument has been presented against a northward migration by *S. t. tenuis* along the Coastal Plain into southern New England during late or post-glacial times, despite an extant range hiatus throughout coastal New Jersey (Holsinger, 1967).

The occurrence of *S. t. tenuis* in subterranean waters well removed from coastal areas begs the question as to whether the subspecies migrated to the Taconic Mountain region following glacial retreat or survived in the Taconic Mountains throughout parts or perhaps all of the Pleistocene Epoch. Discussion of the fate of subterranean animals at the onset of glaciation can be found in several papers (see Holsinger 1976, 1978, for review). Recently Holsinger (1980) has reaffirmed an earlier suggestion for the possible existence of a subterranean refugium in Vermont for *S. borealis*. However, Lewis and Bowman (1981) have restated the possibilty of migration of subterranean crustaceans from sub-glacial refugia into formerly glaciated areas. The principal problems to be addressed are (1) could small, relatively non-vagile troglobites actually transverse large distances through varied aquatic substrates within specified time periods to reach their present locations and (2) are places available in which, due to certain geological and hydrological conditions, troblobitic creatures could have survived, even if the proposed refugium lay well within the area of ice cover.

In order to reach the Taconic Moutains by migration, *S. t. tenuis*, and *S. borealis* as well, would have had to move through portions of the upland massif section of New England. The upland section, which separates the Connecticut River valley and other coastal areas from the Taconic Mountains, does not have the extensive cover of glacial deposits characteristic of the lowlands. Although some capacity for water storage is evident in the upland hills, the low porosity of the metamorphic and igneous bedrocks, combined with the presence of deeply dissecting valleys, prevent the formation of extensive wetlands or subsurface drainage systems. Consequently, the upland section separating the Taconic Mountains from the Connecticut River valley lowland would seem to be somewhat of a barrier to migration of troglobitic organisms. Although hardly conclusive, no troglobitic crustaceans have been discovered in the uplands.

The general location of the presently reported collections of *S. t. tenuis* is in an area of high geologic complexity and is a place where two major sections of the New England province converge. The specific sites of collection, Benton and Brush Hills, are situated within an area characterized by the presence of a large north-south trending arc known as the Monument Mountain thrust slice (Ratcliffe, 1969; Fig. 1, this report). The arc is composed of highly metamorphosed carbonate rocks derived principally from Precambrian and Cambrian limestones. Ordovician tectonic activity (Taconic orogeny) resulted in a massive westward movement of portions of the gneissic Precambrian massif of the upland and the formation of the Monument

Mountain Slice (Zen, 1967). Tongues of upland rocks overthrusted the younger or equivalent aged carbonate formations. In a few cases shear surfaces extend 21 km west to east as measured by the distance between exposures of carbonate units of similar age and composition overthrusted by upland rocks (Ratcliffe, 1975a), and thrust faulting may extend several kilometers beneath the present surface (Ratcliffe, 1975b). Within the areas of contact, considerable fracturing of rock surfaces is assumed to have taken place. Subsequent solution of carbonate facies along the contact surface, as depicted for western New England by Norvitch et al. (1968), would result in the development of deep aquifers. Evidence for deep aquifers is provided by observed high permeability of rocks along parts of the thrust front (Ratcliffe, 1975b) and by constant, and at time volumous, resurgences (1 to 400 gpm) at springs and wells near contact zones (Norvitch et al., 1968). It is important to note that the two springs from which *S. t. tenuis* was collected during this study are situated at points of contact where karst, characteristic of solution activity, has developed and is exposed.

It is possible that these deep, subsurface aquifers were available to *S. t. tenuis* during the entire Pleistocene Epoch. The absolute depth at which *S. t. tenuis* had to occur to escape freezing temperatures during glacial episodes and to avoid meltwater flushing, however, can not be answered at the present time for the extent of permafrost and meltwater influences on subsurface water in New England is unknown. Evidence of permafrost in interior New England has been recently questioned (Black, 1976); presently no unequivecal permafrost-indicative structures are known to occur in central New England. I suggest that these glacial influences did not extend to the depths to which subsurface solution has occurred along contact zones in the area of study. Although post-glacial migration of the subspecies to the Taconic Mountains remains as a consideration it seems more plausible that *S. t. tenuis* survived the Pleistocene ice advances in a subsurface refugium in the southern Taconic Mountains.

Holsinger (1967) hypothesized that prior to the Pleistocene Epoch "ancestral populations" of *S. t. tenuis* and the closely releted *S. allegheniensis* (Holsinger) occurred "along the Peidmont and higher ground of the Coastal Plain of southern New England southwestward to east-central Virginia." If Holsinger's (1967) postulations are correct and if it can be assumed that *S. t. tenuis* survived in a Taconic Mountain refugium throughout the various glacial periods of the Pleistocene Epoch, then the continued persistence of *S. t. tenuis* in the southern Taconc Mountains represents a relict of an early distribution of the species.

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ADDENDA

Since the manuscript was submitted, *Stygobromus borealis* has been collected from Benton Hill, New Marlborough, Massachusetts.