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GEOGRAPHIC VARIATION, DISTRIBUTION AND TAXONOMIC STATUS
OF THE INTERTIDAL INSECT *THALASSOTRECHUS BARBARAE*
(HORN) (COLEOPTERA: CARABIDAE)

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Populations of Thalassotrechus barbarae (Horn), a nocturnal, flightless, intertidal carabid beetle species, are distributed linearly from Point St. George (Crescent City), California to Bahia Magdalena, Baja California, Mexico. Mean elytral lengths vary clinally from 2.68 mm in the extreme southern part of the range to 3.54 mm in the northern part. Elytral color also varies clinally with northern populations being darker. These data are not consistent with recognition of subspecies. Consequently, T. b. barbarae (Horn, 1892; type locality - Santa Barbara, California), and T. b. nigripennis (Van Dyke, 1918; type locality - Moss Beach, San Mateo County, California) are consubspecific, and their names are synonyms. North-South temperature and rainfall gradients may be implicated in selection of local variants along the linear cline of elytral length and color.

Les populations de Thalassotrechus barbarae (Horn), une espèce de carabique nocturne, et aptère se trouvent dans la zone des marées et se rencontrent de la pointe St. George (Crescent City), Californie jusqu'à Bahia Magdalena, Basse Californie, Mexique. La longueur moyenne des élytres varie graduellement à partir de 2.68 mm dans l'extrême sud de leur distribution jusqu'à 3.54 mm dans le nord. La couleur des élytres varie de la même façon avec les populations les plus foncées dans le nord. Ces données ne sont pas compatibles avec notre concept de la sous-espèce. Donc T.b. barbarae (Horn, 1892; localité type - Santa Barbara, Californie) et T. b. nigripennis (Van Dyke, 1918; localité type - Moss Beach, San Mateo County, Californie) ne représentent qu'une seule sous-espèce, et leurs noms deviennent synonymes. Le changement graduel de la température et de la précipitation entre le nord et le sud pourrait expliquer la sélection de variations locales en fonction de changement linéaire de la couleur et de la longueur des élytres.

INTRODUCTION

On most coastlines of the world certain insects are conspicuous on rocky shores and sandy beaches, particularly in those areas characterized by extensive beds of offshore kelp and by diverse intertidal algal communities. During daytime low tide in such places, flies are very evident among cast-up algal masses (wrack) and occasionally swarms of beetles (staphylinids and hydrophilids) are encountered (Leech, 1971); during periods of low tide at night predatory and scavenging beetles are active on sand or rock surfaces (Evans, 1977). However, the majority of intertidal insects, particularly their larval stages, are not easily observed since they inhabit subsurface or rock crevice habitats or algal vegetation.

In general, similar kinds of intertidal insects occur in similar habitats all over the world. Kelp flies of the families Anthomyiidae and Coelopidae, for instance, are found wherever wrack accumulates and an extensive beetle fauna is also associated with this food base either as predators or scavengers. Some beetles eat other insects or small crustaceans stranded by receding tides, and members of *Thalassotrechus barbarae* (Horn) are such predators. Adults and larvae of this species live in cracks in rocks in the intertidal zone; adults are brachypterous, and therefore flightless. Larvae are restricted to crack habitats but adults emerge at night and walk over the rock surfaces; feeding and mating takes place at this time.

Ecological equivalents of this species are undoubtedly found in other parts of the world and probably include carabid beetles of the tribe Trechini such as *Kenodactylus audouini* (Guérin) occurring in the subantarctic islands of New Zealand (the Antipodes Islands, Auckland Islands, Campbell Island, Snares Island, Stewart Island), the Falkland Islands and Patagonia (Darlington, 1964; Johns, 1974), the European *Aepus marinus* (Ström) and *Aepopsis robinii* (Laboulbène) (Glynne-Williams and Hobart, 1952) and *Thalassobius testaceus* Solier from Chile (Jeannel, 1926).

GEOGRAPHICAL DISTRIBUTION OF *THALASSOTRECHUS BARBARAE* (HORN)

The geographic range of *Thalassotrechus barbarae* extends from Point St. George, (near Crescent City) Del Norte County, California to Punta Belcher, Bahia Magdalena, Baja California (Fig. 1), a straight-line distance of approximately 2400 km that spans 17° 10' of latitude and 12° 03' of longitude. Populations of this species occur on rocky shores or on rocky outcrops of sandy beaches along this range and conceivably south of Bahia Magdalena as far as Cabo San Lucas, some 185 km away at the tip of Baja California. A part of this range is in the marine biogeographic zone (based on sea water surface temperature) called Cold-Temperate which extends from Point Conception, California to Alaska (Abbott, 1966) while the remaining part coincides with the Warm-Temperate zone between Point Conception and Bahia Magdalena. So the latter locality is most likely to be very close to the southern limit of the range but as far as I know no collections have been made between Bahia Magdalena and the southern tip of the peninsula. The northern limit of the range is more exactly defined because north of Crescent City, California, where collecting sites are more accessible than in Mexico, I (and presumably other collectors) have failed to find any specimens.

TAXONOMIC CONSIDERATIONS AND GEOGRAPHICAL VARIATION

Taxonomic history of *Thalassotrechus barbarae*

T. barbarae, though trechine in general form and habits, has been placed in the Pogonini on the basis of general structure and particularly on characters of the mouthparts (Van Dyke, 1918) and genitalia (Darlington, 1938). Pogonines are halobiontic (Ball, 1968), that is, they inhabit alkali soils with high concentrations of sodium chloride, but *T. barbarae* is the only member of this predominantly Palaearctic group that is found in the rocky intertidal zone, whereas members of the Trechini are commonly found in this habitat. Adults and larvae of *Trechus ovipennis* Motschulsky, for instance, occur in crevices and under stones of the high intertidal zone on rocky shores from central California to southern Alaska (Evans, 1977; Lindroth, 1961) and the trechine species mentioned above have similar habits. Thus, *T. barbarae* is probably a relict genus derived from a stock that gave rise to the present day halobiontic pogonines (Ball, pers. comm.) but because it has become adapted to living in the rocky marine littoral it has convergently become similar in color and form to marine trechine beetles (Darlington, 1938).

Horn (1892) described *Trechus barbarae* from specimens collected at Santa Barbara, California, the type locality.¹ Van Dyke (1918) transferred this species to the Pogonini, based on it the new genus *Thalassotrechus*, the name indicating resemblance of its members to members of *Trechus*. He also described a second species, *T. nigripennis*, from northern California (type locality - Moss Beach, San Mateo County; see Fig. 1), adults of which were larger and darker, and with proportionately broader prothoraces (Van Dyke probably judged this last feature, as taxonomists generally did at that time, rather than taking measurements). Apparently, however,

1. During 1969, specimens could not be found anywhere near Santa Barbara presumably because of the massive oil spill that occurred early in the year (Evans, 1970).

he later came to regard *T. barbarae* and *T. nigripennis* as subspecies, a conclusion amplified by Darlington (1938) on the basis of comparison of adults from Santa Barbara with adults from the San Francisco area. The elytra of adults of the southern population examined by Darlington were rufotestaceous or castaneous in contrast to the black and dull-textured elytra of adults of the northern group. Also, the anterior prothoracic angles of adults of *barbarae* were less flattened than those of the northern population. Moore (1956) also agreed with this arrangement even though he found no consistent structural difference between series of both populations.

Geographic variation of *T. barbarae*

Since clinal variation is expected to occur in *Thalassotrechus* over the predominantly NW-SE trend of the coastline on which it is found I examined adult specimens loaned by the California Academy of Sciences as well as collected by myself. With the use of an ocular micrometer, measurements of elytral length (base to apex along the suture) and maximum prothoracic width were made of individuals obtained from localities shown in Table 1. These localities represent collecting sites that vary in size from individual rocks (at Bahia Magdalena) to individual beaches (Pismo Beach) to long stretches of coastline (Del Norte, Humboldt and Mendocino Counties).

The data, shown in Fig. 1, clearly indicate that the mean elytral length of *Thalassotrechus* populations increases progressively in a north-westerly direction agreeing with Bergman's Rule (Mayr, 1942) which states that the smallest sized individuals of a species are found in the southern part of the range and the largest in the northern part. This clinal progression consists of consecutive, overlapping ranges of elytral length, and of standard deviations of elytral length (except for San Diego County and Bahia Magdalena) with the largest step occurring between Bahia Magdalena, Mexico and San Diego, California, a straight-line distance of approximately 1060 km. Because of this distance I would expect that further sampling between these two localities would give populations that would reduce this large step to a series of overlapping smaller ones. A population, then, from any locality would not differ significantly in size from an adjacent population. Prothoracic width/elytral length ratios do not differ significantly between adjacent localities or between the most northerly and the most southerly localities (Table 1) indicating that the samples were drawn from a population of individuals of different sizes but not of different form.

As shown in Fig. 1, the rate of change of mean elytral length appears to be greater in the middle of the range than at the ends. Theoretically, this may be expected because there would be a decreasing tendency for selection of variants that reflect submarginal environmental conditions that presumably exist towards the ends of the range. Alternatively, the greater rate of change may be due to an equally greater rate of change of some environmental variable such as sea water temperature. An abrupt change such as this probably occurs in the middle of the range near Point Conception, California (see Fig. 1) a well-known locus of marine inshore faunal discontinuity (Abbott, 1966; Garth, 1955).

Adult specimens were also examined for variation in elytral color. Five color categories could be distinguished and individuals were assigned to a category as accurately as possible by this subjective method. The proportions of the populations from each locality (not identical to the above localities because all the specimens were not available at the time of this analysis) in each of these color categories are shown in Fig. 2 where the suspected color cline is satisfactorily demonstrated. Elytral color progresses from pale testaceous in the extreme south to black in the northern part of the range. It is interesting to note, however, that color varies even at the ends of the range so that the elytra of individuals from Bahia Magdalena are not

all pale testaceous and individuals from Point St. George do not all have black elytra. Finally, color variation is apparently greater in the middle part where the elytral color of individuals may vary from the lightest to the darkest.

Because variation in supposed diagnostic features is either non-existent (ratio to prothoracic width/elytral length) or clinal (elytral length and color), I conclude that recognition of subspecies would be wholly arbitrary, and would serve no useful purpose. Consequently, *T. b. barbarae* and *T. b. nigripennis* are consubspecific, and their names are synonymous. The species is thus monobasic, and a binomial name is sufficient.

Discussion of Pattern of Variation of *T. barbarae*

Clines result from gene flow between populations and from selection of individuals that are adjusted to the local environment (Mayr, 1963). Since *T. barbarae* is distributed along a northwest-southeast trending coastline, that is, linearly (or unidimensionally, Udvardy, 1969), environmental factors that show a north-south gradient are more likely to be implicated in the selection of local variants. One such factor, temperature, is an obvious example, and its role in influencing the body size or body proportions of poikilotherms has been demonstrated by Ray (1960). A north-south gradient for the California coastline is well-documented for air temperature (U.S. Department of Commerce, 1968) and sea water temperature (U.S. Department of Commerce, 1967) both of which must influence metabolism of *T. barbarae* but other factors such as salinity, rainfall, humidity, wave action, and availability and kind of food, are probably also involved. Johns (1974) suggests that body size of marine carabids of the species *Kenodactylus audouini* may be related to the amount of exposure to sea water since the largest specimens of this species are in supralittoral habitats where sea water is much diluted and where prey such as Collembola and Isopoda, and larvae and eggs of various arthropods are more available. A rainfall gradient exists between the ends of the range of *T. barbarae* with Point St. George (Crescent City), California having the highest average annual rainfall, about 178 cm (U.S. Department of Commerce, 1968) and Bahia Magdalena, Mexico receiving less than 25 cm a year (Escoto, 1964). The increasing dilution of sea water in a northerly direction may very well be implicated in the cline of body size in *T. barbarae* but perhaps the rainfall gradient, expressed as a humidity gradient, may be implicated in the clinal variation in elytral color. Discussing Gloger's Rule, Dobzhansky (1937), concludes that pigmentation in insects increases in humid and cool and decreases in dry and hot climates with humidity being more effective than temperature. If, indeed, this is correct, the correlation between elytral color and humidity in *T. barbarae* could be explained but the underlying mechanism for this phenomenon is unknown. In all likelihood, several factors are involved in geographic variation of *T. barbarae* making it difficult to determine the actual cause of this variation even though the distribution of this insect is linear, therefore, seemingly much more simple to analyze than two- or three-dimensional distributions (Udvardy, 1969). In the latter case, for example, a plot of a single character gradient such as color on a distribution map results in, at best, a series of non-parallel, crude isophenes (see Petersen, 1947). Or, when geographic variation in body length of a nonlinearly distributed insect is plotted on a Hubbs-Hubbs diagram, as Ball and Negre (1972) did for a xerocolous carabid, *Calathus ruficollis* Dejean, the resulting pattern can be very complex indeed. But this pattern merely reflects complex gradients of environmental variables. In order to elucidate relationships between biological and environmental variation precise measurements of such parameters as temperature and rainfall or humidity are needed in addition to data on several character states of populations of linearly distributed species. This study suggests that such an approach is possible.

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Table 1. Prothoracic width/elytral length ratios of populations of *Thalassotrechus barbarae* collected at various localities.

Locality	Code (see Fig. 1)	Mean prothoracic width x 100/elytral length ratio	S.D.
CALIFORNIA			
Del Norte, Humboldt and Mendocino Co's.	1	36.04	3.73
Marin Co.	2	36.15	4.04
San Francisco and Contra Costa Co's.	3	35.12	2.27
Pacific Grove	4	35.44	1.42
Pismo Beach	5	34.4	2.7
Santa Barbara Co.	6	37.59	3.3
Los Angeles and Orange Co.	7	36.95	2.4
San Diego	8	37.8	1.19
MEXICO			
Punta Belcher, Bahia Magdalena	9	35.4	2.11

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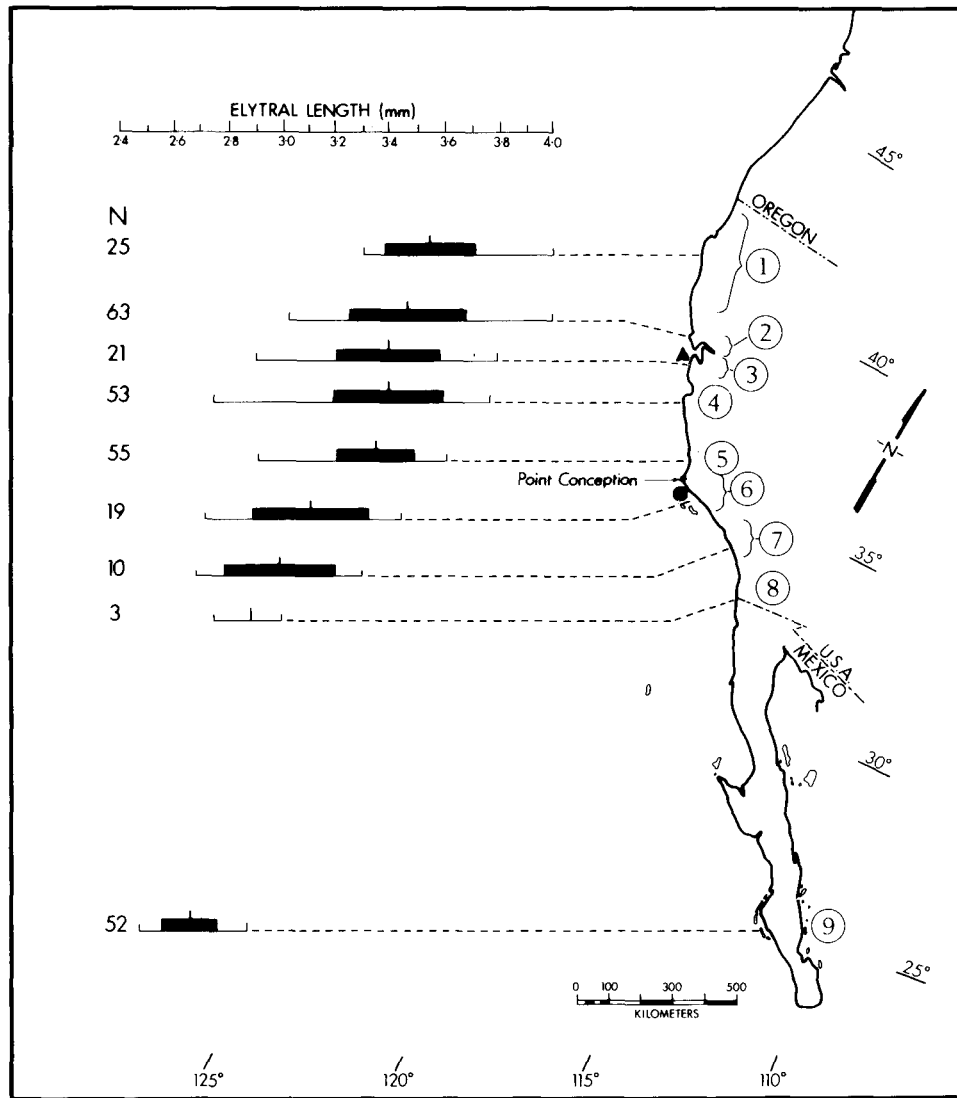


Fig. 1. Mean (vertical line), standard deviation (black bar) and range (horizontal line) of elytral lengths of populations of *Thalassotrechus barbarae* collected from localities given in Table 1. ▲- Type locality for *T. nigripennis*. ●- Type locality for *T. barbarae*.

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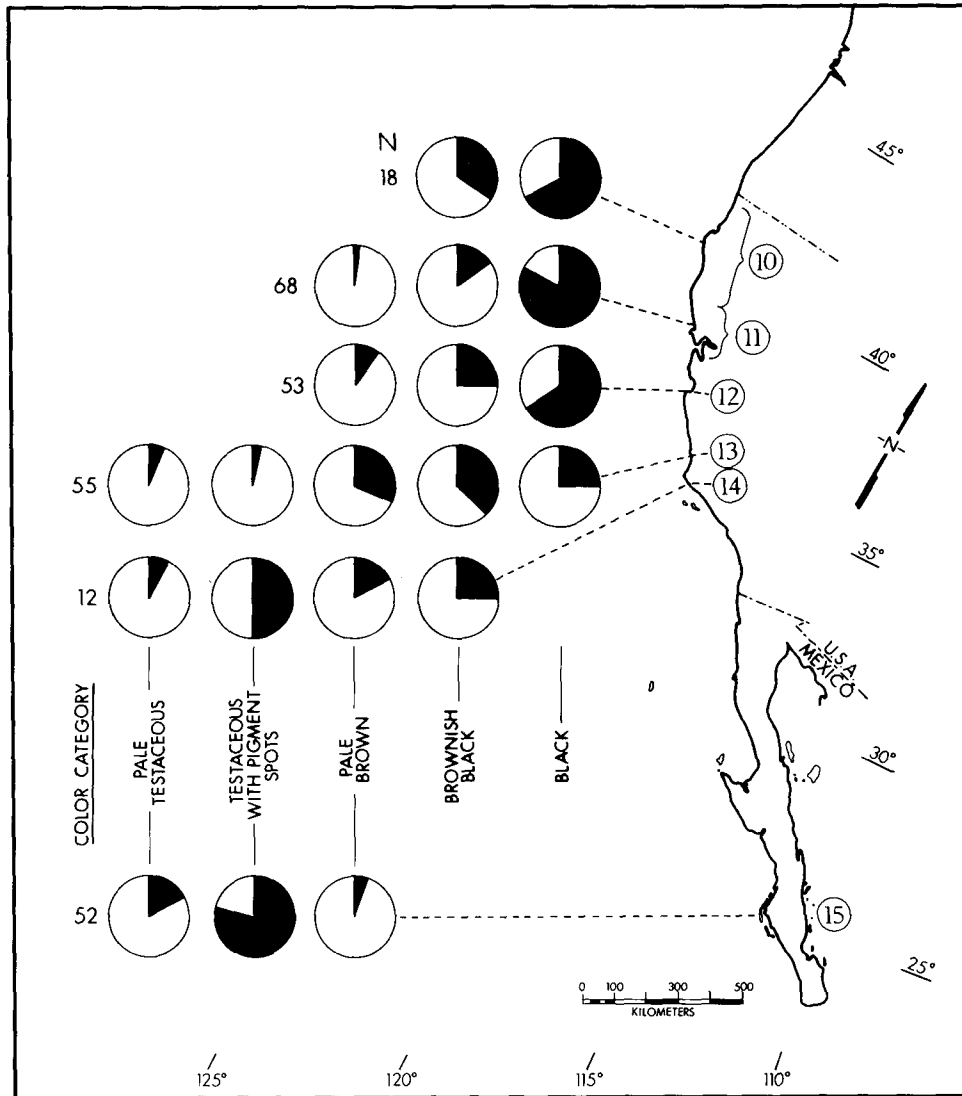


Fig. 2. Proportions of populations of *Thalassotrechus barbara* collected from various localities in five clytral color categories. Black portion of circle represents the proportion of a population in that particular color category. Locations: 10. Mendocino, Humboldt and Del Norte Counties, Calif.; 11. Marin, Sonoma and Contra Costa Counties, Calif.; 12. Pacific Grove, Calif.; 13. Pismo Beach, Calif.; 14. Santa Barbara and Ventura Counties, Calif.; 15. Punta Belcher, Bahia Magdalena, Baja California, Mexico.