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About the malacological subdivision of Curaçao; a review

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Abstract

Burrington Baker (1924) states that Curaçao can be divided into three distinct faunal areas. Stock (1977) mentions the occurrence of three subspecies of hadziid amphipods almost exclusively confined to different parts of Curaçao. The results of a study of the distribution on this island of various subspecies of the gastropods *Cerion uva*, *Brachypodella raveni*, *Tudora megacheilos* and *T. rupis*, however, do not support the hypothesis of a tripartite Curaçao.

Résumé

Burrington Baker (1924) considère Curaçao comme pouvant être divisé en trois zones fauniques distinctes. Stock (1977) mentionne la présence de trois sous-espèces d'amphipodes hadziides presque exclusivement dans les zones distinctes de Curaçao. Les résultats d'une étude de la distribution sur cette île de sous-espèces diverses des gastropodes *Cerion uva*, *Brachypodella raveni*, *Tudora megacheilos* et *T. rupis* ne viennent pas à l'appui de l'hypothèse d'un Curaçao tripartite.

Introduction

Studying Jan Stock's publication on the hadziid Amphipoda of the West Indian area (1977), I was struck by the occurrence of three subspecies of freshwater amphipods on Curaçao, each of them almost exclusively confined to a different part of the island (fig. 1). This reminded me of Horace Burrington Baker's statement (1924: 113), that Curaçao "can be divided into three, quite distinct, faunal areas".

Can the distribution of animals from cavern waters of Curaçao be connected in some way to the occurrence of certain land mollusks restricted to the same limestone area of this arid island? A rather funny question at first sight, but – as the Antillean researches of Stock himself have already yielded so many surprises – this induced me to consult anew Burrington Baker's still unsurpassed paper on the "Land and freshwater molluscs of the Dutch Leeward Islands", 1924.

Geography

It may be clear that the western part of Curaçao was never completely submerged during the formation of the terrace-limestones which still cover almost one third of the island, as the Christoffelberg (372 m) stands high above the Highest Terrace of the neighbouring Tafelberg of St. Hyronimus (230 m). In eastern Curaçao the present situation is quite different as the limestone terrace of the Tafelberg of Santa Barbara (193 m) rises well above the highest part of the interior (89 m). The interior, however, consists of easily weathering rock, so that this part of the island was probably above the sea-surface during the formation of the Tafelberg of Santa Barbara.

Thus, during the Early Pleistocene, the two nuclei of the western and eastern parts of the present-day island remained above sea-level. These two islets became united to form an almost continuous karstic area with corresponding cavern-water complexes. Disintegration of this middle-Curaçao area occurred afterwards.

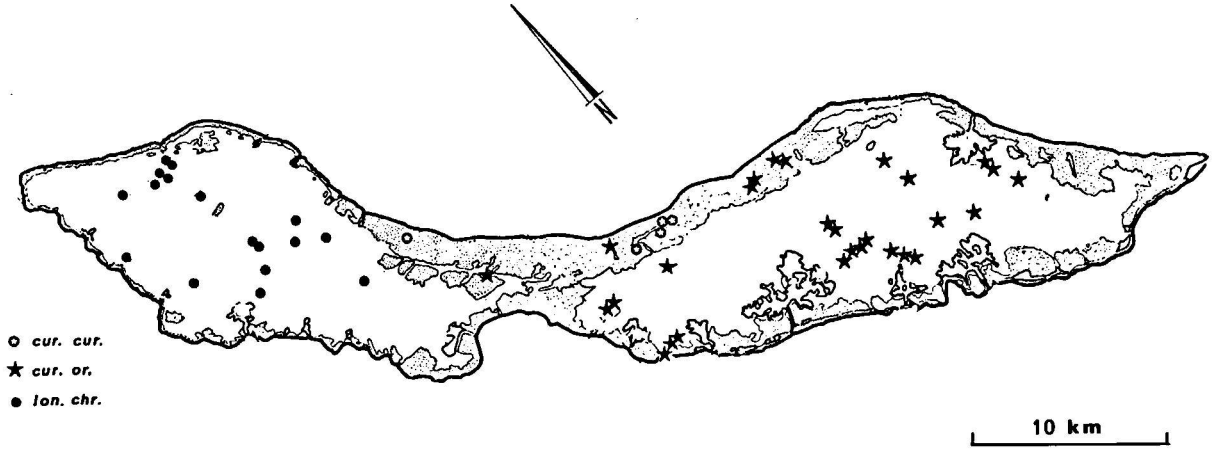

Fig. 1. Map after Stock (1977), showing the distribution of three forms of *Metaniphargus* on Curaçao – which reminded the author of Burrington Baker's statement, that this island can be divided into three quite distinct faunal areas.

As most of the land mollusks are almost exclusively limited to the remaining limestone rim of the island, breaks in these rims constitute quite definite barriers to migration. After several successive breaks, the species of *Tudora* especially often change so much, that there is no intergradation left between the populations thus separated. On such discontinuities Burrington Baker (1924: 113–114) based his subspecies discrimination:

"Curaçao can be divided into three, quite distinct, faunal areas, which appear to have been populated from central hills, which must have been separate islands during periods of higher strandline. [...] The most southern area of Curaçao centers around the Tafelberg of Santa Barbara. *Tudora rupis rupis*, *T. pilsbryi* and *Brachypodella raveni sanctaebarbarae* were only found at the base of the northern and western escarpments of this mesa. The first species is also represented by the subspecies *newportensis*. [...] *Cistulops raveni* appears to be absent from southern Curaçao. – The central area may be considered to center around Ronde Klip and the Hato ridge. It is characterized by the absence of the section *Tudorata* [to which *T. rupis* belongs], and by the presence of *Tudora megacheilos* (4 subspecies) and *Brachypodella raveni raveni*. – The northern area [...] is differentiated by *Tudora muskusi* (3 subspecies), *Guppya molengraaffi*, 3 subspecies of *Tudora fossor*, *Brachypodella raveni knipensis* and *Cerion uva knipensis*. – The northern and central areas agree in the occurrence of *Cistulops raveni raveni*, while the central and southern possess *Cerion uva uva* in common. The presence of the section *Tudorata*, and the resemblance of the subspecies of *Brachypodella* and the species *Tudora fossor* and *pilsbryi*, appear to relate the northern and southern areas more closely to each other than to the central portion."

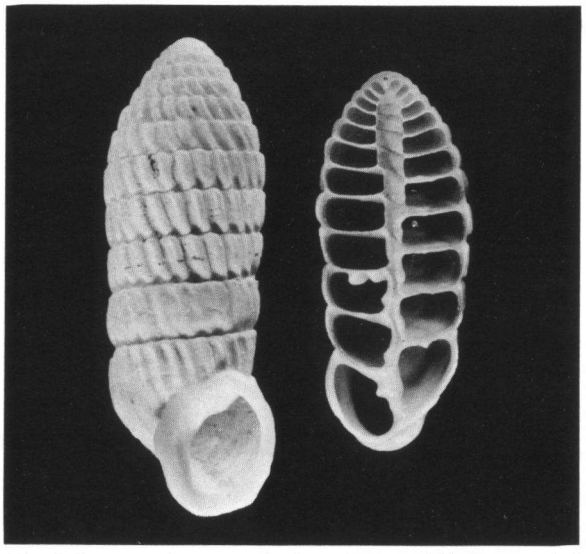

Fig. 2. Large and average-sized specimens of *Cerion uva* (L.) from the Hato ridge on Curaçao, 32 and 25 mm in length.

Malacology

When trying to check Burrington Baker's conception of the malacological tripartition of Curaçao, we may restrict ourselves to the species of *Cerion*, *Brachypodella*, and *Tudora*, of which he made an admirable effort to describe a number of well-defined subspecies.

Cerion uva (figs. 2, 3)

Studying variation in *Cerion uva* (L., 1758) regard-

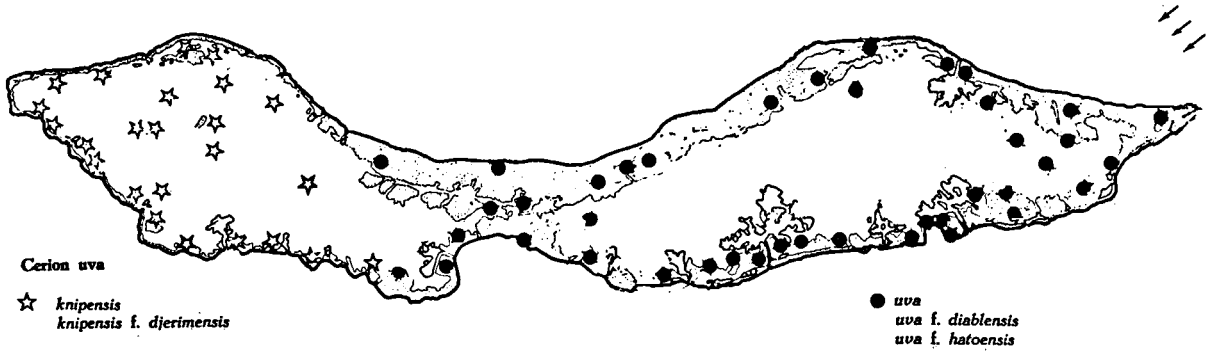

Fig. 3. Localities of *Cerion uva*, mapped according to Burrington Baker who distinguished a subspecies *knipensis*. The species is not strictly confined to areas of terrace limestone.

ing three characters (altitude, diameter and number of whorls), Burrington Baker (1924) distinguished *C. uva uva* (south and middle Curaçao), *C. uva knipensis* (northwestern Curaçao), and furthermore *C. uva arubana* and *C. uva bonairensis*. However, Wagenaar Hummelinck (1940: 102) concluded: "*Cerion uva* does not show such morphological differences, which justify a subdivision of the species in subspecies". De Vries (1974) who undertook a more extensive study of old and new material (231 samples and 6 measures per shell) did not succeed in finding any distinct correlation of geographical distribution and form either. In the mean time, however, Stephen Jay Gould (1969) could confirm Burrington Baker's subdivision after a multivariate study of Baker's and Hummelinck's material. This investigation was followed, in 1984, by an analysis of 135 samples of 20 snails each, based on 19 measures selected to show covariance in patterns of ontogenetic allometry. Gould's fig. 8 (1984) shows a line off Bullenbaai, which separates eastern and western regions.

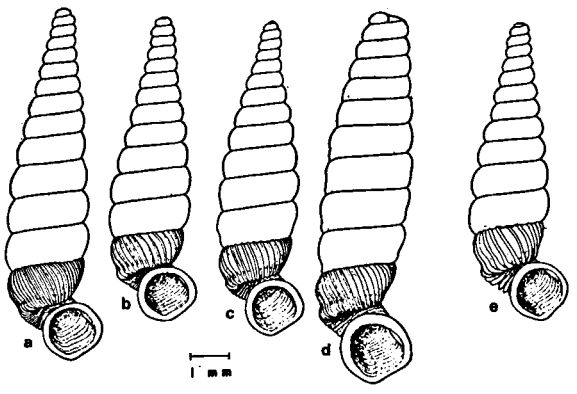

Fig. 4. The species of *Brachypodella* as figured by Burrington Baker (1924): a, *Br. raveni raveni*; b, *raveni sanctaebarbarae*; c, *raveni knipensis* from Curaçao; d, *raveni arubana* from Aruba, and e, *gibbonsi* from Bonaire.

Brachypodella raveni (figs. 4, 5)

Burrington Baker (1924) described two a-typical subspecies of *Brachypodella raveni* (Crosse, 1872) from Curaçao, another from Aruba and a closely related species, *B. gibbonsi* from Bonaire (fig. 4). *Brachypodella raveni raveni* occurs rather commonly in the eastern part of the island; *B. raveni knipensis* is found near the northwestern coast and the Seroe Christoffel, while *B. raveni sanctaebarbarae* was collected only near the northern escarpment of the Tafelberg of Santa Barbara. Burrington Baker stated that *raveni raveni* attains the largest size and has its riblets closest together. The shell of *sanctaebarbarae* is smaller, thinner and more polished, whereas the growth riblets of the last whorls are lower, more rounded, and more widely spaced. The subspecies *knipensis* is only a little bit smaller than *raveni*, often somewhat oval, with growth riblets of the last whorls more widely spaced and slightly heavier (fig. 4).

These differences are small and often indistinct, so I wrote in 1940 (p. 103): "The material from Curaçao and Aruba does not justify a subdivision into subspecies; nor is *B. gibbonsi* from Bonaire specifically separable".

Looking at these differences again, and studying the (hitherto unpublished) measurements taken by J.C. Lindeman some thirty years ago (see table I) I

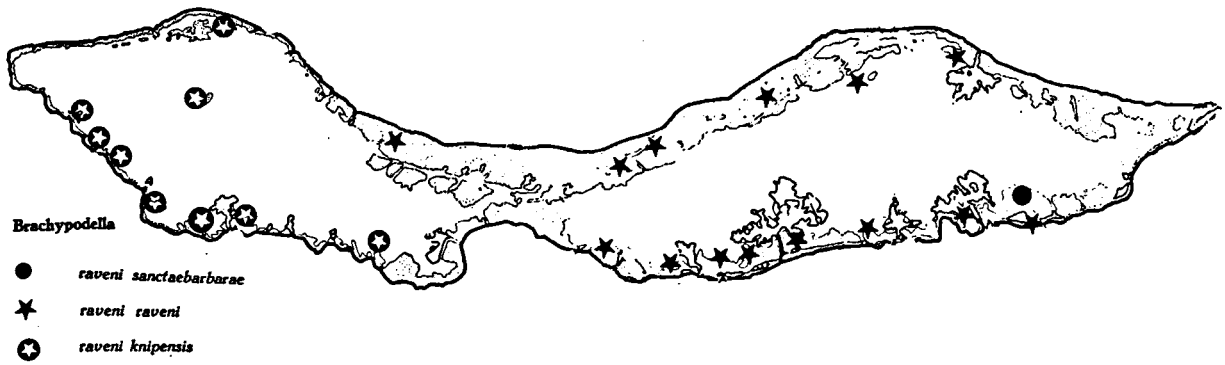

Fig. 5. Samples of *Brachypodella raveni*, mapped according to the classification of Burrington Baker.

Table I. Measurements of *Brachypodella raveni* from Curaçao and Aruba, and *B. gibbonsi* from Bonaire (length of shell restored as the apical whorls are usually missing; average values in italics).

	B. r. raveni	*B. r. sanctaebarbarae*	*B. r. knipensis*	*B. r. arubana*	*B. gibbonsi*
Locality	East Curaçao	Tafelberg S.B.	West Curaçao	Aruba	Bonaire
N	108	100	43	82	19
length of shell (restored, mm)	7.0–*8.2*–8.8	6.5–*7.23*–8.2	6.6–*7.37*–8.0	7.6–*8.61*–10.0	6.5–*7.13*–8.1
width:% length	22.5–*25.0*–27.5	24.0–*26.6*–29.5	23.5–*26.2*–29.0	20.0–*22.7*–25.0	24.5–*26.8*–28.5
height of mouth: % shell length	20–*21*–24	20–*23*–24	20–*22*–25	18–*21*–22	20–*22*–24
number of whorls (restored)	13–*13.5*–14	12–*12.5*–13	12–*12.5*–13	14–*14.5*–16	12–*12.7*–13
diam. 6th whorl: % width	21–*30*–39	25–*37*–50	24–*35*–41	17–*25*–33	30–*38*–46
greatest width on whorls from apert.	2½–3	2–2½	2–2½	3	2–2½
growth riblets per mm	6.5–8.0	4.5–6.5	5.0–8.5	8–9	4–6
status of riblets	well marked	much lower	slightly heavier	lower, more rounded	heavier, more distant

am still convinced that it will be extremely difficult to maintain Burrington Baker's subspecies of *B. raveni* without any further study.

Tudora megacheilos (figs. 6, 7)

Spectacular examples of intra-insular geographic variation can be observed in two representatives of *Tudora* Gray, 1850, a genus which, according to some authors, may be considered to be a junior synonym of *Licina* Gray, 1847.

On Curaçao *Tudora megacheilos* (Potiez & Michaud, 1838) abundantly occurs on limestone. It can also be found in several places of the non-calcareous interior, including gardens.

Burrington Baker distinguished (1924) in the species complex of *T. megacheilos*: *megacheilos megacheilos*, *megacheilos spreitensis*, *megacheilos rondeklipensis*, *megacheilos kabritensis*, *pilsbryi*, *fossor fossor* and *fossor westpuntensis*. Comparing specimens from the type-localities affirms the more

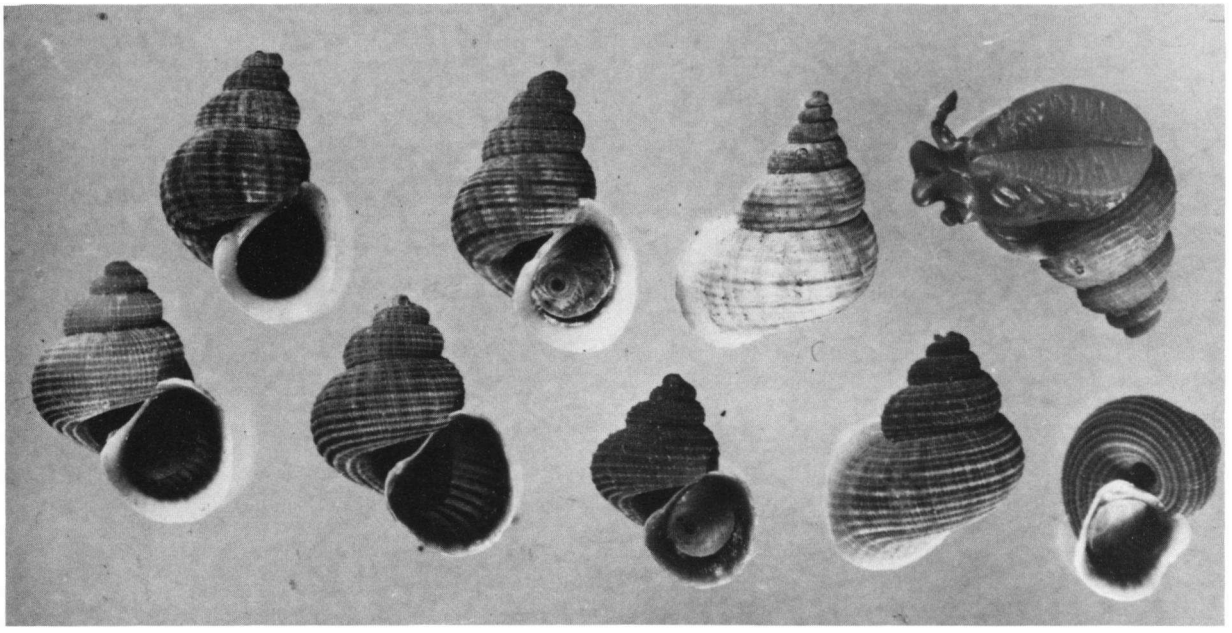

Fig. 6. Specimens of *Tudora megacheilos megacheilos* (upper row, average size 14.3 × 7.3 mm) and of *T. meg. pilsbryi* (average size 14.1 × 8.9 mm) from the southeastern part of Curaçao.

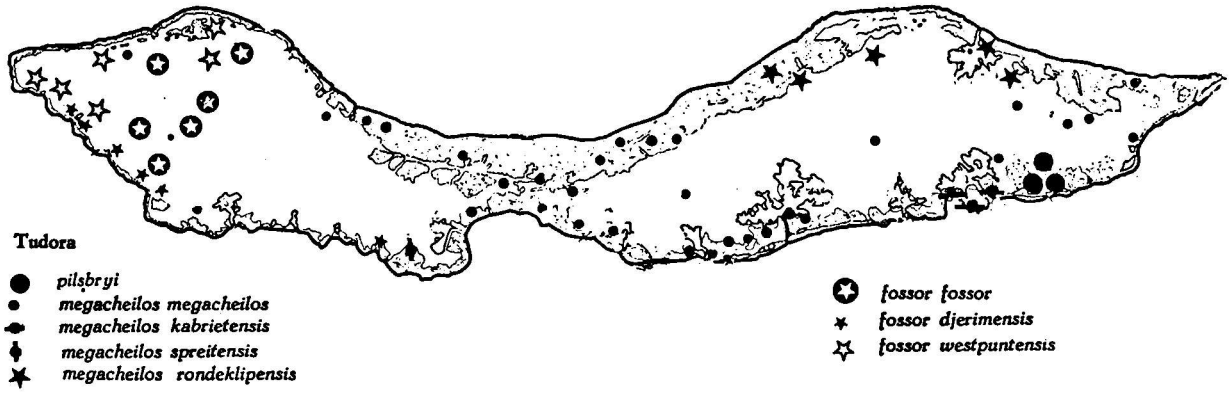

Fig. 7. Localities of *Tudora megacheilos* as much as possible arranged according to the classification of Burrington Baker. The species is not strictly confined to limestone areas.

or less noticeable differences, distinguishing the populations of these places. At other localities, however, the different forms are intergrading, so that a subdivision of *T. megacheilos* into lower taxonomic categories might not be justified. Only *T. pilsbryi*, which was only collected alive at the Tafelberg of Santa Barbara, may deserve a special status within the species complex of *T. megacheilos*.

Tudora rupis (figs. 8–10)

Tudora rupis Burrington Baker (1924) is much less common on the island and strictly confined to limestone areas.

The following subspecies are described by Burrington Baker (1924): *rupis rupis*, *rupis newportensis*, *muskusi muskusi*, *muskusi grandiensis*, and *muskusi bullenensis*. Wagenaar Hummelinck (1940) distinguished as belonging to the species complex of *Tudora rupis*: (a) *T. rupis rupis* (incl.

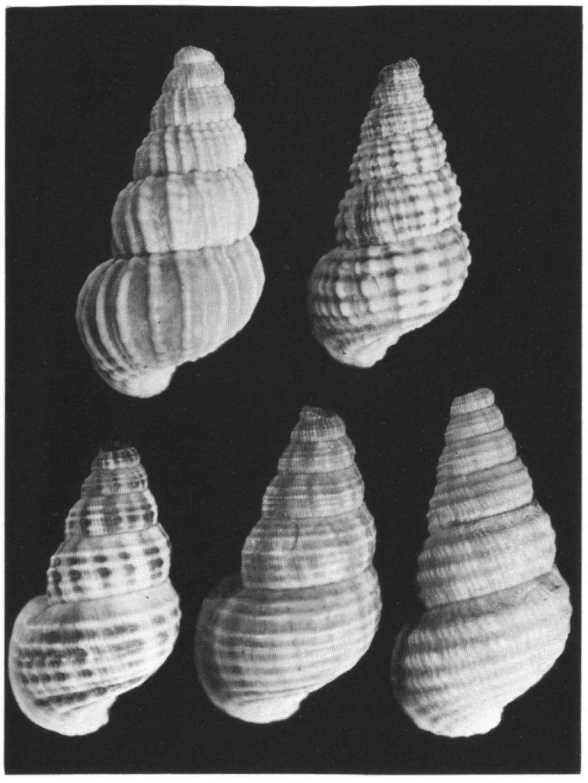

Fig. 8. Typical specimens of *Tudora rupis*, from above, left to right: *T. rupis muskusi* from Seroe Djerimi; *T. rupis grandiensis* from Seroe Cabajé; *T. rupis rupis* (2 specimens) from Tafelberg S.B.; *T. rupis hatoensis* from Hato.

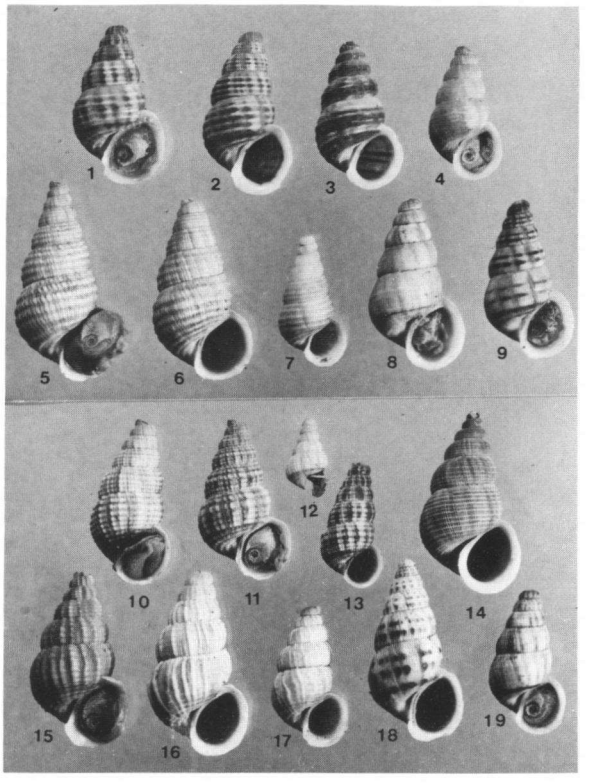

Fig. 9. Variation in *Tudora rupis* on the island of Curaçao (472 km²): *rupis rupis* from Tafelberg (1–4) and Newport (8–9); *rupis hatoensis* from Hato (5–7); *rupis grandiensis* from Seroe Cabajé (10–13) and S. Bartool (18–19); *rupis muskusi* from St. Kruisbaai (15–17); moreover *rupis muskusi* × *megacheilos* from St. Kruis (14). Average size ♀ ♀ 15.0 × 6.9 mm, ♂ ♂ 12.1 × 5.5 mm.

newportensis), endemic to the Tafelberg of Santa Barbara area; (b) *rupis grandiensis* (incl. *bullenensis*), a very variable form, from middle to northwestern Curaçao; (c) *rupis muskusi* from west Curaçao, and (d) a new subspecies *hatoensis* from near the north coast of Hato (fig. 10).

If the centres of the different forms should be isolated, then most malacologists would without any hesitation accept four or more species. The present state of affairs, however, shows distinct intergradation, with the exception of *rupis rupis*.

The eastern boundary of the distribution area of *hatoensis* appears to be a small gully intersecting the belt of limestone along the north coast, along the road to Hato Airport (Wagenaar Hummelinck, 1981, fig. XXXIX b). Several attempts have failed to collect *T. rupis hatoensis* on the Seroe Rondó, whilst it is found on the Seroe Bordo, only a hundred metres or so towards the West.

The peculiar distribution of *Tudora* on the arid and easily explorable island of Curaçao did not arouse much interest in later years. Only a small paper of Hovestadt (1987) may be mentioned. He raised the possibility of the existence of four former islands, having their nuclei at the Christoffelberg, Seroe Grandi, Ronde Klip, and Tafelberg Santa Barbara, characterized by the occurrence of *Tudora rupis muskusi*, *T. rupis grandiensis*, *T. rupis hatoensis*, and *T. rupis rupis*.

Conclusion

The recent distribution of the species of *Cerion*, *Brachypodella*, and *Tudora* may support the assumption that Curaçao has been populated from

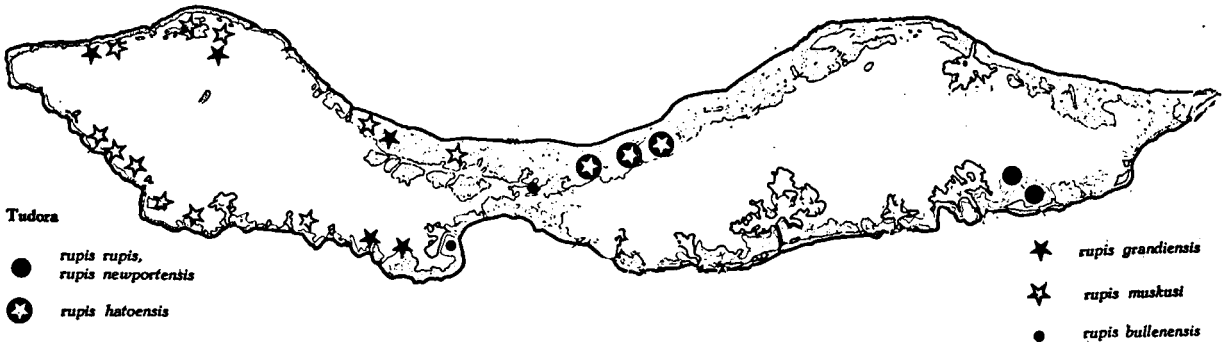

Fig. 10. Distribution of *Tudora rupis*, strictly confined to limestone areas. Burrington Baker's subspecies *newportensis* is considered to be a form of *rupis rupis*; his *bullenensis* might be a more or less smooth form of *grandiensis*.

the nuclei of the eastern and western parts of the island after its almost complete transgression which resulted in the formation of the limestones of the Highest Terrace. It does *not* support the hypothesis that the island can be divided into three rather distinct faunal areas.

This conclusion would appear somewhat disappointing if this paper had not given its author a new opportunity to insist on more malacological research on this interesting island.

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