LAND NEMERTINES OF MADEIRA AND THE AZORES [1]

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With 6 figures and 1 table

I INTRODUCTION

Geonemertes chalicophora is a terrestrial nemertine known only from European greenhouses. It was first recorded by von Graff (1879) from the Palm House at Frankfurt, and later found in the Botanical Gardens, Graz by Böhmig, who compared his specimens with those of von Graff and gave a full description (Böhmig 1898). Since then it has never been found again. Southern (1911) recorded a nemertine in greenhouses near Dublin, but his assumption that this must be *G. chalicophora* cannot be substantiated. None of these specimens can now be traced. All the other *Geonemertes* species occur on oceanic islands or in Australia or New Zealand (Pantin 1961).

Further investigation of *G. chalicophora* is particularly desirable: by now a number of species of land nemertines have been described and *G. chalicophora* can be seen to occupy an isolated position, having fewer specialised characters than any other land nemertine (Pantin 1969).

In 1957, Professors E. Dahl and P. Brinck of the University of Lund surveyed the fauna of Madeira and the Azores (see earlier publications in this Boletim). They found a terrestrial nemertine at several sites on the islands of Madeira, S. Miguel, Faial and Flores. This material was examined by Professor Dahl and Dr. Pantin and was thought to be *G. chalicophora,* but certain identification was not possible (Pantin 1969, Appendix). We are much indebted to Professors Dahl and Brinck for their material and for helpful information.

In March 1971, we visited Madeira and S. Miguel, Azores, and found 21 specimens of the nemertine «*Geonemertes* X» in a number of different sites. The following account

1. records the distribution and habitat of the specimens
2. considers whether the specimens agree with Böhmig's account sufficiently closely to be identified as *G. chalicophora*
3. considers the relationship of the species found to others in the genus *Geonemertes*.

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II DISTRIBUTION AND HABIT

We searched for land nemertines on Madeira, March 13th — 18th 1971, and on S. Miguel, Azores, March 19th — 27th 1971. Special attention was paid to localities in which land nemertines had been found by Brinck and Dahl, and to habitats which appeared most likely to contain specimens. However many apparently unsuitable habitats were also investigated.

Specimens were searched for under boulders, large stones and rotten wood. A record was kept of the number of stones etc. investigated, in order to give an indication of the intensity of search and frequency of occurrence. In localities where conditions appeared to be suitable at

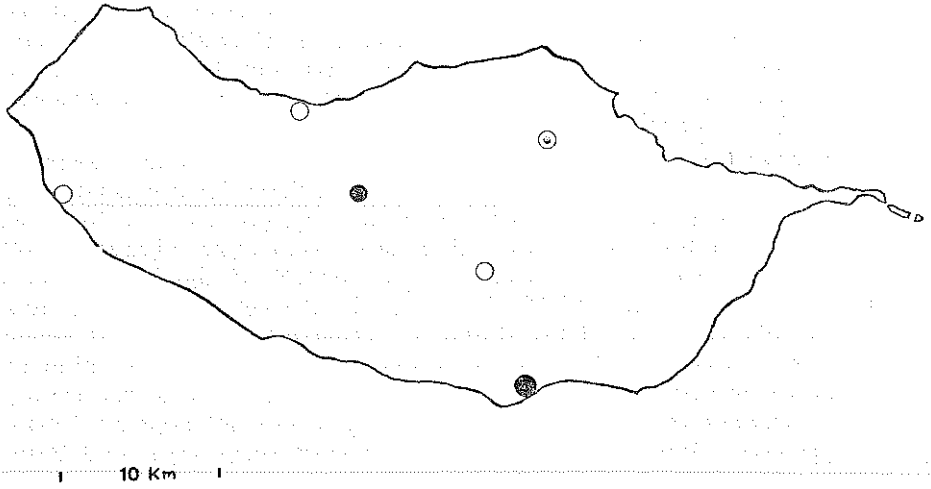

Fig. 1. — *Geonemertes* X (= *G. chalicophora* — see conclusions) in Madeira. — ○ No *G. chalicophora* found 1971 (J.M., N.W.M.). — ◎ *G. chalicophora* found in 1957 (Brinck, Dahl), but not in 1971. — ◍ *G. chalicophora* found in 1971. — ● *G. chalicophora* found in 1957 and 1971.

least 20 stones were examined wherever possible. Notes were made about other animals found under the stones where land nemertines were found, and about the plants growing nearby.

The geographical positions of localities where *Geonemertes* was found are shown in Figures 1 and 2. Notes on the localities and on the habitats of the nemertines are given below.

(i) Localities and general nature of the habitat

A. MADEIRA

1. *Ribeiro Seco* (Loc 111, Brinck — Dahl)
The floor of the wooded ravine between the the sea and the road from Funchal to Câmara de Lobos. Height above sea level 1 — c. 10 m. Vegetation: derelict banana plantation and non-endemic trees, soil variable, in some places unusually deep for uncultivated land in Madeira.

100+ stones investigated, 16 *Geonemertes X* found.

Species found here in 1957 by Brinck and Dahl. No *Geonemertes* found under 20 stones investigated above the road bridge.

This was the richest site for *Geonemertes* which we found in Madeira and S. Miguel. It has a particularly rich soil fauna in general (Brinck and Dahl in this Boletim). It is to be hoped that its great scientific interest will be taken in account in future developments in the area.

2. *Boca da Encumeada* (C. 1200 m west of highest point on Ribeira Brava to S. Vicente road). Steep slope of upper part of nearly inaccessible mountain valley of Ribeira de S. Vicente. Edge

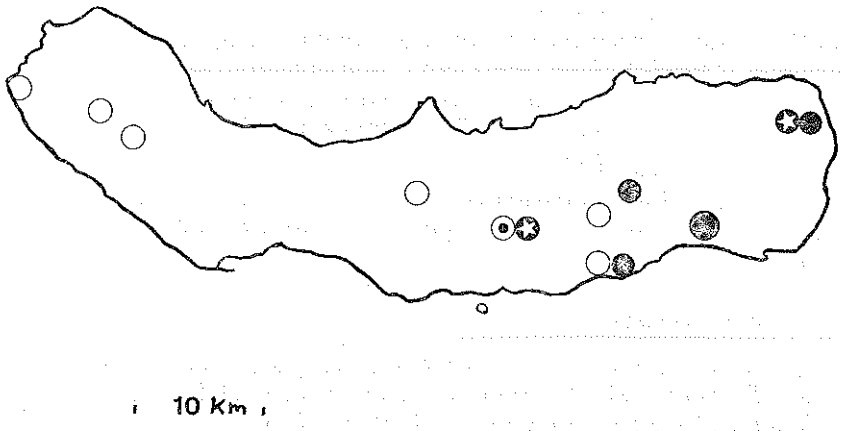

Fig. 2. — *Geonemertes* X (= *G. chalicophora* — see conclusions) and *G. dendyi* in São Miguel, Azores. — ○ No nemertines found 1971 (J. M., N. W. M.). — ◎ *G. chalicophora* found in 1957 (Brinck, Dahl). — ● *G. chalicophora* found in 1971. — ● *G. chalicophora* found in 1957 and 1971. — ✪ *G. dendyi* found in 1971.

of levada. Height above sea level c. 1000 m. Distance from sea c. 5000 m. Endemic woodland *(Ocotea foetens, Erica arborea etc.)*.

40 stones investigated, 1 *Geonemertes X* found.

3. *Casa das Queimadas* (Loc 122). Brinck and Dahl found

Geonemertes X in 1957. We investigated this site, which is ecologically rather similar to Boca da Encumeada, but found no *Geonemertes*.

B. AZORES, SÃO MIGUEL

1. *Ribeira Quente* (c. 1300 m WSW of Ribeira Quente church). Steep wooded valley. Height above sea level c. 100 m. Distance from sea c. 500 m. Derelict land at limit of cultivation, with endemic species present (e. g. *Erica azorica)*
   5 stones and 1 rotten log investigated.
   2 *Geonemertes X* found, one under stone, one under log.
2. *Furnas* (c. 1500 m NW of Caldeiras, Furnas). Open track where *Cryptomeria* forest adjoins pasture in broad valley in Furnas crater. Height above sea level c. 250 m. Distance from sea c. 5,700 m. Edge of cultivated land vegetation mainly non-endemic.
   3 stones investigated, all exposed to midday sun.
   1 *Geonemertes X* found
3. *Povoação* (1 500 m N of Povoação river mouth. Loc 60, Brinck — Dahl). Partly cultivated deep ravine-like valley. Height above sea level c. 100 m. Distance from sea 1 500 m. Vegetation a mixture of endemic (*Myrica faya* etc.) and non-endemic species.
   20 stones investigated. 1 *Geonemertes X* found.
   Species found here in 1957 by Brinck and Dahl.
4. *Nordeste* (c. 1 500 m SW of mouth of R. Guilherme). Wooded valley just above cultivation. Height above sea level c. 150 m. Distance from sea c. 1 100 m. Vegetation a mixture of endemic and non-endemic species.
   53 stones investigated. 1 *Geonemertes X* found.
   1 *G. dendyi* found (see below)
5. *Lagoa do Congro*, east shore. (Loc 34, Brinck — Dahl). Rocky edge of crater lake at foot of steep woods. Height above sea level c. 500 m. Distance from sea c. 4,700 m. Flora a mixture of endemic and non-endemic species including *Myrica faya, Cryptomeria, Alnus, Hedychium*. Ferns included *Osmunda regalis* and *Trichomanes speciosum*.
   20 stones investigated. No *Geonemertes X* found (it was found here by Brinck and Dahl in 1957). 3 *G. dendyi* found.

C. OTHER ISLANDS

In 1957 Brinck and Dahl also found land nemertines on Faial, Azo-

res, at Ribeira dos Flamengos, Horta (Loc 71) and at Porta da Boca da Ribeira, 1 000 m E of Ribeirinha (Loc 74). This was before the 1957

Fig. 3. — Known distribution of *Geonemertes* in the Atlantic region 1971. — ● *G. chalicophora*. — ✪ *G. dendyi*. — ▲ *G. agricola*. — ★ *G. nightingaleensis*.

volcanic eruption. Also on the central plateau of Flores, Azores, S and

SE of Caldeira Comprida (Loc 109).

In 1971, Brinck found two specimens of land nemertines at El Lomo de Marques (Loc 9) Tenerife, Canary Islands.

Specimens of land nemertines found by Brinck and Dahl in all these sites, and in those on Madeira and S. Miguel, have been examined by J. M., and found to be identical to the «*Geonemertes X*» found by us.

(ii) Microhabitat

All 16 *Geonemertes X* found on Madeira and 4 *Geonemertes X* and 2 *G. dendyi* found on S. Miguel were on the underside of stones whose longest dimension was between 10 and 46 cm. One *Geonemertes X* from S. Miguel was found under a log measuring 32 by 10 cm. 9 of the *Geonemertes X* on Madeira and 1 on S. Miguel and 1 *G. dendyi* were under stones lying under or very near to plants of *Tradescantia fluminensis,* a native of Brazil, Uruguay and Paraguay. All 16 *Geonemertes X* on Madeira and all 5 on S. Miguel were found on stones within less than 300 m of this plant, which therefore can be taken as a useful indicator of possible localities for *Geonemertes X.*

The soil fauna found under the same stones as *Geonemertes* included a terrestrial amphipod, an isopod, at least two species of diplopods, a centipede, an ant, at least two species of slug, a zonitid gastropod, an oligochaete and a turbellarian. No taxon was recorded more than three times; it appears that there is no species of the soil fauna particularly associated with *Geonemertes* under stones.

In conclusion; *Geonemertes X* was found in damp stony shaded habitats where native plant species predominated, also where both endemic and non-endemic occurred together and also where there were virtually no endemic species. Specimens were found on Madeira from 27 m from the sea shore, near sea level, to an altitude of 1000 m in the centre of the island; and on S. Miguel from 100 — 250 m above sea level and at distances between 500 and 5,700 m from the coast. The record from Furnas, S. Miguel shows that the species can survive in more open habitats. That we did not find *Geonemertes* in other localities does not necessarily mean that they were absent.

G. dendyi was found on S. Miguel at altitudes of 150 and 500 m, between 1100 and 4600 m from the shore. These are the first records of this species on a Macaronesian island. In the field, *G. dendyi* cannot be distinguished with certainty from *Rhynchodemus* spp unless it shoots its proboscis. One specimen did this, and subsequent examination of serial sections of all four specimens established beyond doubt that they were identical in every way to *G. dendyi* Dakin (Dakin 1915, Pantin 1969).

In five localities (2 in Madeira, 3 in S. Miguel) *Geonemertes X* was found alone, in one locality on S. Miguel *G. dendyi* was found alone (although Brinck and Dahl had recorded *Geonemertes* X there in

1957) and at Nordeste, S. Miguel, both species were found within a few metres. This is the first time two *Geonemertes* species have been found in the same locality at the same time, anywhere in the world. The known distribution of *Geonemertes* species in the Atlantic region is shown in Fig. 3.

III IDENTIFICATION OF G. CHALICOPHORA

Investigation of the structure of «*Geonemertes X*» will now be described.

External Appearance and Behaviour in Life

Böhmig and von Graff described lengths up to 12 mm and the colour as milk-white, with a red anterior end in «fully grown» individuals.

Of the 21 «*Geonemertes X*» found in the present investigation, 9 small ones (3 — 7 mm long) were white, 1 in this size range was white with a red anterior end, 3 were pink (5 — 6 mm) and 8 larger ones (6 — 15 mm) were pink with a dark red anterior end.

The proboscis was readily and repeatedly everted when the animal was disturbed, and the worms fragmented unless handled carefully with a damp paintbrush.

Methods for histological examination. The nemertines were narcotised for about 15 minutes in 7% ethanol. 17 were fixed either in 80% ethanol or in Susa, according to the methods of Pantin (1969). They were sectioned at 8 μ and stained in Mallory's trichrome by Mr. D. J. Buck, and examined histologically. (The remaining specimens were fixed in glutaraldehyde in phosphate buffer for electron microscopy; results not yet available).

Characters agreeing with Böhmig's account are as follows (additional to characters common to all species of *Geonemertes).*

1. ANTERIOR GLANDS. Cephalic glands are well developed in all land nemertines, but their condition in the present specimens, and in the descriptions of *G. chalicophora,* is unique. The characteristic large lobules of weakly basophilic cells (with small nuclei and small acidophilic inclusions) are apparent only at the anteriodorsal tip of the animal. All the rest of the cephalic glandular tissue, which extends from the anterior tip to the posterior part of the pyloric region, is a mass of large acidophilic cells with large prominent nuclei. These cells are either embedded in the cephalic gland or (in most specimens) displace it altogether. The cells resemble the «dorsal gland cells» of Australian species of *Geonemertes,* which also occur in the *G. pelaensis* species group (Pantin 1969) but are there ventral in position (owng to the large dorsal frontal organ). It is these cells, not typical cephalic gland, which Böhmig figures as «Kopfdrüse». Von Graff in his original description also emphasises these cells. They are the most distinctive feature of any anterior transverse section

in all the present specimens. See Fig. 4, also Fig. 6b.

2. THE FRONTAL ORGAN is absent. The glands described above discharge by numerous extemporised openings.
3. THE BLOOD SYSTEM follows the usual hoplonemertine pattern. Two lateral blood vessels arise from a cephalic vascular loop (which here gives off many capillary branches) and in the cerebral region a transverse link between the lateral vessels gives rise to a dorsal vessel underlying the rhynchocoel. More posteriorly, the lateral vessels are connected at intervals by »metameric» commissures and finally by a supra anal commissure.

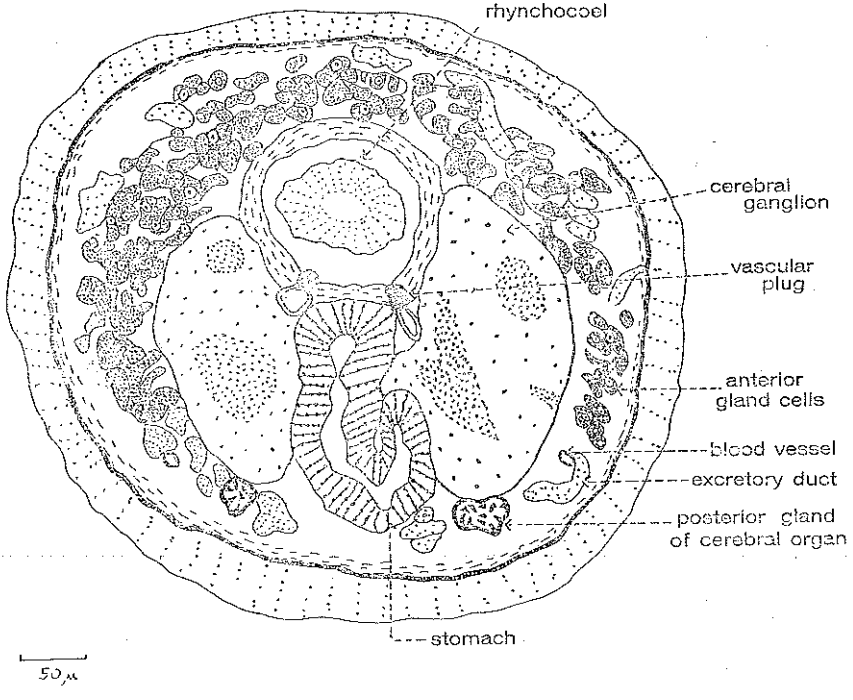

Fig. 4. — T. S. *Geonemertes chalicophora* in cerebral region, showing anterior gland cells, the two vascular plugs and the posterior glands of the cerebral organs

4. THE EXCRETORY SYSTEM extends throughout the body. There are simple mononucleate flame cells scattered in pairs in the parenchyma, connected to fine end canals and then to the thick-walled main excretory ducts. Flame cells are not aggregated round blood vessels.
5. THE CEREBRAL ORGANS extend for 150 — 350 μ between the region

of the posterior eyes (where the oesophagus leaves the rhynchodaeum) and the posterior end of the brain. In occasional specimens the anterior opening is as far back as the ventral brain commissure, but variation in the position of this organ is familiar in *Geonemertes*. The cerebral organs open by the cerebral canal pore near the mid ventral line on either side.

The cerebral canal runs dorsally from the opening and then posteriorly (average 48 μ long). It does not fork but widens into a zone corresponding to an «anterior sac» for 38 μ, and then is surrounded by ganglionic cells which constitute the main part of the organ for 74 μ (see Fig. 5). The posterior end of this region is joined by a large nerve to the middle of the lateral surface of the brain.

6. THE PROBOSCIS has 12 nerves in ten specimens, as recorded by Böhmig, and 13 in one. Variation in this character is usual for

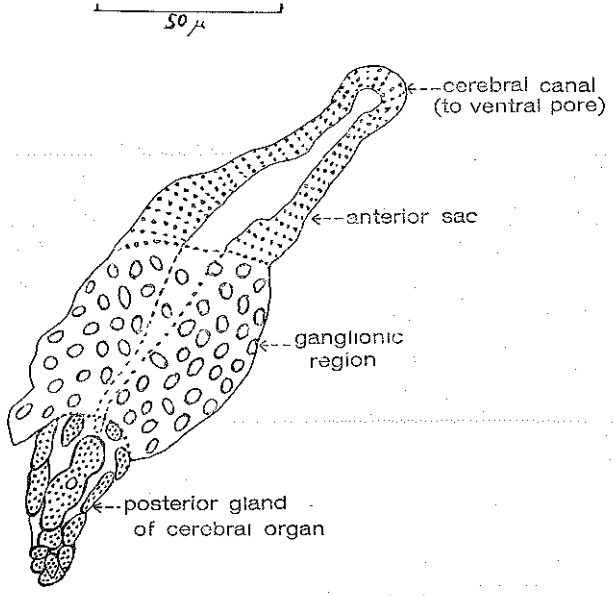

Fig. 5. — H. S. left cerebral organ of *Geonemertes chalicophora*

Geonemertes.

7. AN ACCESSORY LATERAL NERVE is present in all specimens.

8. CALCAREOUS BODIES occur in the parenchyma.

9. THE GUT has a dorsal pyloric tube overlying an unpaired median

caecum (average length 366 μ) which gives rise anteriorly to two blind diverticula (77 μ) which reach to the posterior end of the dorsal cerebral ganglion.

10. FOUR EYES are present in eleven specimens (in one specimen the posterior pair is doubled).
11. GONADS All the specimens are female. As for *G. pantini* in New Zealand, no male has ever been recorded. This may in this instance result from collection at a single time of year, or from different habits of the male. Despite the size range of 3 — 15 mm, all seventeen specimens have fully mature ova. This may suggest that *G. chalicophora* has separate sexes (like *G. australiensis)* rather than protandrous hermaphrodity (like *G. dendyi).*

The two specimens found by Brinck in Tenerife in March 1971 were also female, but immature. All specimens sectioned from Brinck and Dahl's 1957 collection were also female.

In all the above characters, the present specimens agree

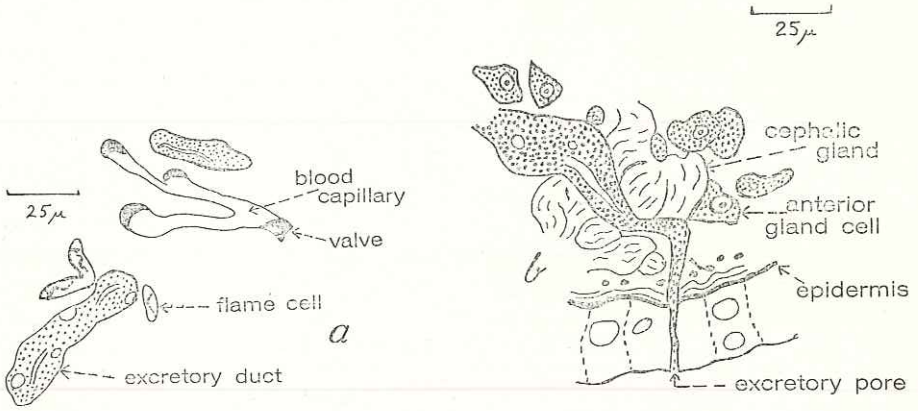

Fig.6. — The excretory system of *Geonemertes chalicophora:* a) H. S. excretory ducts and flame cells; b) T. S. excretory opening in cephalic region

exactly with Böhmig's account of *G. chalicophora.*

Differences from Böhmig's account are as follows: —

1. TWO VASCULAR PLUGS are present (see Fig. 4). They are borne on anterior projections of the dorsal blood vessel which briefly enter the rhynchocoelic sheath, just as described for the Australian and New Zealand species of *Geonemertes* and also *G. nightingaleensis* (Pantin 1969). In the present specimens the plugs are very small (under 20 μ in diameter) and easily overlooked. Böhmig describes the single vascular plug of *Prostoma graecense* which is borne on the main dorsal blood vessel, and states that in *G. chalicophora* the

dorsal blood vessel bears no plug and never enters the rhynchocoel. The present specimens fit the description so far: but Böhmig does not record the paired plugs more anteriorly (yet these had been described in *G. australiensis* by Dendy (1892) in a paper which Böhmig cites). Vascular plugs are hard to find in specimens allowed to shrink on fixation.

2. THE CEREBRAL ORGAN does include glandular tissue. At the end of the cerebral canal, posterior to the ganglionic region and sometimes nearly equal to it in length (average 72 μ), there is a region of basophilic glandular cells (see Figs. 4, 5). Böhmig describes a small cap of these gland cells in *P. graecense* and states that they are strikingly absent from *G. chalicophora*. In the present specimens they are often difficult to find, partly because the cerebral organ nerve arises at the posterior end of the ganglionic region cutting it off from the gland cells, and partly because the organ is closely surrounded by the characteristic anterior glands described above. With Mallory's triple stain however the cerebral organ gland cells can be distinguished, and recognised as very similar to the gland cells of the cerebral organ in other species of *Geonemertes*. With haematoxylin (as used by Böhmig) it would be very difficult to distinguish between these cells and the numerous acidophilic head gland cells.
3. THE EXCRETORY DUCTS are more specialised than those described by Böhmig. He states that the nephridia of *P. graecense* and *G. chalicophora* are essentially similar, and rests his description on *Prostoma* of which he had more specimens. *Prostoma* has an excretory system essentially similar to that of most marine nemertines, except that it extends throughout the body and has 3 — 14 pairs of excretory openings instead of only one pair. Böhmig found the nephridia of *G. chalicophora* to be even more extensive than those of *P. graecense* and counted 20 excretory pores in the single specimen investigated.

   In the present specimens, the excretory ducts are both more subdivided and more specialised.

   (i) After Mallory's triple stain the final ducts look unlike those of *Prostoma,* having granular rather than clear cytoplasm (but lacking the highly organised structure characteristic of the ducts of Australian and New Zealand *Geonemertes)* see Fig. 6a.

   (ii) There is a far greater number of excretory openings (see Fig. 6b). 324 excretory pores were counted in one of the largest (15 mm long) and 161 in one of the smallest (5 mm long). These openings occur at any point on the surface (except middorsally) and are fairly evenly distributed along the length of the worm (except that they are rare in front of the brain). This is still a small number of excretory pores for a land nemertine. In the relatively unspecialised *G. agricola,* Coe at first

counted 15 (Coe 1904) but later amended it to «thousands» (Coe 1929). One specimen of *G. pelaensis* had an estimated 35,000 pores (Schröder 1918) and the Australian species also have tens of thousands of pores (Pantin 1969). Excretory pores, like vascular plugs, are difficult to see unless the worms are fixed with a minimum of shrinkage.

Conclusion. The present specimens of «*Geonemertes X*» can be identified as *G. chalicophora,* on account of their close resemblance to Böhmig's description. They differ from this description on three points, but all these points are difficult to determine without special methods of fixation and staining and therefore could easily have been missed in the earlier description.

IV RELATIONSHIP WITH OTHER GEONEMERTES SPECIES

Relationships within the genus *Geonemertes* are difficult to determine (Pantin 1961, 1969) and convergence may well have occurred. *G. chalicophora* is set apart by lack of specialisation, except in the cephalic glands. Discovery in the present specimens of vascular plugs, posterior gland cells in the cerebral organ and some degree of specialisation in the excretory system reduces its isolation from other species, but it remains difficult to place.

Von Graff originally suggested an Australian origin for his specimens because they were found in the pot of an Australian palm, *Corypha australis.* However the three Australian species *(G. australiensis, G. dendyi* and *G. hillii)* share distinctive specialisations, namely the strong multiplication of the eyes (20 — 80), the specialisation of the excretory ducts and the subdermal capillary network joining the lateral blood vessels. *G. chalicophora* lacks all these features and its structure shows no particular resemblance to this group of species. Nor does it resemble the *G. pelaensis* group, nor the New Zealand group, nor *G. agricola.*

G. nightingaleensis, from the Tristan da Cunha islands of the Southern Atlantic (Brinkmann 1947) is the species which *G. chalicophora* most resembles. *G. chalicophora* differs from *G. nightingaleensis:* —

(a) in possessing an accessory lateral nerve. This is a specialised character occurring also in various other species of *Geonemertes,* but it does not seem to be of great taxonomic value: it is present in *G. pantini* but absent in *G. novaezealandiae,* two New Zealand species which otherwise are very similar indeed.
(b) in the state of the cephalic gland. The typical basophilic lobules are especially extensive and well developed in *G. nightingaleensis,* and there are no acidophilic gland cells.
(c) in the degree of development of the cerebral organ, which is smaller

TABLE I

Summary of Geonemertine characters

(0 = retention of primitive Hoplonemertine character
(+ = special character
(— = suppression of character

Species and distribution	Terrestrial (T) or Littoral (L) or both	Acidophilic head glands	Frontal Organ	Eyes 20-80 0=4 or 6	Cerebral Organ opens ventrally	Vascular plugs	Multiplication excretory ducts and pores	Specialised excretory duct region	Flame cells transv. bars	Acc. lat. nerve	Capill. network for blood commissure	Hermaphrodite or sexes separate Vivip. (v)	Proboscis nerves
G. chalicophora N. Atlantic?	T	++	—	0	+	2	+	0	0	+	0	?	12-13
G. nightingaleensis S. Atlantic	LT	0	—	0	+	2	+	0	0	0	0	?	19
G. agricola Bermuda	LT	0	0	0	0	1	++	0	+	0	+	+V	13-15
G. australiensis G. dendyi G. hillii Australia	T	+	—	+	+	2	++	+	0	+	+	0+	11-19
G. novaezealandiae G. pantini New Zealand	T	0	—	0	+	2	++	+	0	0+	+	0?	12-21
G. pelaensis G. arboricola G. rodericana Indopacific	T	+	0	0	+	1	++	0	+	+	0	+	16-21

and simpler in *G. nightingaleensis*.

(d) in external appearance: *G. nightingaleensis* is brown with white stripes.

The resemblance may only be that of two land living species which have not become greatly modified from their marine ancestors.

Table 1 summarises resemblances and differences between different species of *Geonemertes*. Revision of the genus must await further information, in particular about marine hoplonemertines, but the present hypothesis is that «*Geonemertes*» is a convergent assembly of separately evolved species of land nemertines.

The origin of the two Macaronesian species of *Geonemertes* thus appears to be quite different. *G. dendyi* is known to be a native of Western Australia. It was presumably imported to S. Miguel with Australian plants or among ballast, just as it was imported to European greenhouses (Stammer 1934) and to Britain (Pantin 1961). *G. chalicophora* on the other hand may originate from these islands. This cannot be assumed, in islands which have many imported species. Yet its widespread distribution on these islands, and the fact that it has never been found in the wild anywhere else, leaves this as a reasonable hypothesis.

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SUMMARY

Geonemertes chalicophora, whose origin was previously unknown, was found in Madeira and in the Azores, and its distribution and habitat recorded. *G. dendyi* also was found on S. Miguel, Azores. Contrary to the earlier description of *G. chalicophora,* histological examination revealed two vascular plugs, gland cells in the cerebral organ and many excretory openings. The relationship of this species to other land nemertines is discussed.