The Geonemertes problem (Nemertea)

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(With 3 plates and 7 figures in the text)

A new genus of monostiliferous hoplonemerteans, Pantinoneniertes gen. nov., provides evidence for the separate evolution of terrestrial nemerteans. The genus is established for two new species found in Australia, P. enalios sp. nov., an intertidal form, and P. winsori sp. nov., which lives in fallen timber in the supralittoral brackish water regions of mangrove swamps. One only of the known species of land nemerteans, Geonemertes agricolu from Bermuda, closely resembles these two species morphologically and is transferred to the new genus as Pantinoneniertes agricolu.

A re-examination of all the known species of Geonemertes has shown that two major groups can be distinguished on the basis of morphological characters. In one group the rhynchocoel musculature is in two distinct layers, a frontal organ is present, the mid-dorsal blood vessel has a single vascular plug, and the flame cells are binucleate and reinforced with cuticular support bars. It comprises the genus Pantinoneniertes gen. nov. and the Pelaensis or Indopacific group of terrestrial nemerteans, for which the generic name Geonemertes is retained.

In the second major group the rhynchocoel musculature is composed of interwoven longitudinal and circular fibres, there is no frontal organ, the mid-dorsal blood vessel bears two vascular plugs, and the flame cells are mononucleate and lack support bars. Five genera, three of which are new, are distinguished in this group. Australian species are united in the genus Argonernertes gen. nov. and New Zealand forms comprise the genus Antiponemertes gen. nov., while Acteonernertes bathamae from New Zealand and the Auckland and Ocean Islands remains in a separate genus. Geonemertes nightingaleensis is transferred to a new genus, Katechonentertes gen. nov., and for Geonemertes chalicophor a previously used generic name, Leptonernertes, is adopted.

A key to the terrestrial, brackish-water and marine nemertean species described in the present paper is provided.

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Introduction

Although all terrestrial nemerteans are currently included in a single genus, Geonemertes, this undoubtedly comprises an artificial assemblage of species which have evolved independently (Pantin, 1961a, 1969; Moore & Moore, 1972; Moore, 1973, 1975a, b). Any attempt at tracing these parallel lines of evolution from marine ancestors must depend upon information about closely related species. It is therefore of particular interest to find species which are transitional, both in structure and in habitat, between marine and terrestrial nemerteans. One such species already known is Acteonemertes batharmae from New Zealand, an upper littoral nemertean which has many anatomical features in common with the New Zealand species of Geonemertes and is itself fully terrestrial in the Auckland Islands (Pantin, 1961b; Moore, 1973). The present paper describes two new species found by one of us (R.G.) in Queensland, Australia. One lives intertidally in silty mud or beneath coral boulders on Magnetic and Pelorus Islands in the Great Barrier Reef province. The other occurs beneath the bark or in cavities of rotten timber in the supralittoral brackish water regions of mangrove swamps near Townsville. Both species clearly belong to the same genus. Both are also closely similar to one only of the known species of Geonemertes, G. agricola, which occurs in mangrove swamps and in fully terrestrial habitats in Bermuda (Willemoes-Suhm, 1894; Coe, 1904; Crozier, 1917). Accordingly, these three species are united in the new genus Pantinonemertes, named after the late Professor Carl Pantin as a tribute to his enjoyment of land nemerteans. The Townsville species dwelling in mangroves is named *P. winsori* sp. nov. after Mr Leigh Winsor, who first drew attention to the nemertean and assisted in finding specimens. The intertidal species is named *P. enalios* sp. nov. (in or of the sea). Geonemertes agricola is transferred to the new genus and becomes Pantinonemertes agricola.

The separate evolution of one terrestrial species is thus established on secure morphological grounds which, further, point to those characters of value in establishing the relationships between other terrestrial forms. Accordingly, all the known species of Geonemertes have been re-examined and a division of the genus is proposed.

Materials and methods

Specimens of the two new species, upon which the following descriptions are based, were mainly found by R.G. during his visit to Australia in 1975, but Mr Leigh Winsor and Mr Robert Hardie gave valuable assistance during searches for the mangrove swamp dwelling form.

The nemerteans were anaesthetized in 8% MgCl₂ for external examination prior to fixation in either 4% neutral formalin or Bouin's fluid. Several individuals, after anaesthetization, were used for in toto studies, either as squash preparations (particularly valuable for the examination of the proboscis stylet armature) or following fixation, dehydration and clearing. Others were investigated histologically with sections cut at 6–7 µm in 56°C m.p. paraffin wax and stained by the Mallory trichrome, 1% Alcian blue, periodic acid-Schiff or Mazia et al. (1953) bromphenol blue method.

All known terrestrial nemerteans, assembled in the Pantin Collection at present in the care of J.M., have been re-examined and compared with the new species.

Observations

*Pantinonemertes* gen. nov.

Diagnosis. Monostiliferous marine, brackish-water, supralittoral or terrestrial hoplonemerteans with lateral horizontal cephalic furrows; four eyes; rhyynchocoel full body
length, with wall composed of two clearly differentiated muscle layers; proboscis mostly large or massive, powerfully developed and often used for rapid locomotion; dermis thick; body-wall musculature strongly developed, with slender zone of diagonal muscle fibres between circular and longitudinal layers; frontal organ present, usually well developed; cephalic glands extensive, reaching post-cerebrally on dorsal margins, containing coarsely granular tissues which stain orange with Mallory, discharging either through frontal organ or via improvised pores; cerebral sensory organs small, anterior to brain, opening laterally or ventrolaterally into shallow ciliated grooves separate from head furrows; brain well developed, with long slender dorsal commissure in species with massive proboscis; lateral nerve cords without accessory lateral nerve; foregut with distinct oesophagus, stomach divisible into anterior and posterior regions, and long pyloric duct overlying the ventral intestinal caecum from which a pair of anterior diverticula extend towards the brain; blood system thick-walled with large numbers of extra-vascular pouches and few valves; mid-dorsal blood vessel with one vascular plug; parenchyma extensive; excretory system very well developed, branching throughout the body and opening via a large number of pores, with numerous flame cells of unique type, fused in pairs and reinforced with cuticular transverse bars; sexes separate or cyclic hermaphrodite and ovoviviparous.

_Type species._ Pantinonemertes winsori _sp. nov._

_Pantinonemertes winsori_ _sp. nov._

_Type specimens._ Type material deposited with the Australian Museum, Sydney, consists of stained sections and intact individuals; Registration Numbers are holotype W.5895, paratype W.5896, others W.5897 and W. 5898. Additional material is deposited with the Queensland Museum, Brisbane (G.12100 and G.12101) and the British Museum (Natural History), London (BM(NH)1978.12.1 and BM(NH)1978.12.2).

_Type locality._ Mangrove swamps on south bank of Ross River, south of Townsville, Queensland, Australia, beneath bark or in cavities in rotting fallen mangrove timber (_Avicennia marina_ (Forsk.), _Ceriops tagal_ (Perr.)), upper tidal level. Associated fauna in or on the timber included polychaetes, bivalves (teredinids), crustaceans (especially the grapsid decapod _Sesarma erythroductyla_ Hess), coleopteran larvae and ants.

_Material examined:_

1. Four specimens, collected 5 August 1975 from type locality by R.G.
2. Four specimens, collected 7 August 1975 from mangroves, Three Mile Creek, north of Townsville, by R.G.
3. Six specimens, collected at night 16 August 1975 from type locality by R.G. and Mr Leigh Winsor.
4. Nine specimens, collected 18 August 1975 from type locality by R.G., Mr Leigh Winsor and Mr Robert Hardie.

_External appearance._ Living worms are dorsally a dark purplish-brownish-grey with a single narrow pale longitudinal median stripe (Fig. 1). The pigmentation is darkest adjacent to the stripe and fades towards the lateral body margins. The head is marked by a distinctive pattern (Fig. 1) of a colour similar to, but slightly darker than, the remaining dorsal pigment. On the ventral surface the colour is cream to greyish-white anteriorly, pale reddish-brown posteriorly, with intermediate shades between. The intestinal diverticula show through the ventral body surface as pale yellow pouches. The four eyes are not
visible from above, but are easily distinguished in lateral view; the anterior, larger, pair are black, the posterior pair dark brown. Just behind the posterior pair of eyes the cerebral ganglia can be distinguished laterally and ventrally as circular pink patches showing through the body wall. The everted proboscis possesses a rich creamish-brown colouration.

The only variation in colour pattern seen among the 23 individuals was a reduction in the development of the mid-dorsal stripe; in one specimen the stripe was very faint and barely distinguishable, in another it was restricted to the cephalic region only.

Fig. 1. Pantinonemertes winsori gen. et sp. nov. The anterior end of a living specimen, showing the appearance in lateral (a), dorsal (b) and ventral (c) aspect. The width of the specimen drawn was approximately 6 mm.
These nemerteans have long, rather slender bodies with a firm consistency. Measured after anaesthetisation they ranged from 5.1–24.7 cm in length and from 1.5–8.0 mm in width. The body is rounded or oval in cross-sectional shape; behind the rounded head the body gradually tapers posteriorly to terminate in a bluntly pointed tail. The cephalic furrows, which are usually quite evident, give the head a somewhat bilobed appearance in lateral aspect (Fig. 1).

**Behaviour.** Specimens of *P. winsori* gen. et sp. nov. were mostly found by splitting fallen mangrove logs with a pick-axe. The wood was usually riddled with empty teredinid burrows and the nemerteans, when revealed, attempted to escape along these by using their proboscis as a locomotory organ. This type of rapid movement, a specialized form of escape response, has been observed in a few terrestrial and freshwater species (Dendy, 1892a; Pantin, 1950; Hickman, 1963; Moore & Gibson, 1973).

![Diagram of *Pantinonemertes winsori* gen. et sp. nov.](image)

**Fig. 2.** *Pantinonemertes winsori* gen. et sp. nov. Sagittal section through the anterior tip of the body. Note the long frontal organ duct and massive size of the proboscis. Abbreviations: DCC, dorsal cerebral commissure; EP, epidermis; FOA, frontal organ aperture; FOD, frontal organ duct; JST, junction between anterior and posterior stomach regions; MCG, mucus-producing (basophilic) cephalic glands; OE, oesophagus; PCG, proteinaceous (granular) cephalic glands; PR, proboscis; RC, rhynchocoel; STP, posterior stomach; VCC, ventral cerebral commissure; VP, vascular plug. The arrow indicates the approximate plane of section of Fig. 3.
These brackish water nemerteans appear to be intolerant of higher salinities. Individuals left overnight in tanks of clean aerated sea-water had by the morning emerged to crawl around benches and other laboratory furniture. Their tracks could be followed by a dried slime trail, similar in appearance to those left by terrestrial molluscs, flatworms and nemerteans; the worms appear capable of surviving at least for several hours out of water.

*Internal anatomy.* The internal anatomy of *P. winsori* gen. et sp. nov. is illustrated in Figs 2 and 3 and Plates I–III.

**Fig. 3.** Pantinonemertes winsori gen. et sp. nov. Transverse section through the posterior stomach region of the body. Abbreviations: AD, anterior caecal diverticulum; D, dermis; LBV, lateral blood vessel; LM, longitudinal muscle layer of body wall; LNC, lateral nerve cord. Other abbreviations as in Fig. 2.

*Body wall.* Plate I(b) shows the well-developed epidermis, containing the black granules which give the dorsal pigmentation, and the connective tissue dermis of approximately the same thickness as the underlying circular muscle layer. The longitudinal muscles are strongly developed (see also Fig. 3): anteriorly, just behind the brain, cephalic gland lobules separate an inner layer of longitudinal fibres (Fig. 2) (forming the origin of the pre-cerebral septum) from an outer layer which gives rise to the cephalic retractor muscles. Parenchymatous connective tissue is extensive.
PLATE I. Pantinonemertes winsori gen. et sp. nov. Transverse section through the anterior brain region to show the appearance of the various structures: (a) the two types of cephalic glands; (b) epidermis; (c) cerebral sensory organ; (d) anterior stomach; (e) a portion of the proboscis (note a proboscis nerve arrowed on inset of central diagram); (f) an eye. Abbreviations: CC, ciliated canal of cerebral organ; COG, acidophilic glands of cerebral organ; CON, cerebral organ nerve. Other abbreviations as in Fig. 2. All photomicrographs of section stained with Mallory.
Proboscis apparatus. Figure 2 shows the thin-walled rhynchodaeum and the spacious rhynchocoel which is very nearly the full body length. The rhynchocoel wall contains two distinct muscle layers (outer circular, inner longitudinal) rather than a wickerwork of fibres.

The proboscis is a massive organ, as long as or longer than the body. It has a typical monostiliferous construction and 22–24 proboscis nerves (Plate I). A large-sized proboscis is usual in nemerteans which employ the organ for rapid locomotion. Its stylets, at 200–250 µm long among the largest ever recorded for any nemertean, are capable of penetrating

Plate II. Puntinonemertes winsori gen. et sp. nov. Sagittal section through the dorsal cephalic tip to show the appearance of the frontal organ. Compare with Fig. 2. Improvised ducts leading from the basophilic (mucus-producing) cephalic glands are indicated by arrows. Abbreviations as in Fig. 2. Mallory.

Plate III. (a) Puntinonemertes winsori gen. et sp. nov. Section through a part of a lateral blood vessel to show the thin-walled extravascular pouches characteristic of the genus. (b) Puntinonemertes winsori gen. et sp. nov. Two flame cells showing their binucleate and cuticular reinforced construction. (c) Puntinonemertes enalios gen. et sp. nov. The central stylet and basis. (d) Puntinonemertes enalios gen. et sp. nov. Three accessory stylets; note the lack of variation compared with that shown in Fig. 4. (e) Geonemertes (Argonemertes gen. nov.) dendyi. Two flame cells showing their mononucleate and non-reinforced construction. (f) Geonemertes (Katechnemertes gen. nov.) nightingaleensis. A pair of flame cells showing close similarities to those illustrated in (e). (g) Geonemertes (Puntinonemertes gen. nov.) agricola. A single binucleate and reinforced flame cell; compare with (b). (h) Geonemertes peltangis. Three binucleate flame cells reinforced with both longitudinal and transverse support bars. (i) Geonemertes (Puntinonemertes gen. nov.) agricola. Transverse section through a part of the rhynchocoel wall to show the two distinct muscle layers. (k) Geonemertes (Argonemertes gen. nov.) hilly. Part of the rhynchocoel wall in transverse section to show the wickerwork arrangement of the muscle fibres, typical of most terrestrial nemertean species. (l) Geonemertes peltangis. Transverse section through the head, showing the enormous frontal organ duct surrounded by cephalic gland lobules. (m) Geonemertes (Argonemertes gen. nov.) dendyi. Transverse section through two branches of the submuscular capillary blood network; note the absence of extra-vascular pouches. Compare with (a). (n) Geonemertes peltangis. Transverse section through the single vascular plug. (o) Geonemertes (Antiponemertes gen. nov.) novaezelandiae. Transverse section through the two vascular plugs. (c) and (d) photographed under polarised light, all other photomicrographs of sections stained with Mallory.
PLATE III.
the soft human flesh between fingers; a wound so inflicted produces a sharp stinging sensation which wears off after a few minutes. The proboscis stylets are extremely variable in shape, even within a single individual (Fig. 4).

**Alimentary tract.** The oesophagus (Fig. 2) is a long unciliated tube, leading posteriorly with a progressive increase both in wall thickness and number of acidophilic gland cells. The anterior stomach has characteristically ciliated and folded walls, but lacks gland cells; it is flanked by longitudinal muscle blocks (Plate I(d)) which extend forwards alongside the oesophagus. The posterior stomach is typically hoplonemertean, with strongly ciliated, deeply folded walls containing basophilic gland cells, and is very large (Figs 2, 3). It is ensheathed by longitudinal splanchnic muscle fibres. A long wide pyloric duct, overlying a ventral intestinal caecum, leads from the stomach into the intestine, which bears unbranched lateral diverticula throughout its length. A pair of anterior caecal diverticula (Fig. 3) extend forward to just below the dorsal brain lobes.

**Fig. 4.** *Pantinonemertes winsori* gen. et sp. nov. The proboscis stylet armature; the lower figure shows the central basis with a stylet in position, the upper figures illustrate the variation in accessory stylet shape found within a single individual.
The cephalic glands are extensive, reaching from the anterior tip to well behind the brain (Fig. 3). A characteristic feature of the glands in Mallory stained sections is that the typical vacuolated basophilic lobules are both surrounded and invaded by coarsely granular orange-staining tissues, usually situated peripherally (Plates I(a), II). The basophilic glandular components stain strongly both with the Alcian blue method for acid mucopolysaccharides and the periodic acid-Schiff carbohydrate technique; in contrast the orange-staining granular tissue reacts to neither of these stains but is coloured by the bromphenol blue method for proteins.

The cephalic glands primarily discharge through the frontal organ, but additional improvised ducts can also be found anterodorsally and ventrally (Plate II).

The frontal organ is extremely large and well-developed. From its anterior opening into the transverse cephalic furrow formed by the junction of the two head "lobes" (Fig. 1), an attenuated median dorsal duct, lined by a ciliated columnar epithelium, leads back almost to the dorsal cerebral commissure (Fig. 2, Plate I).

The cerebral sensory organs are comparatively small and anterior to the brain. Each opens into a shallow ventrolateral longitudinal groove which is separate from the main head furrow. The cerebral canal runs inward beside the ganglionic region (Plate I(c)), turns through 90° and enters the more posterior glandular region. The nerve from the ganglionic region leads posteriorly to the lateral edge of the ventral cerebral ganglion.

Glandular tissues form the major components of the organ and are in two parts; a dense mass of lobules (with acidophilic inclusions) forms a saddle around the ganglionic region and a cerebral canal (Plate I(c)) and a more posterior portion (granular cells staining dark brown with Mallory) extends back to the brain.

Eyes. There are four large eyes, of the advanced type found in the reptantic polystiliferous genus Drepanophorus (Gibson, 1972). Each has a distinct lens, pigment cells and retina and is linked with the dorsal cerebral ganglion by a well-defined nerve (Plate I(f)).

One specimen had five eyes. The anterior pair, level with the oesophageal opening, measured 136 μm in diameter, while the posterior eyes, level with the ventral cerebral commissure, measured 144 μm (left) and 192 μm and 80 μm (right). More frequently the anterior eyes are visibly larger than the posterior (Fig. 1).

Nervous system. The brain is well developed. The two dorsal lobes are larger and more widely spaced than the ventral and are transversely joined by a long slender dorsal cerebral commissure; this arrangement reflects the room required for eversion and retraction of the massive proboscis through the cerebral ring.

There is no accessory lateral nerve, i.e. the lateral nerve cords contain only a single fibrous core. They also possess a single longitudinal muscle fibre near the dorsolateral margin of the fibre core.

Blood system. As in most hoplonemerteans, there is an anterior cephalic vascular loop and three main longitudinal vessels, with regular transverse commissures connecting the lateral and mid-dorsal vessels in the intestinal region. Shortly behind the brain the mid-dorsal vessel enters the rhynchocoel wall and forms a single vascular plug.

All the blood vessels are unusually thick-walled, with associated muscle fibres, and possess valves. In addition the vessels are provided with large numbers of extra-vascular pouches which are lined only by slender membranes (Plate III(a)). The size, appearance and distribution of these pouches suggests that they function by locally permitting the volume of the blood vessels to be almost doubled.
Excretory system. An extremely well developed excretory system is present throughout the body, located in the subdermal parenchymatous tissues. It comprises non-specialized, thin-walled and branched excretory ducts which open to the exterior via large numbers of pores distributed over the entire body length. The system is characterized by enormous numbers of clustered binucleate flame cells possessing irregular (i.e. not parallel) transverse cuticular support bars (Plate III(b)).

Gonads. The sexes are separate. The gonads are distributed in the parenchyma between the intestinal diverticula and present a normal hoplonemertean appearance.

Pantinonemertes enalios sp. nov.

Type specimens. Type material is lodged with the Australian Museum and comprises series of stained sections, Registration Numbers W.5900 (holotype) and W.5899 (para-type), and unsectioned material, Registration Numbers W.5901 and W.5902. Additional specimens are deposited with the Queensland Museum (G.12102) and the British Museum (Natural History) (BM(NH)1978.12.3 and BM(NH)1978.12.4).

Type locality. In silty mud beneath rocks and coral boulders, mid- to lower-shore, intertidal, Nelly Bay, Magnetic Island, Queensland, Australia.

Material examined:
1. Thirteen specimens, collected 8 August 1975 from type locality by R.G.
2. Fifteen specimens, collected 4 September 1975 by R.G. from a similar type of habitat, Picnic Bay, Magnetic Island.
3. Nine specimens, collected 6 September 1975 by R.G., from beneath coral debris on outer reef flat, Pelorus Island, Palm Island Group, Great Barrier Reef, Australia.

Fig. 5. Pantinonemertes enalios gen. et sp. nov. The anterior end of a living specimen about 1-2 mm wide viewed dorsally (a) and laterally (b).
**External appearance.** In life these nemerteans are dorsally coloured a pale fawn-brown, orange-brown or orange, with the deepest pigmentation appearing in a crescentic shape over the anterior pair of eyes. Laterally the colouration fades imperceptibly to a ventral cream, off-white or very pale orange shade, through which the intestine and its diverticula appear variously grey or pale green; this intestinal colouration seems to be due to gut contents. The four black eyes, arranged at the corners of a rectangle (Fig. 5), are easily visible, with the anterior pair being considerably larger than the posterior. Behind the eyes the pink cerebral ganglia show through the body wall.

The rounded head has a distinct bilobed appearance in lateral aspect, the upper lobe being delimited by the lateral cephalic furrows which behind the eyes arch upwards to meet mid-dorsally in a rear-pointing V-shape (Fig. 5). At the tip of the head a distinct median notch is usually evident.

The nemerteans possess slender bodies, between 1–1.7 mm wide and 3–6 cm long after anaesthetization. Behind the brain the body margins taper posteriorly to a blunt rounded tail.

The internal anatomy of *P. enalios* gen. et sp. nov., illustrated in Figs 6 and 7, is exactly as described for *P. winsori* gen. et sp. nov. so far as the body wall, rhynchocoel, alimentary tract, frontal organ, eyes, blood system and gonads are concerned. Characters showing differences are as follows:

*Parenchymatous connective tissues* are far less extensive.

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**Fig. 6. Pantinonemertes enalios gen. et sp. nov.** Transverse section through the brain region. Note the relatively much smaller size of the proboscis compared with Fig. 2 and Plate I. Abbreviations: DCG, dorsal cerebral ganglionic lobe; RD, rhynchodaeum; VCG, ventral cerebral ganglionic lobe. Other abbreviations as in Fig. 2.
**Proboscis.** Unlike the mangrove-dwelling species, the proboscis is not a massive structure and is only about $\frac{3}{8}$ of the body length. The organ was never observed being used for locomotion. At the brain level the proboscis is between $\frac{1}{4}-\frac{1}{3}$ of the total body diameter (Fig. 6), whereas in *P. winsori* gen. et sp. nov. it considerably exceeds half the body width. The structure of the proboscis presents no unusual features, but it has only 14–15 proboscis nerves (Figs 6, 7) and the stylet armature is smaller and less variable in form (Plate III(c), (d)).

**Fig. 7.** *Pantinonemertes enalios* gen. et sp. nov. Transverse section through the posterior stomach region of the body; compare with Fig. 3. Abbreviations: MDV, mid-dorsal blood vessel. Other abbreviations as in Figs 2 and 3.

*The cephalic glands* are sparse in the anterior tip, but become plentiful dorsally over and well behind the brain (Fig. 7). Two ventral strands are also present alongside the foregut. In nature and method of discharge they show no difference from *P. winsori* gen. et sp. nov.

*The cerebral organs* are only slightly developed. The marked glandular formation of the mangrove-dwelling species is not found; only a single glandular region is present, lying dorsal to the cerebral canal and not extending posteriorly to the cerebral organ nerve.

*Nervous system.* The dorsal lobes of the brain are better developed and closer together, with a short dorsal cerebral commissure. This can be related to the smaller size of the proboscis. The lateral nerves are as described for *P. winsori* gen. et sp. nov.

*Excretory system.* Whilst the extent and appearance of the excretory ducts and the nature of the flame cells accord with the description for *P. winsori* gen. et sp. nov., the flame cells are not as numerous.

**Pantinonemertes agricola** (Willemoes-Suhm, 1874)

*Tetrastemma agricola* Willemoes-Suhm (1874), Moseley (1879), Hubrecht (1887), Verrill (1902).
Neonemertes agricola Girard (1893), Joubin (1894), Friedrich (1955).

Geonemertes agricola Bürger (1895, 1897-1907), Coe (1904, 1905, 1929, 1939, 1940), Crozier (1917), Pantin (1947, 1961a, 1969), Gibson (1972), Moore & Moore (1972), Moore (1973, 1975a,b).

This terrestrial nemertean from Bermuda was first reported and briefly described by Willemoes-Suhm (1874). Coe (1904) gave a fuller account of the anatomy and ovoviviparous development of the species. Crozier (1917) reported its occurrence below low-water level in mangrove swamps as well as on land, and Pantin (1969) amplified and corrected earlier descriptions of the structure and contrasted the species with other members of the genus Geonemertes. These accounts show that G. agricola bears a striking resemblance morphologically to the two new species described above. In particular, the binucleate flame cells reinforced with irregular transverse bars are identical in the three species and are, furthermore, unique in type.

G. agricola differs from Pantinonemertes gen. nov. species only in the following ways:

Locality. Bermuda.

Habitat. It occurs in moist earth under stones on hillsides, on the borders of mangrove swamps, and also in fully marine conditions below low spring tide level under stones or among matted algae.

External appearance. Unstriped, the nemerteans vary in colour (white, pink, orange, grey, black). The length varies from 15 to 150 mm, larger specimens being found in water.

Reproduction. Geonemertes agricola is a cyclic hermaphrodite and is ovoviviparous.

Internal anatomy. The frontal organ is smaller than in those of the other two species. The walls of the blood vessels are much thinner and with their numerous prominent valves and extra-vascular pouches possess a rather different appearance from the thick-walled system of the two species of Pantinonemertes gen. nov.

Geonemertes agricola resembles Pantinonemertes winsori gen. et sp. nov. more closely than P. enalios gen. et sp. nov. in that the proboscis is very large, is readily everted and is used for locomotion on land. Correspondingly, the shape of the brain resembles that of P. winsori gen. et sp. nov. The degree of development of the excretory system, with flame cells very numerous, more closely resembles that of the Australian mangrove-dwelling species. The cerebral organs, however, have a short and undivided glandular region, resembling that of P. enalios gen. et sp. nov. rather than that of P. winsori gen. et sp. nov.

Geonemertes agricola is accordingly transferred to the new genus and becomes Pantinonemertes agricola. A further subdivision of “the genus Geonemertes” now appears inescapable.

Characters common to all terrestrial nemerteans

All known land nemerteans are monostiliferous hoplonemerteans which share the following characters:

1. Reduction of longitudinal head furrows.
2. Great development of the cephalic glands (mucus producing).
3. Great development of the excretory system; numerous flame cells are present and the excretory ducts branch throughout the body and open by hundreds or thousands of pores.

These characters, however, may well represent convergent adaptations to life on land and cannot by themselves be used in tracing the ancestry of the various species.
Another feature of land nemerteans is that they occur only on oceanic islands, or in Australia (excluding obvious immigrants to, for example, European greenhouses). The reason for such a distribution remains obscure, but could be explained by the colonization of land by marine or littoral ancestors occurring independently in widely separated localities. Such an evolutionary relationship has been established within the new genus, *Pantinonemertes*; it remains to consider the relationships of the other land-dwelling forms.

**Two morphological groups of terrestrial nemerteans**

A full re-examination of all the known species of terrestrial nemerteans makes it possible to divide them into two major groups on the basis of the following clearly defined morphological characters:

1. **Flame cells.** In all land and freshwater nemerteans the excretory system is very well developed and contains large numbers of flame cells. These usually resemble those of marine nemerteans in that each is a simple mononucleate cell with a single ciliary "flame" and a slender canal leading to a wider duct, the flame cells commonly occurring in pairs (Plate III(e), (f)). In *Pantinonemertes gen. nov.*, however, the flame cells are binucleate and reinforced with irregularly arranged transverse bars, having an identical and unique appearance in all three species (Plate III(b), (g)). Binucleate and reinforced flame cells also occur in the Pelaensis or Indopacific group of *Geonemertes*, but here the transverse bars are more regularly arranged and joined by longitudinal supports to give a "bivalve" appearance (Plate III(h)).

2. **Rhynchocoel muscles.** One group of the land species (*Pantinonemertes gen. nov.* and the Pelaensis group of *Geonemertes*) have the muscles surrounding the rhynchocoel divided into two separate layers (outer circular, inner longitudinal), as in Plate III(j). This is the arrangement common to most marine hoplonemerteans. In the other group, however, the longitudinal and circular muscle fibres of the rhynchocoel wall are interwoven into a wickerwork (Plate III(k)).

3. **Splanchnic musculature.** The stomach is surrounded by a longitudinal splanchnic muscle layer in *Pantinonemertes gen. nov.* and the *Geonemertes pelaensis* group, but this is absent from the remaining *Geonemertes* species.

4. **Frontal organ.** In *Pantinonemertes gen. nov.* and the Pelaensis group there is a very large and distinctive frontal organ (Fig. 2, Plates II, III(l)), through which the cephalic glands primarily discharge. In other *Geonemertes* species, however, there is no frontal organ and the cephalic glands discharge entirely through improvised ducts leading through the dermis and epidermis of the pre-cerebral regions.

5. **Blood vessels.** The blood vessels in *Pantinonemertes gen. nov.* and the Pelaensis group have distinct thin-walled extra-vascular pouches in addition to the normal blood vessel valves (Plate III(a)). Other *Geonemertes* species possess valves but entirely lack the extra-vascular pouches (Plate III(m)).

6. **Vascular plugs.** The mid-dorsal blood vessel in the Pelaensis group and in *Pantinonemertes gen. nov.* enters the rhynchocoel floor in the region of the ventral cerebral commissure and bears a single vascular plug which projects into the rhynchocoel; this is particularly prominent when the proboscis is everted (Plate III(n)). In all other *Geonemertes* there are two such vascular plugs, borne on the two anterior branches of the mid-dorsal blood vessel in this region (Plate III(o)).
As indicated in Table I, the above characters enable the land nemerteans to be divided into two groups as follows:

Group 1

The genus *Pantinonemertes* gen. nov.:
- *Pantinonemertes winsori* sp. nov.
- *Pantinonemertes enalios* sp. nov.
- *Pantinonemertes agricola* (Willemoes-Suhm, 1874)

The Pelaensis group:
- *Geonemertes pelaensis* Semper, 1863
- *Geonemertes rodericana* (Gulliver, 1879)

Group 2

- *Geonemertes chalicophora* Graff, 1879
- *Geonemertes nightingaleensis* Brinkmann, 1947

The Australian group:
- *Geonemertes australiensis* Dendy, 1889
- *Geonemertes dendyi* Dakin, 1915
- *Geonemertes hillii* Hett, 1924
- *Geonemertes stocki* Moore, 1975

The New Zealand group:
- *Geonemertes novaезealandiae* Dendy, 1894
- *Geonemertes pantini* Southgate, 1954
- *Geonemertes allisonae* Moore, 1973
- *Acteonemertes bathamae* Pantin, 1961

The Pelaensis group formerly included an additional species, *Geonemertes arboricola* Punnett, 1907, but this has subsequently been shown to be identical with *G. pelaensis* (Moore & Moore, in press).

Further subdivision of the genus *Geonemertes*

A full description of all species of terrestrial nemerteans will not be given here. The salient characters have been defined, with reference to earlier full descriptions, by Pantin (1969) in “the Genus *Geonemertes*” (with the exception of *G. chalicophora*, which was then known only from European greenhouses). Subsequent information has been provided for the New Zealand group (Moore, 1973), the Australian group (Moore, 1975a), *G. pelaensis* (Moore, 1975b; Moore & Moore, in press) and *G. chalicophora* (Moore & Moore, 1972). The principal references for each species are as follows:

- *G. pelaensis*: Semper (1863), Schröder (1918), Hett (1927), Coe (1940), Pantin (1969), Moore (1975b), Punnett (1907: as *G. arboricola*).
- *G. rodericana*: Gulliver (1879), Punnett (1907), Pantin (1969).
- *G. chalicophora*: Graff (1879), Böhmg (1898), Stammer (1934), Pantin (1969), Moore & Moore (1972).
- *G. nightingaleensis*: Brinkmann (1947), Pantin (1969).
- *G. australiensis*: Dendy (1889, 1892a, b), Hickman (1963), Pantin (1969), Moore (1975a).
- *G. dendyi*: Dakin (1915), Stammer (1934), Pantin (1944, 1947, 1969).
- *G. hillii*: Hett (1924), Pantin (1969), Moore (1975a).
# Table I

*Summary of the main morphological characters of terrestrial nemerteans and closely related species*

| Habitat         | Pantinonemertes gen. nov. | Geonemertes | Leptonemertes | Katechonemertes gen. nov. | Argonemertes gen. nov. | Antiponemertes gen. nov. | Acteonemertes |
|-----------------|--------------------------|-------------|---------------|---------------------------|------------------------|--------------------------|--------------|
| Habitat         | enalios sp. nov. | winsori sp. nov. | agricola | pelaeonis | redricana | chalicothora | nightingaleensis | australiensis hiliti | stocki | dendyi | novae-zealandiae | pantini | allisoniae | bathameae |
| Size: length at maturity in mm | Marine | Mangrove swamps | Mangrove swamps or terrestrial | Terrestrial | Terrestrial | Supralitoral and terrestrial | Supralitoral and terrestrial | Supralitoral and terrestrial | Supralitoral and terrestrial |
| 30-60 | 51-247 | 15-150 | 25-75 | 3-15 | 3-29 | 10-84 | 10 | 3-18 | 17-75 | 10 | 30-80 |
| Rhynchocoel muscles: separate layers (○) or a wickerwork of interwoven fibres (+) | ○ | ○ | ○ | ○ | ○ | + | + | i | i | + | + | + |
| Splanchnic longitudinal muscles around stomach present (+) or absent (○) | + | + | + | + | + | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Frontal organ present (+); cephalic glands discharge via improvised ducts (○) | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Flame cells binucleate with irregular transverse support bars (+), binucleate with transverse and longitudinal support bars (+) or simple, mononucleate without support bars (○) | + | + | + | + | + | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Blood vessels thick-walled with valves and extra-vascular pouches (+); thin-walled with valves and pouches (+ ○) or thin-walled with valves but no pouches (○) | + | + | + | + | + | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Number of vascular plugs | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| Cephalic glands: basophilic lobules (○), acidophilic anterior glands (+), granular proteinaceous components (+), other glands dorsally (D) or ventrally (V) | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ | ○ |
| Cerebral organ canal opens from lateral longitudinal furrow (+) or from ventral transverse furrow (○) | + | + | + | + | + | i | i | i | i | i | i | i | i |

*J. Moore and R. Gibson*
| Cerebral organ canal | simple (O) or forked (+) | cerebral organ small (O) or elaborated (+) | cerebral organ gland dorsal (D) or posterior (P) |
|---------------------|--------------------------|------------------------------------------|------------------------------------------|
| Eyes                | 4 (DP) 4 (8) 4 4 4 4 (P) | 4 4 4 20-180 30 20-180 4 4 2 4 (6)       | Eyes                                     |
| Body wall musculature   | strong (+) or weak (O)    | + + + + or O + O + + + + O + + + + + + | Body wall musculature strong (+) or weak (O) |
| Parenchymatous connective tissue extensive (+) or sparse (O) | + + + + O + O + + + + O + + + + + + | + + + + O + O + + + + O + + + + + + |
| Proboscis large, half or more of body diameter (+) or small (O) | + + + O O O + + + + + + O + + + + + + | + + + O O O + + + + O + + + + + + |
| Proboscis used for locomotion | + + + O O O ? + + + + + + + + | + + + O O O ? + + + + O + + + + + + |
| Number of proboscis nerves | 14-15 22-24 10-15 18-20 19-21 12-13 19 | 11-21 10-21 15-18 | Number of proboscis nerves |
| Oesophagus long, stomach well behind ventral cerebral commissure | + + + + O O O O O O O O O O | + + + + O O O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Stomach normal (O) or pushed forward (+) | O O O O O O O O O O O O | + + + + O O O O O O O O | Stomach normal (O) or pushed forward (+) |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Cephalic blood system a simple vascular loop (O) or a capillary network (+) | O O O O O O O O O O O O | + + + + O O O O O O O O | Cephalic blood system a simple vascular loop (O) or a capillary network (+) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Cephalic blood system a simple vascular loop (O) or a capillary network (+) | O O O O O O O O O O O O | + + + + O O O O O O O O | Cephalic blood system a simple vascular loop (O) or a capillary network (+) |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Cephalic blood system a simple vascular loop (O) or a capillary network (+) | O O O O O O O O O O O O | + + + + O O O O O O O O | Cephalic blood system a simple vascular loop (O) or a capillary network (+) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Cephalic blood system a simple vascular loop (O) or a capillary network (+) | O O O O O O O O O O O O | + + + + O O O O O O O O | Cephalic blood system a simple vascular loop (O) or a capillary network (+) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral com- missure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral com- missure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |
| Oesophagus long, stomach well behind ventral cerebral commissure | O O O O O O O O O O O O | + + + + O O O O O O O O | Oesophagus long, stomach well behind ventral cerebral commissure |
| Accessory lateral nerve present (+) or absent (O) | O O O O + + + O + + + + O + + + + + + | O O O O + + + O + + + + O + + + + + + | Accessory lateral nerve present (+) or absent (O) |

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**THE GEONEMERTES PROBLEM**

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$G. \text{ stocki}$: Moore (1975a).
$G. \text{ novaezealandiae}$: Dendy (1894, 1895), Pantin (1969: Appendix), Moore (1973).
$G. \text{ pantini}$: Southgate (1954), Pantin (1969: Appendix), Moore (1973).
$G. \text{ allisonae}$: Moore (1973).

$Acteonemertes \text{ bathamae}$: Pantin (1961b, 1969: Appendix), Moore (1973).

As shown in Table I, the species can further be grouped by morphological characters which coincide with geographical distribution. Separate genera can be established as follows:

**Group 1 (excluding Pantinonemertes gen. nov.). The Pelaensis or Indopacific group**

$Geonemertes \text{ pelaensis}$ and $G. \text{ rodericana}$ are closely similar in most characters, but are distinct in colour. $G. \text{ pelaensis}$ varies from a translucent white to red, with a single dark brown dorsal stripe. $G. \text{ rodericana}$ is dark green with a single white mid-dorsal stripe and four white spots around the eyes. The two species also differ in the size and nature of the stomach.

These two species should, because of their similarities, clearly be placed in the same genus, separate from the other members of Group 1 (which are united in the genus Pantinonemertes gen. nov.). This genus must retain the name of $Geonemertes$ since the name was first erected by Semper (1863) for $G. \text{ pelaensis}$.

**Group 2. The New Zealand and Australian groups**

These species share a number of specialized characters, both within each group and in common:

(i) The final region of the excretory ducts is a highly specialized duct, thick-walled with radial striations in the cytoplasm.

(ii) Throughout the body, in the submuscular layer with the flame cells and excretory ducts, there is a capillary blood network, much branched and with characteristic valves at frequent intervals. In the head this network forms the anterior origin of the two lateral blood vessels and the two vascular plug-bearing cephalic vessels which unite to form the dorsal blood vessel; more posteriorly the network forms cross-connections between the main vessels in place of the usual quasi-m metameric vascular commissures.

(iii) The cerebral canal of the cerebral organs is forked, leading to an anterior sac or to the ganglionic region, behind which it ends in the large glandular region which extends a long way posteriorly.

The Australian species ($G. \text{ australiensis}$, $hilli$, $dendyi$, $stocki$) share the further specialized character of extreme multiplication of the eyes. Between 20 and 180 eyes (the number increasing with the size of the worm) are distributed over the anterior tip, usually in four distinct groups. It is proposed that these four species should be separated into a new genus Argonemertes.

The New Zealand land nemerteans retain the primitive number of eyes (four in $Geonemertes \text{ novaezealandiae}$ and $G. \text{ pantini}$, two in the small $G. \text{ allisonae}$) and may be placed in the new genus Antiponemertes, related to but distinct from Argonemertes gen. nov. Antiponemertes gen. nov. is further characterized by a moveable stomach, probably pushed forward during feeding. In transverse sections the oesophagus and stomach can often be seen as concentric rings.
Acteonemertes bathamae shares many of the characters of Australian and New Zealand land nemerteans (see Table I), including the capillary network in the blood system, but it lacks the specialized excretory ducts and has a small simple cerebral organ. It also has specialized features of the nervous system. It remains in a separate genus, distinct from but close to Antiponemertes gen. nov.

The two remaining species on Atlantic islands, Geonemertes chalicophora and G. nightingaleensis, are not at all close either to the Australian and New Zealand members of Group 2 or to each other. G. nightingaleensis is unspecialized in character and intermediate (supralittoral or terrestrial) in habitat. G. chalicophora is a small, fully terrestrial worm, circular in cross-section, with few specialized characters apart from the acidophilic glands, very extensive and well developed, which largely replace the usual basophilic lobules of the cephalic gland. Until their relationship can be further elucidated each should be placed in a monotypic genus; for nightingaleensis the new generic name Katechonemertes is proposed (to land, as by a ship). Geonemertes chalicophora was separated by Girard (1893) and Friedrich (1955) as Leptonemertes (thin or slender). Now that there is sufficient evidence to support such a division, it is proposed that this name should be adopted.

Generic diagnosis

Seven genera of hoplonemerteans with terrestrial representatives have now been established. Apart from Pantinonemertes gen. nov., for which a diagnosis is provided on page 176, these genera may be defined as follows:

Acteonemertes Pantin, 1961

Upper littoral to terrestrial monostiliferous hoplonemerteans; four (occasionally six) eyes; rhynchocoel full body length, with wall composed of wickerwork of interwoven longitudinal and circular muscle fibres; proboscis small, less than half body diameter, used in locomotion; dermis thin; body-wall musculature strongly developed; frontal organ absent; cephalic glands extensive; basophilic, opening via improvised pores; cerebral sensory organs, small, simple, with posterior glandular region, opening ventrally from transverse head furrow; lateral nerve cords without accessory lateral nerve but with fibres contributed by dorsal brain lobes; blood system with prominent valves but lacking extravascular pouches, developed as a submuscular capillary network which is extensively branched in the head; mid-dorsal blood vessel with two vascular plugs; parenchyma extensive; excretory system well developed, branching throughout the body and opening via large number of pores, with scattered mononucleate flame cells which lack cuticular support bars, excretory tubules without thick-walled terminal region; sexes separate, oviparous.

Antiponemertes gen. nov.

Terrestrial monostiliferous hoplonemerteans; two to four eyes; rhynchocoel full body length, with wall composed of wickerwork of interwoven longitudinal and circular muscle fibres; proboscis large, used in locomotion; dermis thin; body-wall musculature strongly developed; frontal organ absent; cephalic glands extensive, basophilic, opening via improvised pores; cerebral sensory organs large, with anterior sac, forked cerebral canal and posterior glandular region, opening ventrally from transverse head furrow; lateral nerve
cords with or without accessory lateral nerve; blood system with prominent valves but no extra-vascular pouches, developed as an extensive submuscular capillary network, one species with vascular loop replacing cephalic network; mid-dorsal blood vessel with two vascular plugs; parenchyma poorly developed; excretory system extensive, branching throughout the body and opening by large number of pores, with scattered mononucleate flame cells lacking cuticular support bars, excretory tubules with thick-walled terminal region; sexes separate, oviparous.

**Argonemertes gen. nov.**

Terrestrial monostiliferous hoplonemerteans; 20–180 eyes, number increasing with age and size; rhynchocoel full body length, with wall composed of wickerwork of interwoven longitudinal and circular muscle fibres; proboscis massive, powerful, used in locomotion; dermis and body-wall musculature variably developed; frontal organ absent; cephalic glands extensive, basophilic, opening via improvised pores; cerebral sensory organs large, with anterior sac, forked cerebral canal and elongate posterior glandular region, opening ventrally from transverse head furrow; lateral nerve cords with accessory lateral nerve; blood system with prominent valves but no extra-vascular pouches, developed as extensive submuscular capillary network, one species with both vascular loop and capillary branches in head; mid-dorsal blood vessel with two vascular plugs; parenchyma poorly developed; excretory system extensive, branching throughout the body and opening by large number of pores, with scattered mononucleate flame cells which lack cuticular support bars, excretory tubules with thick-walled terminal region; sexes separate or hermaphroditic.

**Geonemertes Semper, 1863**

Terrestrial monostiliferous hoplonemerteans; four to eight eyes; rhynchocoel full body length, with wall composed of two clearly differentiated muscle layers; proboscis small, less than half body diameter, not apparently used in locomotion; dermis thin; body-wall musculature variably developed; frontal organ present, massive, extending back to brain; cephalic glands extensive, basophilic, with characteristic ventral glands in pre-cerebral region, glands primarily discharging through frontal organ but sometimes also via improvised pores; cerebral sensory organs large, with dorsal glandular region, cerebral canal not forked, opening ventrally from transverse head furrow; lateral nerve cords with accessory lateral nerve; stomach with longitudinal splanchnic muscles; blood system thin-walled with valves and extra-vascular pouches, without capillary network; mid-dorsal blood vessel with one vascular plug; parenchyma extensive; excretory system well developed, branching throughout the body and opening by large number of pores, with binucleate flame cells supported by transverse and longitudinal cuticular bars, aggregated around cephalic vascular loop, excretory tubules without thick-walled terminal region; hermaphroditic.

**Katechonemertes gen. nov.**

Supralittoral or terrestrial monostiliferous hoplonemerteans; four eyes; rhynchocoel full body length, with wall composed of wickerwork of interwoven longitudinal and circular muscle fibres; proboscis large but use in rapid locomotion not established; dermis thick; body-wall musculature moderately developed; frontal organ absent; cephalic glands extensive, basophilic, discharging via improvised ducts; cerebral sensory organs small and
simple, with posterior glandular region, opening from transverse head furrow; lateral nerve cords without accessory lateral nerve; blood system thin-walled with valves but no extra-vascular pouches, not developed into capillary network; mid-dorsal blood vessel with two vascular plugs; parenchyma sparsely developed; excretory system extensive, branching throughout the body and opening by large number of pores, flame cells mononucleate without support bars, aggregated around lateral blood vessels, excretory tubules without thick-walled terminal region; sexes probably separate.

Leptonemertes Girard, 1893

Terrestrial monostiliferous hoplonemerteans; four eyes; rhynchocoel full body length, with wall composed of wickerwork of interwoven longitudinal and circular muscle fibres; proboscis small, less than half body diameter, readily everted but not used in locomotion; dermis thin; body-wall musculature not strongly developed; frontal organ absent; cephalic glands extensive, with acidophilic cells in place of basophilic lobules, opening via improvised pores; cerebral sensory organs small and simple, with posterior glandular region, opening from transverse head furrow; lateral nerve cords with accessory lateral nerve; blood system thin-walled with valves but without extra-vascular pouches, not developed into a capillary network; mid-dorsal blood vessel with two vascular plugs; parenchyma poorly developed; excretory system extensive, branching throughout the body and opening by large numbers of pores, with mononucleate flame cells lacking cuticular support bars scattered throughout the body, excretory tubules without thick-walled terminal region; sexes probably separate.

The evolution of terrestrial nemerteans

The occurrence of different species of terrestrial nemerteans on oceanic islands could be explained by the separate independent colonization of land in geographically isolated localities. This may have occurred at the time of dramatic changes in climate and sea-level during and after the Pleistocene (Pantin, 1961a). One such evolutionary sequence was postulated by Pantin (1961b) to relate the upper littoral form Acteonemertes to New Zealand land nemerteans. His theory is reinforced by the occurrence of a fully terrestrial colour variety of Acteonemertes on the remote Auckland Islands (Moore, 1973). Further, the secondary colonization of freshwater by these terrestrial or semi-terrestrial nemerteans was held by Moore & Gibson (1972, 1973) to account for the origin of the freshwater genera Campbellonemertes and Potamonemertes. The present paper establishes for the first time a single genus, Pantinonemertes gen. nov., in which marine, brackish-water and terrestrial species are known. The marine species (P. enalios sp. nov.) and the brackish-water intermediate (P. winsori sp. nov.) found in Australia are widely separated geographically from the fully terrestrial P. agricola in Bermuda. This provides tantalizing evidence that other related species of Pantinonemertes gen. nov. remain to be discovered. There is a reference in private correspondence between Mr F. Crandall and Professor Pantin, dated 1959, to an upper littoral nemertean with binucleate reinforced flame cells in California, but this species has never been described, nor apparently found since. What is certain is that the Pantinonemertes gen. nov. group makes possible a further division of the known species of terrestrial nemerteans. Although the two genera may not have a recent common ancestor, Pantinonemertes gen. nov. is more closely related to the Pelaensis group, Geonemertes, than to any other species.
Within Group 2, the Australian land nemerteans share a number of specialized characters with New Zealand terrestrial forms, but have the further specialization of extreme multiplication of the eyes. This suggests that the Australian group (here separated as the genus *Argonemertes gen. nov.*) represent an offshoot from the New Zealand genus *Antiponemertes gen. nov.*, which in turn is closely related to the ecologically transitional form *Acteonemertes*. However, the relationship to these genera of the two separate Atlantic forms, *Katechonemertes gen. nov.* and *Leptonemertes*, remains obscure. Again, although it appears likely that all Group 2 land nemerteans are more closely related to each other than to any Group 1 species, it cannot be assumed that they share a terrestrial or even a brackish-water ancestor. A fuller picture of the evolution of terrestrial nemerteans must await further evidence about their marine precursors.

**Key to the terrestrial nemerteans of the world**

The known terrestrial nemerteans of the world can be identified by the following key which, for the sake of completeness, includes the two new related marine and transitional species described in the present paper. The known geographic distribution of each species is also indicated.

1. Rhynchocoel musculature in two distinct layers (outer circular, inner longitudinal); frontal organ present; blood vessels with valves and thin-walled extra-vascular pouches; mid-dorsal vessel with single vascular plug; flame cells binucleate, reinforced with cuticular support bars; stomach with longitudinal splanchnic muscle fibres

2. Rhynchocoel musculature composed of a wickerwork of interwoven longitudinal and circular fibres; frontal organ absent; blood vessels with valves but without extra-vascular pouches; mid-dorsal vessel anteriorly branched, with two vascular plugs; flame cells mononucleate, without support bars; stomach without longitudinal splanchnic muscle fibres

3. Flame cells with irregular transverse support bars only; cephalic glands with proteinaceous granular components in addition to typical mucus-producing basophilic lobules; genus *Pantinonemertes gen. nov.*

4. Flame cells with regular transverse and longitudinal support bars; cephalic glands normal, without proteinaceous granular components; genus *Geonemertes* Semper, 1863

5. Marine, littoral, pale fawn-brown, orange-brown or orange dorsally, ventrally cream, off-white or pale orange; four eyes, arranged at corners of a rectangle; Magnetic and Pelorus Islands, Great Barrier Reef, Australia

6. Brackish-water, in fallen mangrove timber, dark purplish-brownish-grey dorsally with single narrow pale longitudinal median stripe, ventrally cream to greyish-white; four eyes, not visible from above but easily distinguished in lateral aspect; mangrove swamps near Townsville, Queensland, Australia

7. Littoral to fully terrestrial, white, pink, orange, grey or black, without stripes; Bermuda

8. Terrestrial, translucent white to red, with single dark brown mid-dorsal stripe; Indopacific islands (New Guinea, Seychelles, Ceylon, Celebes, Palau, Caroline Islands, Samoa, Kei, Mauritius) and West Indies (Dominica, Jamaica)

* Since the completion of this paper a specimen of a terrestrial nemertean found at Coral Gables, Miami, Florida, during November 1978, has been sent to us by Dr W. R. Kem, Department of Pharmacology and Therapeutics, University of Florida, Gainesville. The nemertean is a specimen of *Geonemertes pelaensis* and is the first recorded terrestrial species from the North American continent.
4(a) Terrestrial, dark green with single white mid-dorsal stripe and four white spots around the eyes; Rodriguez Island. *Geonemertes rodericana* (Gulliver, 1879)

5 Eyes 2–6

5(a) Eyes 20–180; genus *Argonemertes* gen. nov.

6 Terrestrial, white, yellow or brown with median dark brown stripe, with or without additional slight lateral stripes, eyes in four groups, posterior glandular portion of cerebral organs extends below brain, lateral to oesophagus, cephalic glands well developed, posteriorly extending over brain; South-eastern Australia, Tasmania

6(a) Terrestrial, purplish-brown or scarlet with two deep red or orange-red lateral bands, eyes in four groups, posterior glandular portion of cerebral organs extends below brain, lateral to oesophagus, cephalic glands poorly developed, not extending over brain; South-eastern Australia. *Argonemertes hillii* (Hett, 1924)

6(b) Terrestrial, dark brown dorsally and dorsolaterally with abrupt transition to lateral and ventral cream colour, eyes in two groups; New South Wales, Australia

6(c) Terrestrial, cream with two brown dorsolateral stripes, eyes in four groups, posterior glandular portion of cerebral organs extends laterally to brain, cephalic glands small, hermaphroditic; South-western Australia (also as immigrant to British Isles, European greenhouses, Azores, Canary Islands). *Argonemertes stocki* (Moore, 1975)

7 Terminal portion of excretory ducts thick-walled and specialized, cerebral organs large, elaborated, cerebral organ canal forked; genus *Antiponemertes* gen. nov.

7(a) Terminal portion of excretory ducts not thick-walled and specialized, cerebral organs small, cerebral organ canal not forked

8 Terrestrial, cream with four dark brown dorsal stripes, outer pair thinner than median pair, accessory lateral nerve absent, four eyes, cephalic blood system a capillary network; New Zealand (North and South islands), Ocean Island

8(a) Terrestrial, cream with two rich brown dorsal stripes, occasionally divided for part or all of their length, accessory lateral nerve present, four eyes, cephalic blood system a capillary network; New Zealand (North and South islands), Stewart Island. *Antiponemertes pantini* (Southgate, 1954)

8(b) Terrestrial, dorsally mottled brown without pigment stripes, accessory lateral nerve present, two eyes, cephalic blood system a simple vascular loop; New Zealand (South island). *Antiponemertes allisonae* (Moore, 1973)

9 Accessory lateral nerve present; genus *Leptonemertes* Girard, 1893. Terrestrial, milk-white or pink with red anterior end, cephalic glands replaced by or containing acidophilic cells; Madeira, Azores, Canary Islands (also as immigrant to European greenhouses. *Leptonemertes chalicophora* (Graff, 1879)

9(a) Accessory lateral nerve absent

10 Parenchymatous connective tissues extensive, proboscis small, cephalic blood system a capillary network; genus *Acteonemertes* Pantin, 1961. Upper littoral to fully terrestrial, cream dorsally with two broad chocolate brown stripes separated by narrow pale line, ventrally pale, or uniformly light grey without stripes; New Zealand (South island), Auckland Island, Ocean Island

10(a) Parenchymatous connective tissues poorly developed, proboscis large, cephalic blood system a simple vascular loop; genus *Katechonemertes* gen. nov. Supralittoral or fully terrestrial, olive-grey or yellowish-white, with two broad brown stripes dorsally; Nightingale Island (Tristan da Cunha Group). *Katechonemertes nightingaleensis* (Brinkmann, 1947)
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Note added in press

Since this paper was accepted for publication in June 1980 Professor R. I. Smith of the Bodega Marine Laboratory, California, has kindly drawn our attention to two references previously unknown to us relating to the Californian species of Mr F. Crandall, referred to on p. 197. Hedgpath (1964: 58) records that “one terrestrial species, Geonemertes, is common under boards and stones on the marshes” and Haderlie (1975) lists the localities as Tomales Bay and Elkhorn Slough. More recently Professor Smith has both sent us examples of these nemerteans and put us in touch with Mr Crandall. The nemerteans, which are not Geonemertes although they belong with the Group 1 species described in the present paper, will be reported fully in a future publication.

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