Annotations on freshwater planarians
(Platyhelminthes Tricladida Dugesiidae)
from the Afrotropical Region

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Accounts are given of six species of freshwater planarians of the genus *Dugesia* Girard 1850 and two of the genus *Neppia* Ball 1974 from the Afrotropical Region, based on samples from new localities as well as re-examination of original preparations of previously described species. The study resulted in the description of one new species, an improved understanding of the distinguishing features and taxonomic status of several species, and a re-assessment of the taxonomic status of several populations described earlier in the literature. The diversity of freshwater planarians of the Afrotropical Region is compared with that of the Palearctic section of Africa.

KEY WORDS: Platyhelminthes, Tricladida, *Dugesia, Neppia*, taxonomy, biogeography, Afrotropical Region, new species.
INTRODUCTION

After De Vries (1988a) published her synopsis of the species of Dugesia from Africa and Madagascar, freshwater planarians from the Afrotropical Region did not receive any further attention for a long period of time. It was only recently that some new contributions to our knowledge of the diversity of these animals in this biogeographic region were published when Stocchino et al. (2002, 2004) described the anatomy and karyology of a new species.

When worms collected from South Africa, Uganda, and Yemen were made available to me, I had the opportunity to add some new data on the distribution and diversity of dugesiids in the Afrotropical Region. The comparative studies accompanying the description and identification of this material necessarily involved detailed re-examination of several species and populations reported from the African continent. This re-examination was greatly facilitated by the availability of original preparations of these species or populations, including very old type material, which were in my custody. The study of these original preparations resulted in a more detailed and improved understanding of the anatomy and taxonomic status of several species and led to a completely different taxonomic status of some populations. The present paper details both the new material from South Africa, Uganda and Yemen and the results of the re-examinations by providing accounts on six species of Dugesia Girard 1850, including one new to science, and two species of the genus Neppia Ball 1974.

MATERIAL AND METHODS

Specimens from Dhamar, Ruwenzori Mountains, Bell River and Carlisle Bridge were postfixed in Steinmann's fluid, sectioned at intervals of 6 µm or 8 µm, and stained in Mallory-Cason; other material was already available in the form of histological sections mounted on glass slides. All of the material examined for this paper has been deposited in the Zoological Museum of the University of Amsterdam (ZMA). As usual, microscopical reconstructions of the anatomy of the copulatory apparatus were made with the help of a camera lucida.

Abbreviations used in the figures: bc, bursal canal; ca, common atrium; cb, copulatory bursa; cg, cyanophilic glands; ed, ejaculatory duct; eg, erythrophilic glands; go, gonopore; ma, male atrium; mo, mouth; od, oviduct; pb, penis bulb; pc, parenchymatic cavity; pg, penis glands; pp, penis papilla; rf, retractor fibres; sg, shell glands; sph, spermatophore; sv, seminal vesicle; te, testis; vd, vas deferens; vi, vitellaria

SYSTEMATIC ACCOUNT

Order Tricladiida Lang 1884
Family Dugesiidae Ball 1974
Genus Dugesia Girard 1850

Dugesia aethiopica Stocchino, Corso, Manconi & Pala 2002

Material examined and distribution. Paratypes: ZMA V.Pl. 6410.1 (originally numbered as DIZAB Pla 2.3), Lake Tana, Bahir Dar, Ethiopia (11°36'N 37°23'E), May 1988, sagittal sections on 18 slides; V.Pl. 6410.2 (= DIZAB Pla 2.4), ibid., transverse sections on 42 slides.
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Other material: ZMA V.Pl. 6411.1, Dhamar, Yemen, alt. 1500 m, sagittal sections on 20 slides; V.Pl. 6411.2, ibid., sagittal sections on 16 slides.

Discussion. Examination of the paratypes revealed that the testes are situated dorsally and that the follicles are underdeveloped in that they do not contain mature spermatozoa, in contrast to the statement by Stocchino et al. (2002) that "the testes are well developed".

The original description of the copulatory apparatus is basically correct, although somewhat confusing. The authors mention for the bursal canal a "longitudinally pleated epithelium" and depict in their fig. 3 a considerably enlarged and folded section of the bursal canal immediately ental to the oviducal openings. However, pleated or folded and enlarged sections of the bursal canal are completely absent in their fig. 4, but again suggested in their figs 5C and 5D. Reconstruction of the available paratype specimens showed that the section of the bursal canal directly ental to the openings of the oviducts is greatly expanded, especially in the lateral direction, showing large folds. The sagittal reconstruction of the copulatory apparatus (Fig. 1) can only show this situation to a limited extent since most of the folds occur in the lateral direction. The rest of the bursal canal is also provided with some irregular folds, but these are much smaller than the ones in the proximal section of the bursal canal.

Stocchino et al. (2002) suggested that the presence of a copulatory bursa with many pleats and folds is diagnostic for *D. aethiopica*. However, the copulatory bursa of planarians is usually a rather irregular structure that does not lend itself for the definition of diagnostic characteristics. As another diagnostic feature, Stocchino et al. (2002) mentioned the symmetrical, ventral openings of the oviducts into the bursal canal. This is indeed the case in the type specimens and is related to the fact that the most proximal section of the bursal canal runs more or less parallel to the body surface. Although such a horizontal approach of the bursal canal to the atrium is rare, it has also been reported for specimens of *Dugesia austrostasiatica* Kawakatsu et al. 1985 (cf. Kawakatsu et al. 1985: fig. 3D), *D. benazzii* Lepori 1951 (cf. De Vries 1984a: fig. 1), *D. brigantii* De Vries & Benazzi 1983 (cf. De Vries & Benazzi 1983: fig. 1) and *D. indica* Kawakatsu 1969 (cf. Kawakatsu 1969: fig. 2). Moreover, in these species, the oviducts also open into the ventral part of the bursal canal, as is the case in *D. aethiopica*.

With respect to the penis, Stocchino et al. (2002) considered its shape to be diagnostic, as well as the presence of a parenchymatic cavity. The shape of the penis papilla is not very different, of course, from other species of *Dugesia* with a plump papilla and ventral opening of the ejaculatory duct, such as *D. astrocheta* Marcus 1953, *D. batuensis* Ball 1970, *D. neumanni* (Neppi 1904), *D. leспорii* Kawakatsu & Mitchell 1995, *D. lindbergi* De Beauchamp 1959, *D. nанophallus* Ball 1970, *D. novaguineana* Kawakatsu 1976, *D. sicula* Lepori 1948 and *D. tamilensis* Kawakatsu 1980. The penial groove may well result from conservation artefacts, in view of the fact that the paratype has two penial grooves (Fig. 1A), in contrast to the single groove reported for the holotype.

The cavity or cleft in the apical section of the penis papilla is partly filled with a finely granular, erythrophilic substance, probably the secretion of penis glands. Such a structure has not been reported for other species of *Dugesia*. In some species, the penis is provided with so-called parenchymatic zones, e.g. *D. leспорii* Pala, Stocchino, Corso & Casu 2000, *D. liguriensis* De Vries 1988 and *D. subten-taculata* (Draparnaud 1804). However, these parenchymatic zones are symmetrically
arranged, with one dorsal to the ejaculatory duct and the other ventral to it, and are made up of vacuolated tissue, in contrast to the single and more open cavity in *D. aethiopica*.

Another feature considered to be diagnostic by Stocchino et al. (2002: 49) concerns the "... unusual length and diameter ..." of the bursal canal. However, the length is not unusual, while the diameter of the major part of the duct is not unusual either. What is unusual and diagnostic is the spacious proximal section of the canal with its elaborate, mainly lateral folds; such a feature has not been reported for other species of *Dugesia*.

In conclusion, there are only two characters that set *D. aethiopica* apart from its congeners, viz. the cavity in the parenchyma of the penis papilla and the spacious, elaborately folded proximal section of the bursal canal.
The discussion presented above is based solely on the examination of the type material. Nevertheless, the specimens examined from Dhamar in Yemen are here provisionally assigned to *D. aethiopica*, albeit that there are some differences between these animals and the type specimens.

The largest preserved specimen from Dhamar measures 18 × 3.25 mm; head of low triangular shape; dorsal surface mottled brown. The mouth opening is situated at the posterior end of the pharyngeal pocket. The ovaries are hyperplastic but the dorsal testes are poorly developed; due to their poor development, it was impossible to determine how far the follicles extend into the posterior end of the body. The proximal section of the bursal canal is highly folded, mostly in the lateral direction, and receives the separate openings of the oviducts; the rest of the bursal canal also has many folds, but they are much smaller. The bursal canal is lined with an infranucleated epithelium and is surrounded by a well-developed layer of circular muscle; neither a subepithelial layer of longitudinal muscle nor ectal reinforcement could be discerned. The oviducts open asymmetrically, with one oviducal opening situated at the postero-ventral section of the bursal canal, precisely at the level where the canal communicates with the atrium, and the other opening located more dorsally. Shell glands discharge their secretion into the bursal canal ectal to the openings of the oviducts. A cavity in the parenchyma of the penis papilla comparable to the one present in the type specimens is absent. A small diaphragm separates the seminal vesicle from the ejaculatory duct.

Evidently, the reproductive apparatus of the Dhamar specimens (Figs 2-3) very much resembles that of the type specimens, apart from the asymmetrical oviducal openings and the absence of a subepithelial longitudinal muscle layer on the bursal canal of the animals from Yemen. However, it may well be that the morphology of the spacious and highly folded proximal section of the bursal canal is subject to preservation artefacts, such that in some specimens the oviducts appear to open asymmetrically, whereas in others symmetrical openings appear to be present.

![Fig. 2. — *Dugesia aethiopica*. V.Pl. 6411.1. Sagittal reconstruction of the copulatory apparatus of a specimen from Dhamar, Yemen.](image_url)
There are also additional reasons for provisionally assigning the Dhamar specimens to *D. aethiopica*. Deri et al. (1999) described the chromosome portrait of the Dhamar animals, which were first mentioned by Benazzi & Deri (1988), as consisting of (1) aneuploid complements of 27 chromosomes plus 1 B chromosome, or (2) aneuploid complement of 26 chromosomes. This chromosome portrait corresponds to that reported by Stocchino et al. (2004) for *D. aethiopica*, viz. \(3n = 27 + 1\)-2 B chromosomes or \(2n = 18 + 0\)-1 B chromosome, the triploid complement being the dominant one. However, according to Deri et al. (1999), the haploid complement of the Dhamar animals consists of 8 chromosomes, whereas that of the type specimens consists of 9 chromosomes (Stocchino et al. 2004); thus, from this perspective, the karyology of the animals from Yemen and Ethiopia is different.

Evidently, attribution of the Dhamar specimens to the species *D. aethiopica* is open to debate. Nevertheless, an account of the Yemen population is included in the present paper because it presents information on the anatomical features of the Dhamar animals that was formerly absent. Future studies, based on more material and on the analysis of molecular data, may be able to ascertain whether the Dhamar specimens belong to *D. aethiopica* or another known species of *Dugesia*, or even represent a new species. The present paper follows a conservative approach to taxonomy by assigning the animals from Yemen to *D. aethiopica*, being anatomically and geographically the nearest species.

From a biogeographic perspective, it is interesting to note that the populations of *D. aethiopica* from Lake Tana and Dhamar may have had the possibility of contact until the Red Sea started to open at about 10 Mya (Scotese 2004). Contact between Arabian and African populations may have been possible again during a comparatively short interval of time during the last Glacial Maximum about 18,000 years ago when the Red Sea shrank considerably. During this period, the Red Sea lost its connection with the Gulf of Aden and there may have been a freshwater corridor between its southern end and the Gulf coast.
Dugesia astrocheta Marcus 1953

Material examined and distribution. Syntypes: ZMA V.Pl. 6412.1, locality 2503, Mware, affluent of the Lufira, Upemba National Park, Democratic Republic of Congo, alt. 950 m, 20 June 1949, sagittal sections of posterior end on 3 slides; V.Pl. 6412.2, ibid., sagittal sections of front end and pharynx on 1 slide; V.Pl. 6412.3, ibid., transverse sections of copulatory apparatus on 2 slides.

Discussion. Marcus’ (1953) account on this species is basically correct. De Vries (1988a) already provided a short re-description of the species, based on re-examination of the same material listed above. However, she did not publish a reconstruction drawing of the copulatory apparatus. Therefore, the reconstruction figure presented here (Fig. 4) is the first one after Marcus’ (1953) original account on this species and on this material.

Fig. 4. — Dugesia astrocheta. V.Pl. 6412.1. (A) sagittal reconstruction of the male copulatory apparatus; (B) sagittal reconstruction of the female copulatory apparatus.
De Vries (1988a) already noted correctly that the testes extend from the level of the ovaries well into the posterior end of the body, in contrast to Marcus (1953), who wrote that the follicles extend to the level of the gonopore. Marcus (1953: 25) observed correctly that D. astrovcheta lacks transverse muscles in the ventral body region. According to Marcus and De Vries, ectal reinforcement on the bursal canal extends from the atrium to the copulatory bursa. However, my observations on the material examined showed that the ectal reinforcement extends to about halfway along the bursal canal (Fig. 4B).

Marcus (1953) listed a number of features in which D. astrovcheta differs from D. sicula. But De Vries (1988a) correctly observed that these features carry no taxonomic weight and that, consequently, D. astrovcheta cannot be reliably distinguished from D. sicula. A difference between the two species not noted by these two workers concerns the presence of transverse muscles in the ventral body region of D. sicula and the absence of such muscles in D. astrovcheta.

Dugesia capensis n. sp.

Paratype: V.Pl. 6413.2, ibid., sagittal sections on 5 slides.
Other material: ZMA V.Pl. 6414.5, Dolomitic Spring at Fountains, Pretoria, Transvaal, 10 April 1971, alt. approx. 2000 m, sagittal sections on 4 slides (mature specimen); V.Pl. 6414.1-4, ibid., sagittal sections of 4 not fully mature animals.
ZMA V.Pl. 6415.6, stream in Klip Rivier crossed by Johannesburg-Vereeniging Road, Transvaal, 13 August 1971, alt. approx. 2000 m, sagittal sections on 14 slides; V.Pl. 6415.1-5, 7, 8, ibid., sagittal sections of 7 immature specimens; V.Pl. 6415.9, ibid., whole mount on 1 slide.

Etymology. The specific epithet is taken from the Cape Province, the southernmost area of the Republic of South Africa. The geographical name “Cape” is derived from the Latin noun “caput”, meaning “head”.

Diagnosis. Dugesia capensis n. sp. is characterized by: under-developed testes and hyperplastic ovaries; acentral ejaculatory duct opening at the tip of the penis papilla; infranucleated bursal canal, receiving the asymmetrical openings of the oviducts, being provided with an ectal reinforcement layer of longitudinal muscles that extends from the vaginal area to the copulatory bursa. The species lacks an extra layer of longitudinal muscle in the outer pharynx musculature and also lacks transverse muscles in the ventral body region.

Ecology. Specimens were collected from under stones in streams and from a spring. Animals originally collected from Bell River have been kept as a laboratory
population at the Institute for Water Research, Rhodes University. Most of the animals in this laboratory population multiplied by fissioning. However, some cocoons were also observed. One of these cocoons was opened and two newly hatched flatworms appeared (Elmari de Kock pers. comm.). This shows that the worms are able to reproduce at least parthenogenetically, despite their poorly developed testes and their hyperplastic ovaries. Such animals are frequently triploid and thus cannot produce through regular meiosis and syngamy (Charni et al. 2004).

Description. Living animals slender; head of low triangular form with bluntly pointed auricles. The two eyes are situated in conspicuous pigment-free patches. An unpigmented auricular groove is positioned laterally, directly posterior to the auricles (Fig. 5). Dorsal surface mottled brown-black; body margin pale. Ventral surface pale. Preserved specimens measure up to 9 × 2 mm.

The pharynx is located in the middle of the body and measures about 1/8 of the body length in preserved specimens; it does not have an extra longitudinal muscle layer in the outer zone of muscles. The mouth opening is located at the posterior end of the pharyngeal pocket.

The testes are situated dorsally and extend throughout the body length. However, the follicles are under-developed and do not contain spermatozoa.

The vasa deferentia open separately into the proximal, anterior section of the intrabulbar seminal vesicle. Through a small diaphragm, located at its distal end, the seminal vesicle communicates with the ejaculatory duct. The diaphragm receives the openings of erythrophilic glands, while the ejaculatory duct is penetrated by the openings of cyanophilic glands. The ejaculatory duct runs slightly acrally, i.e. ventrally displaced, through the stubby penis papilla, opening at the tip of the latter.

The mid-point of the hyperplastic ovaries is located at 1/3-1/4 of the distance between the brain and the root of the pharynx. Ovarial tissue fills the entire dorso-ventral space over a distance of about 400 µm.

The oviducts open separately into the proximal section of the bursal canal. These oviducal openings into the bursal canal are placed asymmetrically, with one opening being located very close to the point where the canal communicates with the atrium, whereas the other opening is situated higher on the canal, directly dorsal to the openings of the shell glands (Fig. 6).

The bursal canal originates relatively high on the atrium and is lined with a tall, probably infranucleated, epithelium. The entire canal is surrounded by three layers of muscles: (1) a thin, subepithelial layer of longitudinal muscle, (2) a thick layer of circular muscle, followed by (3) a thin layer of longitudinal muscle. The bursal canal communicates with a relatively large copulatory bursa.

Discussion. The description of the species presented above is based solely on the type specimens. However, the other material examined (V.Pl. 6414, V.Pl. 6415) is also assigned to D. capensis. These specimens were described first by Kawakatsu (1972), who identified the animals as Dugesia neumannii (Neppi 1904). Re-examination of Kawakatsu’s specimens revealed a close similarity between these animals and those from Bell River.

Apart from their blackish-brown dorsal surface and bluntly triangular head (cf. Kawakatsu 1972), the reproductive apparatus of the animals from Transvaal is also very similar to that of the Bell River specimens. Kawakatsu (1972) described the ovaries of the Transvaal animals as “moderate to large in size” and the tes-
tes as "very small". Re-examination of his specimens revealed that the ovaries are hyperplastic and that the testes are under-developed (cf. Kawakatsu 1972: plate IV, fig. A), as is the case in the Bell River specimens. The copulatory apparatus of the Transvaal animals is very similar to that of the Bell River worms, particularly with respect to the acentral course of the ejaculatory duct, the “angled” course of the bursal canal, and the extension of the ectal reinforcement (i.e. the third, longitudinal muscle layer on the bursal canal) up to the copulatory bursa. According to Kawakatsu’s account, the oviducts of the Transvaal specimens open symmetrically into the most proximal portion of the bursal canal. However, re-examination of his material showed that the oviducts open asymmetrically into the bursal canal, similar to the situation in the Bell River specimens. A reproduction of Kawakatsu’s reconstruction of the copulatory apparatus of the Transvaal animals, but with the course of the oviducts adapted according to current insights, underscores the great similarity between the copulatory apparatuses of the Transvaal and Bell River worms (Fig. 7). Further details on the anatomy of the reproductive apparatus of the Transvaal specimens can be obtained from Kawakatsu (1972).

Since Kawakatsu (1972) identified his animals as *D. neumanni*, it is necessary to compare *D. capensis* with the animals that Marcus (1955) described from the Makheka Mountains in Lesotho and that he identified as *D. neumanni*. According to Marcus’ (1955) description, these worms show (a) a subterminal, ventral opening of the ejaculatory duct at the tip of the penis papilla, (b) symmetrical openings of the oviducts into the bursal canal, (c) ectal reinforcement that is confined to the proximal, ectal half of the bursal canal, (d) a nucleated epithelium of the bursal canal, and (e) a small copulatory bursa. All of these five character states in Marcus’ specimens differ from the conditions found in *D. capensis* (it must be noted that the infranucleated state of the bursal canal epithelium could not be observed unequivocally in the type specimens but was easily detected in the Transvaal specimens). Therefore, it is here concluded that Marcus’ animals represent a different species than those from Transvaal and Bell River, which are here described as *D. capensis*.  

![Fig. 6. — *Dugesia capensis*. Holotype, V.Pl. 6413.1. Sagittal reconstruction of the copulatory apparatus.](image-url)
Furthermore, it is debatable whether Marcus’ animals from Lesotho are representatives of *D. neumanni* (see below).

The only other species of *Dugesia* that has been described from southern Africa is *D. monomyoda* Marcus 1953, which was reported from Pietermaritzburg (Marcus 1953). The gross morphology of the copulatory apparatus of *D. monomyoda* is very similar to that of *D. capensis*, certainly when one takes into account De Vries’ (1988a) correct observation that the ejaculatory duct of *D. monomyoda* is slightly ventral, in contrast to the central course depicted by Marcus (1953). In both species, the oviducts open asymmetrically into the bursal canal. However, in *D. monomyoda*, the ectal reinforcement is restricted to the proximal half of the bursal canal, as observed by De Vries (1988a), while the lining epithelium of the canal is nucleated, in contrast to the situation in *D. capensis*. Furthermore, *D. monomyoda* possesses normal, non-hyperplastic ovaries and fully developed, mature testes. Another difference between *D. monomyoda* and *D. capensis* concerns the presence of transverse muscles in the ventral body region of the first-mentioned species. These muscles are located directly ventral to the gut and dorsal to the ventral nerve cords. Such transverse muscles are absent in *D. capensis* but distinctly present in *D. monomyoda* and also in the type material of *D. neumanni*. For a more detailed account on *D. monomyoda*, see below.

In view of the above, it is concluded that the specimens from Bell River do not resemble *D. neumanni*, *D. monomyoda* or any other known species, either from Africa or from another part of the geographic range of the genus *Dugesia* (cf. Sluys et al. 1998).

It is noteworthy that besides *D. capensis*, hyperplastic ovaries have been reported for a number of other species: *D. sicula*, *D. gonocephala*, *D. benazzii*, *D. minotaurus*, *D. subtentaculata*, *D. biblica*, *D. hymanae*, *D. notogaea* and *D. aethiopica* (cf. Char-
Usually, hyperplastic ovaries indicate that in the particular animal sexualization has been induced, either spontaneously or experimentally. A further sign of such sexualization is the presence of poorly developed testes, as is the case in *D. capensis*. In the same way, hyperplastic ovaries and poorly developed testes were found in ex-fissiparous specimens of *Fonticola morgani* (Benazzi & Ball 1972). The term "sexualization" in these cases refers only to the presence of hyperplastic ovaries, testes and copulatory apparatus because such ex-fissiparous animals are almost completely sterile (Benazzi 1974, Benazzi & GreMigni 1982).

**Dugesia lanzai** Banchetti & Del Papa 1971

*Material examined and distribution.* ZMA V.Pl. 6416.1, Bujuku River (0°22’N 29°58’E), Ruwenzori Mountains, Uganda, 26 January 1994, alt. 3400 m, sagittal sections on 30 slides; V.Pl. 6416.2, Bujuku River, Ruwenzori Mountains, Uganda, 24 January 1994, alt. 2600 m, sagittal sections on 11 slides; V.Pl. 6417.1, Bujuku River, Ruwenzori Mountains, Uganda, 28 January 1994, alt. 4000 m, sagittal sections on 20 slides; V.Pl. 6417.2, ibid., sagittal sections on 9 slides; V.Pl. 6417.3, ibid., sagittal sections on 8 slides; V.Pl. 6417.4, ibid., sagittal sections on 8 slides; V.Pl. 6417.5, ibid., sagittal sections on 8 slides; V.Pl. 6417.6, ibid., sagittal sections on 11 slides; V.Pl. 6417.7, ibid., sagittal sections on 14 slides.

ZMA V.Pl. 811.1, mountain stream in bamboo forest, station no. 41, Mount Kenya, alt. 2870 m, January 1912, sagittal sections on 5 slides [material originally described by de BeauChamp (1913) as *Dugesia gonocephala* but transferred to *D. lanzai* by de Vries (1988a: fig. 13)].

*Description.* Preserved specimens measure up to 17 × 7 mm. Head rounded, with hardly any indication of auricles; most specimens clearly show an unpigmented auricular sense organ on either side of the head. Eyes very small, situated in small, unpigmented eye spots.

Dorsal surface dark brown, with a broad, pale band along the body margin and with an equally pale and broad mid-dorsal stripe (Fig. 8A). Ventral surface pale, with two longitudinal blackish stripes running from the head to the tail (Fig. 8B).

The ventral body region shows transverse muscles, located directly ventral to the gut and dorsal to the ventral nerve cords.

The pharynx is located in the middle of the body and measures between 1/6-1/8 of the body length in preserved specimens; it does not have an extra layer of longitudinal fibres in the outer zone of muscles. The mouth opening is located at the posterior end of the pharyngeal pocket.

The relatively small testes are situated dorsally and extend from the level of the ovaries far into the posterior end of the body. Within the penis bulb the vasa deferentia open separately into an elongated seminal vesicle, the openings of the ducts being located about halfway along the vesicle (Fig. 9). The seminal vesicle is surrounded by a layer of loosely arranged circular muscle fibres. Via a small diaphragm, the seminal vesicle communicates with a broad ejaculatory duct. The latter follows a slightly acentral, ventrally displaced course through the penis papilla and also opens acentrally at the tip of the papilla. The diaphragm receives the secretion of erythropoietic glands and especially the ejaculatory duct receives the abundant secretion of orange-staining penis glands. Similar glands open abundantly through the distal posterior half of the lining epithelium of the penis papilla. Remnants of a spermatophore are present in the ejaculatory duct of some of the specimens examined.
The small ovaries are located at about 1/5 of the distance between the brain and the root of the pharynx. The infranucleate oviducts, arising from the dorsal side of the ovaries, open separately and symmetrically into the bursal canal, directly above the zone of shell glands (Fig. 9B). The bursal canal is lined with glandular, nucleated cells and is surrounded by a subepithelial layer of longitudinal muscle, a well-developed layer of circular muscles, and a thin layer of longitudinal fibres. The last-mentioned layer constitutes the so-called ectal reinforcement layer and extends from the atrium to the copulatory bursa.

Discussion. In all essential details, the specimens examined from the Ruwenzori Mountains agree with the description of *D. lanzai* as provided by De Beaufchamp (1913), Banchetti & Del Papa (1971) and De Vries (1988a).

De Beaufchamp (1913) described that specimens from Mount Kenya fixed in Bouin’s fluid had retained their triangular head with auricles but that the heads of animals fixed in alcohol were rounded and provided with auricles so small that they were hardly visible, as was the case in the Ruwenzori specimens.

De Beaufchamp (1913) described the dorsal surface of his specimens as dark brown and their ventral surface as pale with two dark, longitudinal stripes. Banchetti & Del Papa (1971) mentioned for their specimens from Mount Kenya two dark stripes on the dorsal surface, running at 1.5 mm from the body margin, but this may be a lapsus calami in view of (a) De Beaufchamp’s observation that the stripes are ventral, and (b) the fact that Banchetti & Del Papa also described the entire dorsal side of their animals as dark brown. Two distinct ventral stripes are also present in the Ruwenzori specimens (Fig. 8B).

Four other species of *Dugesia*, anatomically somewhat similar to *D. lanzai*, have been reported from countries around Uganda: *D. sudanica* Dahm 1971, *D. congoensis* De Beauchamp 1951, *D. astrocheta*, *D. neumannii* (Neppi 1904) (cf. De Vries 1988a: fig. 15). According to De Vries (1988a), *D. sudanica* is a species inqui-
renda known only from the original description since the type material could not be traced. However, the species was described with a third, extra layer of longitudinal fibres in the outer zone of pharyngeal muscles, a feature not present in *D. lanzai*, including the Ruwenzori animals. An outer zone of pharyngeal muscles with three layers was also reported for *D. congolensis*, while this species is also characterized by a short common oviduct (De Vries 1988a), features that are absent in *D. lanzai*. In *D. astrocheta* and *D. neumanni*, the oviducal openings into the bursal canal are highly asymmetrical, in contrast to the symmetrical openings in the Ruwenzori specimens and *D. lanzai* in general.

Fig. 9. — *Dugesia lanzai*. V.Pl. 6417.1. (A) sagittal reconstruction of the male copulatory apparatus; (B) sagittal reconstruction of the female copulatory apparatus.
**Dugesia monomyoda** Marcus 1953

**Material examined and distribution.** Paratype: ZMA V.Pl. 6418.1, one specimen of which the anterior end is sectioned sagittally (2 slides), the pharyngeal region transversally (3 slides) and the posterior end sagittally (2 slides), collected at Pietermaritzburg, Natal, South Africa.

**Description.** According to Marcus (1953), preserved specimens measure up to 14 × 2 mm and have a dorsal surface that varies from pinkish-brown to almost oливaceous, becoming paler towards the body margins. The mouth opening is located at the posterior end of the pharyngeal pocket.

The ventral body region shows well-developed transverse muscles, located directly ventral to the gut and dorsal to the ventral nerve cords.

The small, rounded and well-developed testes are situated dorsally and extend from directly behind the ovaries into the posterior end of the body. The vasa deferentia open separately into the anterior section of the intrabulbar seminal vesicle, which is separated from the ejaculatory duct by a small diaphragm. The ejaculatory duct follows a slightly ventral course through the penis papilla, opening at the tip of the latter. Numerous, well-developed, erythrophilic penis glands discharge their secretion into the ejaculatory duct (Fig. 10).

The small, rounded ovaries are located at some distance posterior to the brain; according to Marcus (1953: fig. 19), the ovaries are situated at about 1/6 of the distance between the brain and the root of the pharynx. The oviducts open separately into the most proximal section of the bursal canal, i.e. close to the point where the canal communicates with the atrium. Shell glands open into the bursal canal ventral to the openings of the oviducts as well as at the level of the oviducal openings.

The bursal canal is lined with a nucleated epithelium and is surrounded by a thin, subepithelial layer of longitudinal muscles, followed by a thicker layer of circular muscle. A third, thin ectal layer of longitudinal muscle could be discerned on the ventral side of the proximal section of the bursal canal (Fig. 10).

**Discussion.** De Vries (1988a) presented a short re-description of this species, based on examination of the same material listed above, but she did not provide a reconstruction drawing of the copulatory apparatus. Therefore, the reconstruction presented above (Fig. 10) is the first after the one depicted by Marcus (1953).

De Vries (1988a) remarked that in her opinion the ejaculatory duct follows a slightly ventral course, in contrast to the central course described by Marcus (1953), a conclusion that is supported by the present study.

With respect to the extension of the ectal reinforcement along the bursal canal, Marcus (1953: 23) remarked that “in some places there is an outer layer of scattered longitudinal fibres”, while De Vries (1988a: 369) wrote: “ectal reinforcement extends halfway along the bursal canal”. In his reconstruction drawing of the copulatory apparatus, Marcus (1953: fig. 23) depicted a few longitudinal fibres precisely at the position where I found the fibres to be present in the specimen examined, i.e. at the ventral, proximal section of the bursal canal.

De Vries (1988a) wrote that the testes are “... large ...” and “... distributed throughout the body length”. However, I found the follicles to be rather small and rounded and to be completely confined to the most dorsal body region. Although the testes extend into the posterior region of the body, the material examined does not allow one to establish precisely how far the follicles extend towards the posterior body margin because the tail end has been cut off and thus is missing from the
histological sections. However, Marcus (1953: fig. 19) depicted that the testes extend well beyond the copulatory apparatus but by far do not reach the tail end (contrary to de Vries' (1988a: 375) remark that this situation was not mentioned by Marcus).

My observations on the openings of the oviducts into the bursal canal differ somewhat from those of Marcus (1953), who wrote that the ducts “... do not enter at symmetrical points from both sides, but one ... higher and farther behind, the other ... lower and more in front”. My reconstruction of the course of the oviducts suggests that the ducts open much more symmetrically into the bursal canal.

**Dugesia neumannii** (Neppi 1904)

*Material examined and distribution.* Syntypes: ZMA V.Pl. 6419.1, Buka-Weri, southern Kefa, Ethiopia (approx. 7°00′N 36°37′E), altitude 2300 m, sagittal sections on 21 slides; V.Pl. 6419.2, ibid., sagittal sections on 16 slides; V.Pl. 6419.3, ibid., sagittal sections on 13 slides; V.Pl. 6419.4, ibid., transverse sections of pharyngeal region on 4 slides; V.Pl. 6419.5, ibid., transverse sections of anterior part on 8 slides.

*Description.* According to Neppi (1904), the dorsal surface of preserved specimens is pigmented, with a blackish median stripe; eye spots and auricles unpigmented; ventral surface also pigmented. The maximum dimension of preserved specimens mentioned by Neppi (1904) is 1 × 0.6 mm.

The ventral body region shows distinct transverse muscles, located directly ventral to the gut and dorsal to the ventral nerve cords.

Pharynx located in the middle of the body; the mouth opening is at the posterior end of the pharyngeal pocket. The well-developed testes are dorsal, extending from directly behind the ovaries into the posterior end of the body.
The vasa deferentia open separately into the most proximal, anterior section of the intrabulbar seminal vesicle. The latter narrows before communicating with a relatively wide ejaculatory duct; a small diaphragm separates the vesicle from the ejaculatory duct, which has a strongly subterminal opening at the ventral part of the penis papilla (Fig. 11). The ejaculatory duct receives the abundant secretion of numerous erythropilic penis glands and contains parts of a spermatophore. The penis papilla is a thick and blunt cone that completely fills the male atrium; the penis bulb is weakly muscular.

The small egg-shaped ovaries are located at 1/4-1/5 of the distance between the brain and the root of the pharynx. The oviducts, which originate from the dorsal surface of the ovaries, open separately into the proximal section of the bursal canal. The oviducal openings are located asymmetrically in that one oviduct opens virtually at the point where the canal communicates with the atrium, whereas the opening of the other oviduct is located more dorsally. Shell glands open into the bursal canal directly ventral to the most dorsal oviducal opening.

The bursal canal is lined with a rather thick epithelium and is surrounded by three layers of muscle: (a) a thin subepithelial layer of longitudinal fibres, (b) a thick layer of circular muscle, (c) a thin layer of longitudinal fibres that extends all the way from the proximal section of the canal to the point of communication with the copulatory bursa. It could not be established unequivocally whether the bursal canal is lined with nucleated or infranucleated cells.

Discussion. Basically, Neppi’s (1904) description is accurate, albeit that she did not observe the presence of the small diaphragm in the specimens, as noted by de Vries (1988a).

Fig. 11. — Dugesia neumanni. Syntype, V.Pl. 6419.1. Sagittal reconstruction of the copulatory apparatus.
In her description, Neppi (1904) mentioned that the oviducts open separately and distinctly asymmetrically into the female atrium and that the shell glands open into the bursal canal, dorsal to the oviducal openings. Meixner (1928) considered this situation to be physiologically impossible, re-examined the slides and, subsequently, concluded that the oviducts open into the bursal canal dorsal to the openings of the shell glands into the canal. The reconstruction presented above (Fig. 11) vindicates the opinions of both Neppi and Meixner. Although Neppi (1904) mentioned that the oviducts open into the female atrium, her drawing of the copulatory apparatus shows one oviduct opening at the point of communication between bursal canal and atrium, with the opening of the other oviduct being located somewhat more dorsally; this resembles very much the reconstruction presented above (Fig. 11). However, in contrast to Neppi's observations, the shell glands open into the bursal canal ventral to the most dorsal oviducal opening; this situation is more or less in agreement with Meixner's (1928) observation, albeit that it applies to only one of the oviducts since the opening of the other oviduct into the bursal canal is not located dorsal to the openings of the shell glands.

In the account on D. capensis (see above), it was pointed out that Kawakatsu's (1972) presumed D. neumanni specimens from Transvaal do not belong to the last-mentioned species but are members of D. capensis and that it is debatable whether Marcus' (1955) specimens of D. neumanni from southern Africa have been correctly assigned to this species. Marcus (1955) mentioned D. neumanni from three localities in southern Africa but only the animals from one site in the Makheke Mountains in Lesotho were identified on the basis of sectioned, mature animals. Marcus' (1955) material from Lesotho was not available during the present study but his descriptions of flatworms are usually detailed and accurate. When Marcus' (1955) account on the Lesotho specimens is compared with the type material of D. neumanni, a number of differences are apparent.

Although Marcus (1955) described a subterminal, ventral opening of the ejaculatory duct for his specimens, the situation seems to be less extreme than in the case of the type specimens since in the Lesotho animals the opening is still close to the tip of the penis papilla; however, in the case of the type specimens, preservation artefacts cannot be excluded. Furthermore, the penis bulb of the type specimens of D. neumanni is only weakly muscular, whereas Marcus (1955) depicted a strongly muscular bulb for his Lesotho animals.

In the Lesotho specimens, the ectal reinforcement muscle layer around the bursal canal is restricted to its "ectal half" (Marcus 1955: 114), whereas in the type specimens this layer of longitudinal muscles occurs on the entire canal, i.e. from atrium to copulatory bursa. Marcus (1955) described the lining epithelium of the bursal canal of the Lesotho specimens as being of the nucleated type; in the type specimens, the canal may be lined with an infranucleated epithelium, albeit that this could not be determined unequivocally. According to Marcus (1955: 114), the copulatory bursa of the Lesotho animals is "small", whereas the bursa of the type specimens appears to be relatively large.

From Marcus' (1955) description, it can be deduced that the oviducts open symmetrically into the bursal canal, directly above the zone of shell glands; this contrasts with the situation in the type specimens of D. neumanni (see above).

Lastly, in the type specimens, there is a distinct layer of transverse muscles in the ventral body region, located directly ventral to the intestinal branches and dorsal to the ventral nerve cords. Such a layer of transverse muscles was described by Marcus (1953) for D. monomyoda and D. didiaphragma (identified as D. gono-
cepha by Marcus, cf. De Vries 1988a), while he mentioned that such a layer is absent in *D. astrocheta* and *D. ectophysa*. Since Marcus (1955) did not mention the presence of this layer of transverse muscles for his Lesotho specimens, it is here assumed that such a layer is absent in these animals.

In view of the differences listed above, it is here concluded that Marcus’ Lesotho specimens do not belong to *D. neumanni*. They may well represent a third, new species of *Dugesia* in southern Africa, different from *D. capensis* and *D. monomyodya*. However, in the absence of new material and of Marcus’ (1955) slides of the Lesotho specimens, I refrain from coining a new species name for these animals.

Genus **Neppia** Ball 1974

**Neppia jeanneli** (De Beauchamp 1913)

*Material examined and distribution.* Topotypes: ZMA V.Pl. 6420.1, Mt Kilimanjaro, Tanzania, station no. 71, altitude 2700 m, coll. Alluaud and Jeannel, 3 February 1912, sagittal sections on 5 slides; V.Pl. 6420.2, ibid., horizontal sections on 3 slides.

*Description.* According to De Beauchamp (1913), preserved specimens are 8-10 mm long, with a uniform blackish colouration on the dorsal surface; the ventral body surface is only slightly paler. A distinct auricle is present on either side of the head (De Beauchamp 1913).

The pharynx is provided with an extra layer of longitudinal muscle in its outer zone of muscles (Fig. 12A); the mouth opening is located at the posterior end of the pharyngeal pocket.

The testes are situated dorsally, extending from directly behind the ovaries to the root of the pharynx. The testes follicles are located in a zone directly lateral to the anterior gut trunk; the vitellaria occupy the lateral zones of the body (De Beauchamp 1913).

The vasa deferentia are swollen to form spermiducal vesicles, which narrow considerably at the point where they separately penetrate the penis bulb. Within the bulb, the sperm ducts expand again somewhat in diameter and subsequently unite to form a short common section that opens into the proximal part of the ejaculatory duct. The latter has a wide, irregularly shaped lumen with several folds; it is lined with a tall epithelium that is penetrated by numerous openings of penis glands. The ejaculatory duct opens at the tip of the penis papilla; in some specimens, this opening may be slightly more ventral than terminal (Fig. 13; cf. Ball 1974: fig. 6B).

The penis papilla is lined with a cuboidal, nucleated epithelium and is provided with a relatively thick layer of circular muscles and a much thinner layer of longitudinal muscle; in addition there are longitudinal retractor fibres. The penis bulb is well-developed, consisting of a thick zone of criss-cross-arranged muscle fibres.

The ovaries are rather small and situated directly behind the brain. The oviducts open separately into the bursal canal; the oviducal openings are asymmetrically located in that one oviduct opens directly dorsal to the zone of shell glands, whereas the other duct opens more ventrally and penetrates this zone of glands (Fig. 13; see also Ball 1974: 20).

The bursal canal is lined with a tall, probably infranucleated, epithelium. It is surrounded by a thin layer of longitudinal muscle, a thick zone of circular muscle, and a thin ectal layer of longitudinal reinforcement muscles. Part of the copulatory bursa
may be located lateral to the penis bulb (Fig. 13; cf. De Beauchamp 1913: fig. 1) or the bursa may be situated anterior to the bulb, as is the case in specimen V.Pl. 6420.2. In specimen V.Pl. 6420.1 (Fig. 13), a spermatophore is present in both the bursa and the ejaculatory duct; in specimen V.Pl. 6420.2, a spermatophore is present in the copulatory bursa. In the type material, spermatophores are also present (Ball 1974).

Discussion. The description presented above is the first one based on other specimens after De Beauchamp (1913) and Ball (1974) published their accounts on the type material. A re-description of the species is necessary because (1) it resembles Neppia paeta (Marcus 1955), especially the not fully mature specimens of this species (see below), (2) examination of the new specimens revealed some differences between their anatomy and De Beauchamp's (1913) description of the type specimens.
Ball (1974) already corrected De Beauchamp’s (1913) description that the testes are situated in the middle region of the body by observing that the follicles are dorsal, an observation that agrees with the condition in the specimens examined in the present study.

Furthermore, De Beauchamp’s (1913) description of the lateral position of the testes is completely contradicted by the situation in the newly prepared material. Notably, the horizontally sectioned topotype specimen V.Pl. 6420.2 reveals that the testes are arranged close to the anterior gut trunk and that the well-developed vitellaria are located in the lateral regions of the body (Fig. 12B). In view of De Beauchamp’s (1913) fig. 1, which is probably based on the whole mounted specimen (cf. Ball 1974: 20), it looks as if he has mistaken the vitellaria for the testes.

**Neppia paeta** (Marcus 1955)

*Material examined.* ZMA V.Pl. 6421.1, Hekpoort, South Africa, 25°55’S 27°38’E, July 1977, sagittal sections on 16 slides; V.Pl. 6421.2, ibid., sagittal sections on 2 slides; V.Pl.
Fig. 14. — *Neppia paeta*. V.Pl. 6421.7. Dorsal view of whole mounted specimen.

6421.3, ibid., sagittal sections on 3 slides; V.Pl. 6421.4, ibid., horizontal sections on 2 slides; V.Pl. 6421.5, ibid., sagittal sections on 6 slides; V.Pl. 6421.6, ibid., sagittal sections on 2 slides; V.Pl. 6421.7, ibid., 2 whole mounts on 1 slide.

ZMA V.Pl. 6422.1, Johannesburg, South Africa, 26°10’S 28°02’E, April 1977, sagittal sections on 4 slides; V.Pl. 6422.2, ibid., 1 whole mount on 1 slide.

ZMA V.Pl. 6423.1, Great Fish River, Carlisle Bridge, South Africa, 33°04’59.8”S 26°13’8”E, October 2005, sagittal sections on 4 slides.

**Distribution.** Marcus (1955) reported the species from the following localities: South Africa: Lundean’s Nek, 32 km NW of Rhodes; Drakensbergen, about 20 km ENE of Rhodes (altitude 2440 m); De Hoop Vlei at Windhoek Farm, 32 km E of Bredasdorp; Lesotho: Makheke Mountains, 16 and 24 km ENE of Mokhotlong; Quthing. Marcus (1955) also mentioned four immature specimens from Swartberg Pass, Platberg in South Africa that may belong to *N. paeta*; however, these records need to be substantiated by examination of sexual animals and therefore have not been included in the distribution map of the species (Fig. 17). The new records for the species detailed in the present paper imply a notable northward extension of the distribution range of the species.

**Description.** Preserved specimens measure up to about 8.5 × 2 mm. Head bluntly triangular, with short, rounded auricles; eyes situated in pigment-free patches. Dorsal surface mottled brown or with the pigment arranged in an irregular, reticulate pattern (Fig. 14); ventral surface pale. According to Marcus (1955), the anterior border is nearly black, with the black rim extending over the auricles; however, in my material, the body margins are devoid of pigment.

Marcus (1955) described that the two posterior gut trunks unite in the posterior end of the body, a situation that was also evident in specimens V.Pl. 6421.4 and V.Pl. 6421.7.

The pharynx is located in the posterior half of the body and measures between 1/7-1/9 of the body length. The outer zone of pharynx muscles is provided with an extra layer of longitudinal muscle, located ental to the layer of circular fibres. The mouth is at the posterior end of the pharyngeal pocket.

The testes are dorsal, extending from a short distance behind the ovaries to a short distance anterior to the root of the pharynx. The spermiducal vesicles narrow considerably at the point where they separately penetrate the penis bulb. Within the bulb, the sperm ducts open into the proximal section of the ejaculatory duct. This proximal section of the ejaculatory duct is lined with a nucleated epithelium and is surrounded by a well-developed coat of circular muscle, in contrast to the distal part of the duct, which is lined with an infranucleated epithelium and lacks the coat of muscle. The distal section of the ejaculatory duct is more spacious than the proximal part, has several irregular folds and is penetrated by the openings of penis glands; the duct opens at the tip of the penis papilla (Fig. 15).
The penis bulb is provided with a well-developed coat of muscles. The penis papilla shows the usual thin coat of subepithelial circular and longitudinal muscle fibres but there is also a coat of longitudinal retractor fibres ental to the layer of circular muscle.

The ovaries are situated at a short distance behind the brain, i.e. at about 1/6 of the distance between the brain and the root of the pharynx. The oviducts open separately into the bursal canal slightly ventral to the point where the canal shows a distinct anteriorly directed bend. A major portion of the bursal canal ventral to the oviducal openings receives the secretion of abundant shell glands. The relatively narrow bursal canal is lined with an infranucleated epithelium and is surrounded by a thin layer of longitudinal muscle, followed by an extremely thick zone of circular muscle. The muscle coat on the distal section of the bursal canal, i.e. ventral to the oviducal openings, is set off from the coat of circular muscle around the horizontal section of the canal by a narrow stretch of parenchyma devoid of muscle fibres that is generally more developed and obvious on the anterior wall of the canal (Fig. 15). The bursal canal communicates with a relatively large copulatory bursa.

Discussion. The specimens from Hekpoort and Johannesburg agree in all essential details with the description of *N. paeta* published by Marcus (1955). Furthermore, I have been able to examine the same type material that was studied by Ball (1974) and this re-examination underscored the identification of the new animals as *N. paeta*. According to Marcus’ (1955) account and the type material, the ejaculatory duct opens on the ventral side of the penis papilla. However, this ventrally displaced opening may be due to preservation artefacts since in most of the new material examined the duct opens at the tip of the penis papilla.

The specimen from Carlisle Bridge (V.Pl. 6423.1) is also assigned to *N. paeta*, although its reproductive apparatus shows some differences from the type material.

![Fig. 15. — *Neppia paeta*. V.Pl. 6421.5. Sagittal reconstruction of the copulatory apparatus.](image-url)
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...and the animals from Hekpoort and Johannesburg. Notably, the copulatory apparatus of this animal is relatively small (Fig. 16), with the lining epithelium of the bursal canal being nucleated and the canal surrounded by a less extensive coat of muscles. Furthermore, the ovaries of this animal are hyperplastic. In these four respects, the animal from Carlisle Bridge resembles a specimen from Johannesburg, viz. V.Pl. 6421.4. Both worms are in full possession of testes and very much resemble the partly mature specimens discussed by Marcus (1955), which also were “completely mature” (Marcus 1955: 109) in the sense that all reproductive organ systems were present and functional, although the copulatory apparatus did not appear fully developed. It is not known whether Marcus’ (1955) partly mature specimens also had hyperplastic ovaries. In the single, partly mature specimen available from the original type material (the “fourth slide”; cf. Ball 1974: 25) only the posterior end of the animal has been preserved.

It is well known that in dugesiid freshwater planarians with an infranucleated lining of the bursal canal, the epithelium is nucleated in not fully mature animals and that only fully mature individuals have their epithelia infranucleated (De Vries 1984b, Sluys 1996).

**GENERAL DISCUSSION**

Although in the above accounts I have made several taxonomic decisions with respect to the species status of particular populations, I have generally followed a

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**Fig. 16.** — *Neppia paeta*. V.Pl. 6423.1. Sagittal reconstruction of the copulatory apparatus of a not fully mature specimen.
conservative approach to taxonomy. However, in view of (a) the descriptions, re-
descriptions and comparative discussions presented above, and (b) the remarks of
De Vries (1988a) that the differences between D. sicula, D. astrocheta and D. neu-
manni are obscure or problematic, it is useful to review the taxonomic status and
differences of a number of species that are very similar in the gross morphology of
their reproductive apparatus.

Notably D. sicula, D. astrocheta, D. neumanni, D. lanzai and D. monomyoda
are species for which it is difficult to establish their identity. For these species,
Table 1 lists the character states of a number of features that may differentiate
these taxa: course of the ejaculatory duct through the penis papilla (a central course
or an acentral, ventrally displaced course); opening of the ejaculatory duct to the
outside (at the tip of the penis papilla or a subterminal, ventrally displaced open-
ing); presence or absence of transverse muscles in the ventral body region; openings
of the oviducts into the bursal canal (symmetrical or asymmetrical); presence or
absence of an extra, third layer of longitudinal fibres in the outer zone of pharyn-
geal muscles; extent of ectal reinforcement on the bursal canal (confined to vaginal
area, up to the copulatory bursa, from atrium to halfway along bursal canal, less
than halfway and confined to ventral side of bursal canal); point of communication
between vasa deferentia and seminal vesicle (at the beginning, most anterior end of
the vesicle or halfway along the vesicle).

On the basis of these characters, it is possible to differentiate between these
five nominal species. However, it is also evident from Table 1 that particularly D.
sicula and D. neumanni are very similar, differing only in the extent of the ectal
reinforcement on the bursal canal. D. sicula is a Palearctic species with a circum-
Mediterranean distribution, whereas D. neumanni is a species from the Afrotropical
Region (Fig. 17; De Vries 1988b: fig. 4), known unequivocally only from the type
locality in Ethiopia (see above). Although it is certainly not impossible for a spe-

Table 1.
Selected character states in five species of Dugesia. For further explanation, see text.

<table>
<thead>
<tr>
<th>Species</th>
<th>Course ejaculatory duct</th>
<th>Opening ejaculatory duct</th>
<th>Transverse muscles</th>
<th>Opening oviducts bursal canal</th>
<th>Third muscle layer pharynx</th>
<th>Extent ectal reinforcement</th>
<th>Opening vasa def. seminal vesicle</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. sicula</td>
<td>acentral</td>
<td>subterminal</td>
<td>present</td>
<td>asymmetrical</td>
<td>absent</td>
<td>vaginal area</td>
<td>anterior</td>
</tr>
<tr>
<td>D. neumanni</td>
<td>acentral</td>
<td>subterminal</td>
<td>present</td>
<td>asymmetrical</td>
<td>absent</td>
<td>up to copulatory bursa</td>
<td>anterior</td>
</tr>
<tr>
<td>D. astrocheta</td>
<td>acentral</td>
<td>subterminal</td>
<td>absent</td>
<td>asymmetrical</td>
<td>absent</td>
<td>halfway bursal canal</td>
<td>anterior</td>
</tr>
<tr>
<td>D. lanzai</td>
<td>acentral</td>
<td>tip</td>
<td>present</td>
<td>symmetrical</td>
<td>absent</td>
<td>up to copulatory bursa</td>
<td>halfway</td>
</tr>
<tr>
<td>D. monomyoda</td>
<td>slightly acentral</td>
<td>tip</td>
<td>present</td>
<td>symmetrical</td>
<td>absent</td>
<td>less than halfway bursal canal; ventral</td>
<td>anterior</td>
</tr>
</tbody>
</table>
cies to straddle the boundaries of biogeographic regions, I interpret the different distributions of these two nominal species as an additional sign of their separate taxonomic status.

With respect to biogeography, Sluys et al. (1998) recognized for the genus *Dugesia* the presence of two major phyletic lineages in the Afrotropical Region that they labelled as Group 1 and Group 2. The African representatives of the last-mentioned group are characterized by the apomorphic presence of an acentral ejaculatory duct with a subterminal opening. This suggests that the new species *D. capensis*, with an acentral ejaculatory duct, falls within Group 2. However, the opening of the ejaculatory duct is located at the tip of the penis papilla, i.e. is terminal and not subterminal.

![Geographical distribution of the focal species of this paper.](image)
As far as current knowledge goes, diversity of freshwater planarians in the Afrotropical part of the African continent seems rather low compared with the Palearctic section of the continent. From the Afrotropical Region, only three genera have been reported, according to current taxonomy, viz. *Dugesia*, *Neppia* and *Cura* (see above; cf. Grant et al. 2006: fig. 71). In contrast to the two last-mentioned genera, *Dugesia* is also present north of the Sahara (cf. Charni et al. 2004 and references therein), together with various other genera such as *Polycelis*, *Crenobia*, *Acromyadenium*, *Dendrocoelum* (*Dendrocoelides*), and *Schmidtea* (cf. Marcus 1955 and references therein, Gourbault 1972, Harrath et al. 2004). Vandel (1922) reported that de Beauchamp had written him about the finding of *Phagocata vitta* (Dugès 1830) in Algeria; Gauthier (1923: 34) remarked that this probably concerned the specimens that he had collected and subsequently forwarded to de Beauchamp for identification. However, this finding apparently has never been substantiated by any detailed descriptions, because Kenk (1974) registered with a question mark the occurrence of this species in North Africa. Lauterborn (1921) reported *Crenobia alpina* for Algeria but this record may also need verification in view of the fact that Kenk (1974) did not mention the species for North Africa.

The current pattern of freshwater planarian diversity of the Afrotropical Region is presumably a poor reflection of the real situation, in view of the fact that large areas of this region have never been thoroughly sampled for these animals.

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