A case study on the Trichoptera fauna of springs in the escarpment mountains of southern Africa (Insecta, Trichoptera)

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Abstract

The Trichoptera assemblages of three springs in the escarpment and on the Waterberg of Namibia, and of two springs in the Great Escarpment of South Africa were collected at irregular intervals. The species composition of each spring is presented and discussed in terms of permanence and stability of spring areas. The study has revealed a poor fauna in the Namibian escarpment, which consists of widespread species whereas the springs on the Waterberg and in the Great Escarpment are more speciose and contain relict and possible endemic species as well as widespread and euryoecious species. The differences are due to different degrees of isolation and distance from other freshwater ecosystems and suitable aquatic biotopes in the arid and semiarid environment of southwestern Africa.

Key words: faunistics, taxonomy, Great Escarpment, Waterberg, Namibia, South Africa, Eastern Cape

Introduction

The south-western part of Africa is a predominantly arid and semiarid region. Annual precipitation is below 300 mm, and the resulting sparse vegetation is typically composed of grasses, low bushes and succulents up to 50 cm in height. Within this dry landscape the escarpment arises as a peculiar, orographical entity. It forms a series of mountain ranges with dramatic scarp slopes on the western and southern sides, separating the highlands of the interior from the coastal lowlands. The escarpment represents the ancient continental margin of the African plate since its separation from Western Gondwanaland about 120 Mya (Matmon et al. 2002). It extends parallel to the coastal line from southern Angola through Namibia into South Africa (RSA). Springs and small headwater streams occur all along the foothills of the escarpment. They represent widely separated freshwater biotopes isolated from other, permanent freshwater systems of the more humid regions.

The caddisflies found in these biotopes are almost completely unknown. Among other aquatic insects, only Odonata have attracted some interest and were studied quite recently (Suhling & Martens 2007; Suhling et al. 2009). The dragonflies and damselflies encountered in the Namibian escarpment were found to belong to widespread species which are able to live in a variety of different aquatic biotopes, not only spring streams. In permanent springbrooks, however, they form unique assemblages (Martens et al. 2010). Many odonate species are even capable to crossing the Namib Desert in search of suitable breeding sites. The high dispersal abilities of Odonata make them rapid colonisers of remote localities, periodic waters or newly created dams or pools. Endemic species were not found. Their absence in a number of water bodies is probably a consequence of the high dispersal power, which counteracts or prevents the occurrence of long isolation phases of widely scattered populations, a prerequisite of evolutionary processes. Most caddisflies are not as good as Odonata in their dispersal and flying abilities. Although able to fly or to drift passively over long distances too, the soft-bodied adults are prone to desiccation and tend to remain in the vicinity of their aquatic habitats, especially when the localities are in a hot and arid environment. This applies especially to species adapted to spring environments (Danks & Williams 1991). Isolated spring populations of caddisflies therefore remain isolated for longer periods of time, which would facilitate the onset of speciation processes. If an aquatic environment is permanent and stable, distinct species could develop. The occurrence of such neo-endemics is therefore...
evidence for the stability and permanency of springs or spring systems. Such ecosystems and biotopes might also serve as refuges for species which are relics of populations that were abundant during a more humid climate phase. Evidence for the occurrence of humid periods in the past was published by Blümel et al. (2009), Heine (2004) and Vogel (1989). At least six non-arid and arid phases since 40 000 BC were suggested by Brook et al. (1999). In contrast to the fauna of an old spring, any caddisfly fauna of a younger or intermittent spring should be a composition of migrants and euryoecous species, which have a wide distribution and which are not confined to spring areas. A study of the composition of the caddisfly faunas of springs in the escarpment is an interesting venture. It throws light on the durability/history of these aquatic ecosystems which are tightly connected with climatic oscillations in the recent and more distant past. The aims of the study are to find arguments for answering the following questions:

1. Are there endemic or relict species in the springs or spring streams of the escarpment?
2. Do the springs have a unique assemblage of species?
3. How are the species distributed along the escarpment? Does or did the escarpment provide a pathway for the dispersal of species in a similar way as described for plant species by Clark 2010, Clark et al. (2009, 2011, 2012) and Galley et al. (2007)?

The study of escarpment springs is difficult. Most localities are remote and not easily accessible. Water is a limited resource and of prime importance for livestock, wildlife and people. Many springs are anthropogenically altered and only remnants of the original fauna and flora exist. Pristine spring sites are rare and are only preserved in conservation areas, where they are also under pressure (Martens et al. 2010). From a conservation viewpoint it is an urgent task to investigate these sites and to take measures for their protection, even if biological data are not available.

Four spring areas were selected for the present study, two in the Namibian escarpment and two in the Great Escarpment in South Africa. They may serve as examples for the caddisfly fauna of springs and spring streams in the escarpment. For comparative purposes one spring on the Waterberg in the inland region of Namibia was also chosen.

Material and methods

Adult caddisflies, active during day-time, were collected using a conventional hand net. The vegetation of stream banks was shaken and beaten and all caddisflies were taken.

Crepuscular and night active species were sampled with a light-tower (company F. Weber, Stuttgart) equipped with two 15-Watt super-actinic light-tubes (Philips). The tower was battery powered (Panasonic, 12 V, 10 Ah) and was in operation for 2–3 hours starting at sunset. The tower is a very mobile device and very useful for collecting adult caddisflies in remote and difficult-to-reach aquatic ecosystems. All caddisfly specimens arriving at the lights were sampled and preserved in alcohol. Some specimens were pinned or micro-pinned. The coordinates were registered with a GPS 60 (Garmin).

Study area. Field work was conducted in the Western Escarpment Mountains and on the Waterberg of Namibia, and in the Great Escarpment in the Eastern Cape of South Africa (Fig. 1). Five springs were visited several times at irregular intervals. The word “spring” refers herein to the spring source and the first 50–100 m of the drainage below the spring source.


The spring stream starts in a rheocrene spring and is a first order tributary of the Hoanib River. Only the first 300–500 m have a permanent water flow. The river bed of the Hoanib further downstream has several stretches with permanent surface water.

FIGURE 1. Location of study sites in southwestern Africa (Namibia: 1—Ongongo Falls, 2—Waterkloof Trail, 3—Waterberg; RSA, Asante Sana: 4—Waterkloof, 5—Zuurkloof).

The spring stream (Fig. 2) is a first-order headwater tributary of a third-order stream (unnamed) which cuts through Naukluft Mts. (Fig. 3) and ends in the Namib sand dunes north of Sossusvlei. The spring stream source has a short stretch of about 200 m with surface water, whereas the third order stream has an intermittent flow of water including a number of isolated pools.


The Waterberg is famous for its springs which are distributed around this isolated table mountain. The spring sites are at the foothills below the steep cliffs. Usually, the spring streams are short, not exceeding 100-200 m. The studied spring above the Tourist Camp is used for water supply for the camp and for the nearby, old police station since historical times.
FIGURE 2. Carstic spring stream on Waterkloof Trail in the Naukluft Mountains.


On the Asante Sana Game Farm, the Waterkloof and the Zuurkloof are deep geomorphological incisions into the steep escarpment (Fig. 4). The valleys exhibit dense vegetation with thickets and forests along the river courses. The two springs on Asante Sana that emerge at the foot of the steep cliffs (Figs 5–6) are first-order headwater streams that unite at Petersburg to form the Melk River which flows into the Sundays River. Both streams are intermittent over most of their courses. The Sundays River flows into the Indian Ocean north-east of Port Elisabeth. The aquatic fauna of this river is little known, but probably is as poor as the fauna of the neighbouring Great Fish River (O’Keeffe et al. 1989; Scott 1974).
Results and discussion

Namibian escarpment. The caddisfly fauna of Ongongo Falls and Waterkloof Trail comprise three and five species, respectively. They are listed in Table 1. Endemic species were not found. Two species occur at both sites. Chimarra caboverdensis Nybom 1960 is known from a moderate number of localities on the African continent. Hydroptila cruciata Ulmer 1912 also has a wide distribution in Africa. In the mountains of the Western Cape the species is a common dweller in different stream types. The remaining species are regular inhabitants of smaller and larger rivers where they usually occur in large populations. All spring species except Chimarra caboverdensis and Cheumatopsyche rhodesiana (Jacquemart 1963) are known, for example, from the lower Orange River and Fish River which cut through the escarpment in the south of Namibia (Mey 2011).

TABLE 1. Caddisfly species of two springs in the escarpment of Namibia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ongongo Falls</th>
<th>Waterkloof Trail</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydroptila cruciata Ulmer, 1912</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Orthotrichia sanya Mosely, 1948</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Chimarra caboverdensis Nybom, 1953</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Cheumatopsyche rhodesiana (Jacquemart, 1963)</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Cheumatopsyche thomasetti (Ulmer, 1931)</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Ecnomus thomasetti Mosely, 1932</td>
<td></td>
<td>x</td>
</tr>
</tbody>
</table>
Samples collected during different seasons revealed that the species are not confined to a single generation per year; there are probably two or more, or they may even be aseasonal with continuously running breeding cycles. During repeated visits, at least one species of the assemblage was found to be on the wing, even in winter (Table 2).

The larvae of the spring species belong to only two functional feeding types. The *Chimarra*, *Ecnomus* and *Cheumatopsyche* species are mainly predators and collectors, but they also ingest algae and detritus. The larvae of the hydroptilid genera *Hydroptila* and *Orthotrichia* feed on green algae and diatoms. The ecological niches of detritus aggregations and stone surfaces normally occupied by shredders, filter-feeders and grazers are void of Trichoptera. Springs in the northern Hemisphere are usually dominated by larvae of these functional feeding types (Danks & Williams 1991). According to the theory of the River Continuum Concept (Vannote et al. 1980; O’Keeffe et al. 1989), a comparable composition could also be expected to occur in African springs. Unfortunately, I have no data or references on African spring Trichoptera for comparison, but given that the River Continuum Concept is applicable, an ecologically more diverse fauna would be expected. The dominance of collectors and predators is typical for larger, lowland rivers. Since most of the collected spring region species in the Namibian escarpment are also inhabitants of these rivers, the spring and spring streams seem to be colonised from these areas. The Orange River in the south and the Kunene River in the north are the only large permanent rivers in the escarpment and probably represent permanent source areas, from which a constant dispersal of migrating specimens into the escarpment may have its origin.

In the interior of Namibia, springs are also rare landmarks. A remarkable exception is the Waterberg with a number of springs located around this famous table mountain. The easily accessible spring near the Tourist Station was sampled several times and the collected species are listed in Table 3. In comparison with the escarpment springs there are two shared species: *Hydroptila cruciata* and *Ecnomus thomasseti* Mosely 1932. Both are widespread species in Namibia, the latter also occurring in reservoirs and artificial pools. *Oecetis vulgata* (Marlier 1956) was found to be the dominant species of the small Trichoptera assemblage. It is the
first record of the species in Namibia and South Africa. On the basis of current knowledge on the distribution of African Trichoptera, the population on the Waterberg seems to be displaced from the main range of the species, for which the southernmost records previously are from Zimbabwe (de Moor & Scott 2003). The Waterberg is an isolated mountain in the vast dry thorn-bush savannah. The nearest localities with spring areas are in the Otavi Mountains, about 50–100 km to the north. However, the Otavi Mountains are as isolated as the Waterberg. If populations of the species also occur there, they can be regarded as similarly isolated relicts of a distant past with a more humid climate.

**TABLE 2.** Phenology of adult caddisfly species at Ongongo Falls.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hydroptila cruciata</em> Ulmer, 1912</td>
<td>11/3</td>
<td>22/29</td>
<td>-</td>
<td>-</td>
<td>2/15</td>
</tr>
<tr>
<td><em>Chimarra caboverdensis</em> Nybom, 1953</td>
<td>5/1</td>
<td>(2 la)</td>
<td>-</td>
<td>1/0</td>
<td>3/4</td>
</tr>
<tr>
<td><em>Cheumatopsyche rhodesiana</em> (Jacquemart, 1963)</td>
<td>19/60</td>
<td>0/4 (3 la)</td>
<td>1/3</td>
<td>4/17</td>
<td>2/0</td>
</tr>
</tbody>
</table>

**TABLE 3.** Caddisfly species of the spring on the Waterberg.

<table>
<thead>
<tr>
<th>Species</th>
<th>1993</th>
<th>2005</th>
<th>2008</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hydroptila cruciata</em> Ulmer, 1912</td>
<td>1/0</td>
<td>2/2</td>
<td>0/1</td>
</tr>
<tr>
<td>Orthotrichia spec.</td>
<td></td>
<td>0/2</td>
<td></td>
</tr>
<tr>
<td><em>Ecnomus thomasetti</em> Mosely, 1932</td>
<td>0/3</td>
<td>0/8</td>
<td>1/2</td>
</tr>
<tr>
<td><em>Oecetis vulgata</em> (Marlier, 1956)</td>
<td>4/0</td>
<td>11/0</td>
<td></td>
</tr>
</tbody>
</table>

**FIGURE 5.** Spring stream in the Waterkloof valley.
In summary, between the springs in the escarpment and the spring on the Waterberg a fundamental difference is evident. The presence of a relict species on the Waterberg points to a long permanence of the studied spring or the entire spring system of this mountain, whereas the absence of those species in the escarpment springs points to impermanence and instability during the same time span.

Great Escarpment, South Africa. The species collected at Asante Sana are summarised in Table 4. From the nine recorded species only one is also present in the Namibian springs: *Hydropilha cruciata*, a common species with a continental distribution. A similarly large range is seen in *Cheumatopsyche afric* (Mosely 1935). Ecologically, both species represent the euryoecous component of the spring fauna. The second *Hydropilha* species is *H. capensis* Barnard 1934, closely related to the former species, but restricted to South Africa. The name was treated as a synonym of *H. cruciata* by Moore & Scott (2003), but it is applicable to a separate species (Mey in preparation). This is the first record outside the Cape Fold Mountains (de Moor & Scott 2003). The same applies to *Chimarra georgensis* Barnard 1934, known hitherto from the Western Cape and KwaZulu-Natal only (de Moor & Scott 2003). Both species are probably outposts or relicts of the Cape fauna, being isolated in the Great Escarpment. A species with an eastern distribution in South Africa is *Lepidostoma caffrariae* Barnard 1934. It occurs from the Eastern Cape to KwaZulu-Natal and Mpumalanga. It is a characteristic species of all springs visited on Asante Sana. The larvae are shredders, feeding on leaf litter and detritus. They are also dwellers of pools and spring sources further downstream. The record of this species in the escarpment suggests a continuous distribution along the Great Escarpment with a connection to the Drakensberg Mountains in the east. This dispersal route could also have been used by other species, originating from the Cape or from the Natal Drakensberg Mountains (e.g., *Chimarra georgensis*). The detection of those species, including *L. caffrariae*, at localities further east of the Great Escarpment would corroborate this hypothesis.

**TABLE 4.** Caddisfly species of two springs in the Great Escarpment of South Africa.

<table>
<thead>
<tr>
<th>Species</th>
<th>Waterkloof</th>
<th>Zuurkloof</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hydropilha cruciata</em> Ulmer, 1912</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>Hydropilha capensis</em> Barnard, 1934</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Orthotrichia spec.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td><em>Chimarra georgensis</em> Barnard, 1934</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>Cheumatopsyche afric</em> (Mosely, 1935)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>Cheumatopsyche spec.</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lepidostoma caffrariae</em> Barnard, 1934</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>Athripsodes spec.</em></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Leptecho spec.</td>
<td>x</td>
<td></td>
</tr>
</tbody>
</table>

*Orthotrichia spec.*, *Cheumatopsyche spec.*, *Leptecho spec.* and *Athripsodes spec.* are undescribed species. They possibly represent the endemic element of the Trichoptera fauna in the escarpment. A botanical exploration of the escarpment has revealed a high diversity and the presence of a number of endemic species (Clark *et al.* 2009). Especially the Sneeuberg range to which Asante Sana belongs is recognised as a centre of endemism. Though Trichoptera are aquatic insects, they seem to support the biogeographic significance of the Sneeuberg, which was deduced from terrestrial biota. However, the undescribed species are not typical for the spring biotopes, because they were sampled there in small numbers only. They have their main distribution in the lower epihrithral section of the streams, where they occur together with a number of additional caddisfly species. These species will be described in a future article on the Trichoptera of Asante Sana.

In comparison with the studied springs in Namibia, the springs in the Great Escarpment are much less isolated. The spring streams are more extensive and unite with other tributaries into larger streams forming one of the main headwaters of the Melk River on Asante Sana. The river becomes intermittent when reaching the lowlands. The permanent river system in the escarpment valleys is multi-branched and connects a variety of streams and aquatic biotopes at elevations between 1000–2000 m. This small but permanent watershed supports a rich and diverse Trichoptera fauna, which also effects the springs leading to more speciose assemblages than in Namibia. The richer fauna on Asante Sana is composed not only of widespread species but includes possible endemic and relict species, and seems to support the notion of a long permanence and
stability of the fluvial systems in the escarpment. But how far back in time does this presumed permanence go? Evidence for a long history might be the presence of stoneflies (Plecoptera) (Erman 1998). Up to now, not a single representative of this aquatic insect order was collected on Asante Sana or in the Namibian escarpment. Years of drought could have caused extinction. The group is known to have weak dispersal abilities, making recolonisation difficult and demanding time spans that are probably more extensive than necessary for Trichoptera, Odonata or Ephemeroptera. Further collecting in the Great Escarpment should be performed to search for Plecoptera and other Trichoptera species in order to gather additional evidence for providing more detailed explanations on the origin and composition of the spring fauna in these arid and semiarid regions.

FIGURE 6. Origin of springs and spring streams at the base of the cliffs in the Waterkloof valley.

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