Ecological effects of impoundments in the Buffalo River, eastern Cape, with particular reference to the distribution of blackflies (Diptera: Simuliidae).

THESIS

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DOCTOR OF PHILOSOPHY

by

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DECLARATION

In accordance with regulations for the award of the degree of Doctor of Philosophy, I declare that:

1. This thesis forms part of a co-operative research programme between the Institute for Freshwater Studies, Rhodes University, and the Freshwater Research Unit, University of Cape Town. Base-line field data from the Buffalo River were collected by Dr J. H. O'Keeffe and myself, with the assistance of numerous students and friends. Unless otherwise stated or acknowledged in the text, the contents of this thesis (including photographs and diagrams) are my own work. Publications which have arisen from the main research programme (Appendix C) bear the names of the authors in order of the importance of their contribution to the research. Technical assistance in sorting and counting of invertebrates is separately acknowledged.

2. Neither the whole nor any part of this thesis has been, is being, or shall be submitted for a higher degree at any other University.

R. Palmer

R. W. Palmer
November, 1991.

CONTENTS

ABSTRACT

This thesis examines the extent and intensity of the effects of impoundments on selected physical, chemical and biotic conditions in an impounded southern African river. Life-history characteristics and environmental requirements which determine the success of impoundment-outlet blackflies in southern Africa were studied. Difficulties with the identification of immature blackflies led to a search for additional diagnostic characters, the description of larvae of seven species previously unknown, and the development of new keys to the species of *Simulium* (larvae and pupae) in southern Africa. Distribution records for each species are presented, and their ecology is summarised. Three pairs of closely related species, which were formerly indistinguishable, can now be recognised by differences between the structure of their cephalic fan microtrichia.

Monthly physical, chemical and invertebrate samples at 16 sites upstream and downstream of four impoundments in the Buffalo River, eastern Cape, were taken over a period of two years. The downstream effects of impoundments on these parameters depended on the variable examined, the position of the impoundment along the river profile, the depth from which water was released, and the quality of the inflowing water. Impoundments in the Buffalo River caused an upstream shift of the thermal and suspended organic conditions, and the distribution of blackfly species. Surface-release impoundments in the clean, upper-reaches of the river caused increases in water temperature (by as much as 8°C) and chlorophyll *a* (by as much as 600%). Recovery to riverine conditions was within 2.6 to 18.4 km, depending on flow. A polluted, surface-release impoundment in the middle-reaches of the river had a slight dampening effect on river temperatures, converted the particle size spectrum of the river from small (<80 μm) to large (250-1000 μm), and improved the water quality of the downstream reaches (with the exception of nitrate concentrations, which were higher in the tailwaters compared to inflowing water). An impoundment in the lower reaches caused reductions in maximum temperature of up to 6°C when releasing water from the surface, and up to 16°C when releasing water from the bottom. Bottom-released water carried high concentrations (36 to 190 g m^3) of small (<5 μm) and largely inorganic (86 to 93%) material.

Twenty species of blackflies were found in the Buffalo River, of which 18 were distinguishable as larvae. They were divided into those which were widespread (5 taxa), those restricted to waterfalls and mountain torrents (2 taxa), those found in the foothill stony run zone (6 taxa), and rare taxa (5 taxa). Impoundments in the Buffalo River did not alter population densities of blackfly larvae, but did alter blackfly species composition, favouring five species commonly found in mid-order streams in southern Africa (*S. meduseaforme*, *S. hargreavesi*, *S. nigritarse*, *S. adersi* and *S. damnosum* s.l.) at the expense of upper-reach species (*S. rutherfoordi*, *S. letabum* and *S. impukane*). These five species are regarded as typical of impoundment-outlets, and were small, multivoltine flies whose larvae shared a generalised cephalic fan microtrichial structure, consisting of a single row of moderately differentiated microtrichia. A strong relation was found between cephalic fan microtrichial structure and larval habitats: Taxa found in fast-flowing, clear water had a more complex fan structure compared to those found in slow-flowing, turbid water. It is concluded that impoundment-induced changes to hydrodynamics and transported material (food) are important factors which have changed the distribution of blackflies in southern Africa in recent times. These changes are more severe downstream of upper-reach impoundments than middle or lower-reach impoundments.

1 GENERAL INTRODUCTION

The distribution of animals in time and space is the product of a long history of chance and survival. Changes in the environment, as a result of the rapidly increasing human population, have led to widespread changes in species distribution, composition and abundance (MacDonald et al., 1986). Such changes are useful for understanding underlying biological processes, upon which management decisions can be based.

In southern Africa the human population is increasing at an estimated 2.7% per annum, and demands for water are increasing proportionately (Department of Water Affairs, South Africa, 1986: 9.10; Huntley et al., 1989). Natural freshwater lakes and good groundwater supplies are scarce in southern Africa, with the result that the rivers are heavily exploited (O'Keeffe, 1989). Limnological research in southern Africa has shifted emphasis from largely taxonomic studies up until the 1950's, to broad-based ecological investigations of a few selected rivers (Berg, Vaal, Jukskei-Crocodile, Eerste, Tugela), eutrophication problems in impoundments (Hartbeespoort Dam and others) and river management (reviewed by O'Keeffe, 1990). These changes in research emphasis reflect changes in the economic importance of water availability: Fresh water is fast becoming a commodity which has good 'investment potential', given the limited supply and increasing demand. Most major rivers in southern Africa have been impounded (Davies, 1979), and together these impoundments store 40-50% of the mean annual runoff (Allanson & Rabie, 1983; Department of Water Affairs, South Africa, 1986).

The consequences of impounding rivers have received considerable

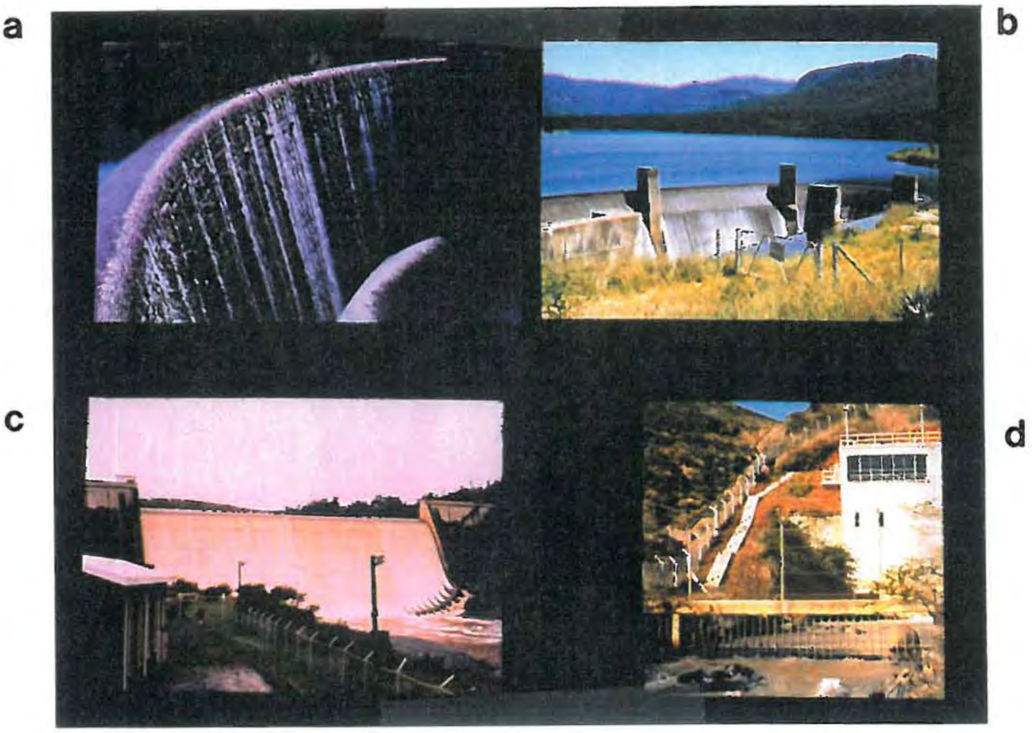

Fig. 1.1 Impoundments in the Buffalo River, eastern Cape: **a**, Maden Dam (B1) during overflow. **b**, Rooikrans Dam (B2) during overflow. **c**, Laing Dam (B3) in spate. **d**, Bridle Drift Dam (B4) showing low-level outlet.

Fig. 1.2 *Simulium medusaeforme* larval head showing extended cephalic fans used in feeding. Each fan consists of about 50 primary rays which bear one or two rows of microtrichia.

attention in the world media since the construction of large-sized dams, which began in the 1950's (Petts, 1984). Major problems include the relocation of people, the spread of diseases, sedimentation, earthquakes and flooding (Balon, 1978; Petts, 1984). These issues have been addressed by the scientific community, resulting in numerous publications on the effects of impoundment in recent years (see reviews by Ward, 1976a; Baxter 1977, 1985; Baxter & Glaude, 1980; Lillehammer & Salviet, 1982; Ward & Stanford, 1983; Petts, 1984; Walker, 1985; Craig & Kemper, 1987; Boon, 1988). The bulk of dam-impact studies have been undertaken in North America and Europe. A current debate in stream ecology is whether the findings on such systems can be usefully applied to rivers in Australia and southern Africa, which are unpredictable, warm and turbid by comparison (Winterbourne et al., 1981; Alexander, 1985; Lake et al., 1985). With the exceptions of the Nile River in the vicinity of the Aswan High Dam (Baxter, 1977; Mancy 1979; Ramadan, 1979), and the Zambezi River in the region of the Cabora Bassa Dam (Davies, 1975), little is known about the effects of impoundments on African rivers (Davies, 1979).

In 1986 the Institute for Freshwater Studies at Rhodes University, and the Freshwater Research Unit at the University Cape Town, initiated a three year research programme to investigate the downstream ecological effects of impoundments in different parts of southern Africa. The multiply-impounded Buffalo River, eastern Cape, and the Palmiet River, south-western Cape, were selected as study sites by the respective institutions. The Buffalo River has four mainstream impoundments (Fig. 1.1), two of which are situated in the near-pristine upper catchment, and two of which are situated in the degraded middle and lower reaches. The river provides a wide range of conditions where the downstream effects of impoundments of different sizes, in different parts of a river and with different water release mechanisms, may be studied.

A common feature of impoundment [and lake] tailwaters worldwide, is the development of dense populations of filter-feeding invertebrates, particularly blackfly larvae (Sheldon & Oswood, 1977; Wotton, 1987a & b; Einarsson 1988; Morin & Peters, 1988). Blackflies which inhabit impoundment and lake outlets are usually restricted to a few typical 'outlet' taxa, and are replaced by 'riverine' taxa with distance downstream (Carlsson et al., 1977; Wotton, 1987a & b). This thesis forms part of the main Buffalo and Palmiet River Research Programme, and is primarily concerned with the effects of impoundment on the downstream reaches of the Buffalo River, and particularly, on blackfly distribution. Blackflies were chosen for study because of their well-known association with impoundments, and because their larvae were found at high population densities (up to 146 000 m^{-2}) in rapids throughout the Buffalo River. Furthermore, most ecological studies of blackflies in southern Africa have focused on the pest *S. chutteri** [See Begemann (1986), Car & de Moor (1984), Chutter (1963, 1967, 1968, 1969, 1970), Coetzee (1982), de Moor (1982a & b, 1983, 1986), Howel et al., 1981), and Jordaan & van Ark (1990)], and little is known about the other species. Steenkamp (1972) assessed the economic importance of blackflies on Agriculture along the Vaal River, and found that blackflies caused a 30-50% reduction in milk production, and 10-15% reduction in fowl egg production. Chutter (1972a) surveyed the blackflies in the Great Fish River before and after a drought, and found that *S. nigritarse* s.l. was the most common blackfly, and that *S. chutteri* and *S. gariepense* appeared once the drought had been broken. Chutter (1972b) described the

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* Authors names to all species of Simuliidae in southern Africa are provided in Appendix A.

oviposition, eggs, development times and cannibalism of *S. nigritarse* s.l.. The bionomy of common blackflies in southern Africa were described by Begemann (1980a & b, 1986), and the energetics of *S. medusaeforme/hargreavesi* in the Buffalo River, eastern Cape, were studied by Scott (1990).

The building of the P. K. le Roux Dam in the Orange River has created ideal conditions for the pest *S. chutteri* for over 1000 km downstream. Likewise, the introduction of Orange River water into the Great Fish River has changed that blackfly species composition from several non-pest species to a dominance of *S. chutteri* (O'Keeffe & de Moor, 1988). The reasons for these changes are poorly understood. Blackflies are generally opportunistic, and have rapid development times and large numbers of eggs (de Moor, 1989). High population densities imply optimal conditions, and impoundment and lake outlets provide an opportunity of studying important factors which may influence the distribution and abundance of blackflies.

Impoundments cause a number of changes in rivers which may be judged *a priori* as important to downstream inhabitants. Firstly, impoundments alter the natural hydrodynamics of rivers by regulating the flow, creating short-term flow pulses, or reducing natural flow fluctuations by releasing set quotas of water as required by downstream users. Flow is important to blackfly larvae because velocity dictates the rate at which microseston (food) flows past the cephalic fans (Kurtak, 1973, 1978; Chance, 1977). Furthermore, flow is important because it influences habitat availability. High population densities of blackfly larvae in impoundment tailwaters have been attributed to stable and predictable flow conditions (Valett & Stanford, 1987; Ward & Stanford, 1983), and favourable hydrodynamic conditions created by spillway architecture (Quelennec et al., 1968).

Impoundments also reduce the annual temperature range of the receiving stream by reducing summer temperatures and elevating winter temperatures (Pearson et al., 1968; Hilsenhoff, 1971; Lehmkuhl, 1972). In addition, diurnal temperatures in impoundment tailwaters tend to be more stable than temperatures in natural river systems (Lavis & Smith, 1972; Hannan & Young, 1974; Ward, 1974, 1976b; Armitage, 1976). The importance of temperature to biological processes, particularly to poikilotherms such as blackfly larvae, is axiomatic (Vannote & Sweeney, 1980; Sweeney et al., 1986). Increases in temperature have been shown to *increase* larval feeding rates (Mulla & Lacey, 1976; Lacey & Mulla, 1979; Morin et al., 1988a), *reduce* filtration efficiencies (Kurtak, 1978), and affect the size and development rates of blackfly larvae (de Moor, 1982a).

Impoundments have a significant effect on the water chemistry of the downstream reaches, particularly when water is released from low-level outlets (Ward, 1975a; Petts, 1984; Walker, 1985). The influences of water chemistry on the distribution of immature blackflies are not well known (Ross & Merritt, 1987), but pH, conductivity and ammonium have been shown to be important (Grunewald, 1976; 1981).

Impoundments alter the suspended particle (food) spectrum of the receiving stream. Armitage (1977) found that 91% of the particulate matter entering Cow Green Reservoir sank. Bottom-released water therefore carried more suspended material than water released from the surface. Water from deep withdrawal systems is often low in POM (Gore, 1977; Ward, 1974, 1976b), although high in nutrients (Spence & Hynes, 1971). Surface-released water, on the other hand, tends to support seasonal blooms of algae and microcrustacea, and may have higher POM fractions than inflowing water (Ward & Stanford, 1983). High densities of blackflies in impoundment and lake tailwaters have been attributed to nutrient-rich seston generated within the impoundment or lake

(Chutter, 1967; Hynes, 1970a; Armitage, 1976; Carlsson et al., 1977; Wotton, 1978a & b, 1979; Richardson, 1984; Morin & Peters, 1988); Other factors which have been implicated include the ingestion of faeces egested by larvae upstream (Wotton, 1979), and the termination of upstream flight of adult females, resulting in aggregation at spillways (Carlsson et al., 1977).

Ward and Stanford (1983) provide a general theory, the Serial Discontinuity Concept (SDC), which predicts the downstream effects of impoundments. The concept assumes the validity of the River Continuum Concept (RCC) of Vannote et al. (1980), and suggests that dams disrupt the natural continuum of physical, chemical and biotic changes down an impounded river. Ward and Stanford (1983) suggest that dams shift variables longitudinally upstream or downstream (the 'discontinuity distance'), and that the type of shift depends on the position of the dam along the river profile. As the river progresses downstream from the dam, riverine conditions are restored as a result of natural processes and tributary inflows. For example, they predict that nutrient availability (with the possible exception of nitrates) will be unaffected by dams in the upper and middle reaches (to sixth order streams), but will be increased by impoundment of larger rivers, due to 'increased clarity and substrate stability'. The SDC provides a useful tool for predicting the likely effects of a proposed impoundment. The SDC assumes that there are no perturbations in the catchment other than impoundment. There are few rivers left today which have not been in some way modified (particularly in their mid- and lower reaches), and this raises the question of how applicable the SDC is to disturbed river systems.

The aims of this thesis were to:

1. Examine the effects of impoundments on the physical and chemical characteristics of a southern African river,

2. Examine the effects of impoundment on the distribution and abundance of blackflies in a southern African river,

3. Identify biological characteristics and environmental requirements which determine the success of impoundment-outlet blackflies in southern Africa.

In order to achieve these aims, it was necessary to identify the aquatic stages of blackflies accurately. Keys to African blackflies (Freeman & de Meillon, 1953; Crosskey, 1960b, 1969) are now dated, and could not be used with confidence. For many species of blackflies in Africa, the adults and pupae are described, but the larvae are unknown. With the exceptions of detailed studies on the *Simulium damnosum* complex in West Africa*, there have been few taxonomic studies of African blackflies since Freeman and de Meillon's (1953) publication and Crosskey's (1969) revision. Car (1983a) described the larvae of *S. gariepense*, Elsen (1984) described the

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* Detailed taxonomic studies using chromosomes, cuticular hydrocarbons, morphometrics and DNA hybridization on the pest *S. damnosum* complex in West Africa have been undertaken (Dunbar, 1966, 1969; Vajime & Dunbar, 1975; Meredith & Townson, 1981; Elouard, 1978; Garms, 1978; Quillevere & Sechan, 1978; Dang & Petersen, 1980; Dunbar & Vajime, 1981; Petersen & Dang, 1981; Meredith et al., 1983; Phillips et al., 1985; Crosskey, 1987b; Elsen & Post, 1989).

larvae of *S. rotundum* and Fain and du Jardin (1983) revised the taxonomy of the *S. nigritarse* complex, based largely on pupal morphology. The most detailed keys to African blackflies are in Freeman and de Meillon (1953; adults & pupae only), Crosskey (1960b: larvae from West Africa) and Crosskey (1969: all stages to Subgenus & group level). Certain characters on which these keys are based have been shown to be variable or redundant. For example, some species may build both shoe- or slipper-shaped cocoons (Disney, 1970; Lewis & Raybould, 1974b), and the presence or absence of hairs on the pleural membrane is sometimes variable. [A specimen from the Buffalo River, eastern Cape, (*S. dentulosum*: Cat. BRSO 350e) had pleural membrane hairs on the right-hand side but was bare on the left-hand side.] Similarly, the larval key to the Subgenus *Pomeroyellum* in Crosskey (1969: 43) no longer works because not all African *Pomeroyellum* larvae have negative head-patterns.

A priority of this thesis was therefore the development of keys to the identification of blackflies in southern Africa. This involved describing previously undescribed larvae, and the search for useful diagnostic characters. Peterson and Dang (1981) list the morphological characters which are used in descriptions of blackflies. With few exceptions, blackfly larvae feed by modified premandibular appendages (cephalic fans) with which they remove small suspended and dissolved material from the water column (Fig. 1.2; Mulla & Lacey, 1976; Craig, 1977a; Wotton, 1977, 1982b; Colbo & Wotton, 1981; Chance & Craig, 1986; Wotton, 1990). Studies which have examined blackfly larval cephalic fan structure conflict in their conclusions: some found only slight structural differences between species (Chance 1970; Nübel 1984), whereas others found that fan structure may be useful in separating closely related species (Yankovskiy 1977), and that fan structure may influence larval habitat preferences (Lewis 1953;

Carlsson 1962; Kurtak 1978). This thesis examines the use of microtrichial structures of cephalic fans as a potential taxonomic character.

The thesis is based on the assumption that the distribution of blackflies is determined by the survival of aquatic stages, rather than that of adults. Catchment development and the introduction of domestic animals (sheep & cattle) into southern Africa since 2000 BP, may have affected adults (and therefore distribution) of certain species by changing host distribution, and disrupting cues for oviposition (Colbo & Wotton, 1981). However, the association of blackflies with river regulation indicates the importance of the aquatic environment to their distribution. Furthermore, adults are not usually host-specific (Rubtsov, 1956), and are easily dispersed by winds (Garms et al., 1979; Johnson et al., 1985), whereas the aquatic stages are less mobile (other than during floods), and their survival depends on suitable water conditions (Rubtsov, 1956).

This thesis begins by describing the physical and chemical conditions of the Buffalo River, paying particular attention the downstream effects of impoundments on flow (Chap. 2), water temperature (Chap. 3), water chemistry (Chap. 4) and transported material (Chap. 5). The taxonomy of the aquatic stages of all blackflies which are known south of (and including) the Orange and Limpopo River catchments is then revised (Chap. 6), to enable a more detailed assessment of the response of blackfly taxa to environmental changes. This is followed by a detailed study of the distribution and abundance of blackflies in the Buffalo River (Chap. 7). The final chapter (Chap. 8) summarises the distribution and ecology of blackflies in southern Africa, and aims to identify the life-history characteristics and environmental requirements which determine the success of impoundment-outlet species.

A basic tenet of this thesis is that an understanding of the ecological processes which govern river systems, and the responses of aquatic organisms to changing environmental conditions, is fundamental for the conservation and management of our rapidly diminishing fresh water resources. I have therefore tried to interpret the results presented here in terms that will provide predictive understanding of the consequences of impoundments, so that future impoundments can be built and managed so as to minimise environmental disturbances.

2 STUDY AREA

2.1 SOUTHERN AFRICA

Southern Africa south of, and including, the Orange and Limpopo River catchments (Fig. 2.1), covers an area of roughly 1,75 million km^2, most of which (over 85%) is over 1000 m above sea level. The most prominent geographical feature is the Drakensberg Mountain range, with peaks over 3 200 m in altitude. These mountains form the primary watershed which divide the subcontinent into a wet (>500 mm MAP) eastern region, with short, fast-flowing rivers, and a dry (<500 mm MAP) central and western region, drained by the Orange/Vaal River system (Noble & Hemens, 1978; Alexander, 1985; Davies & Day, 1986).

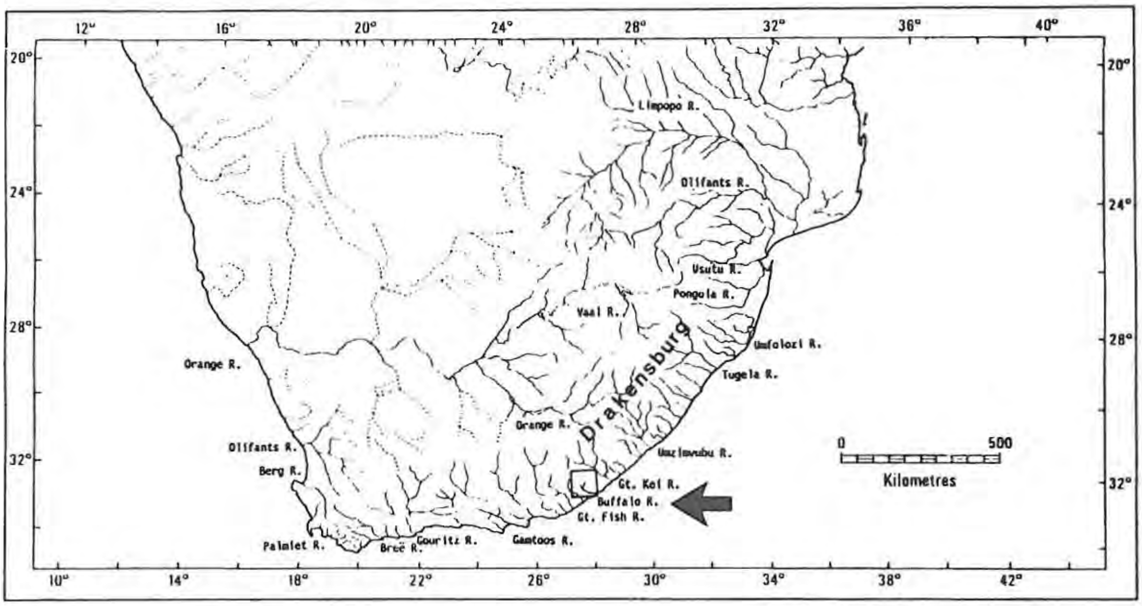

Fig. 2.1 Map of southern Africa showing major rivers, the Drakensburg Mountains, and the location of the Buffalo River, eastern Cape, indicated by an arrow.

2.2 THE BUFFALO RIVER

The Buffalo River is situated in the eastern Cape (Fig. 2.1). The river rises in near-pristine indigenous forest of the Amatola Mountains at an altitude of 1 300 m, flows through the urban and industrial complex of Kingwilliamstown and Zwelitsha, and enters the sea at East London (32° 02'S, 27° 45'E) as a fourth order stream (*sensu* Strahler, 1957; Fig. 2.2). The river is 140 km long, and is divisible (*sensu* Harrison & Elsworth, 1958) into a mountain source zone, a mountain torrent zone (Site 0), an upper foothill stony run zone (Sites 1, 2b & 2c), and a lower foothill stony run zone (Sites 3 to 13; Fig. 2.3). The catchment area of 1 230 km^2 consists primarily (78%) of easily erodable Beaufort Series sandstones and mudstones, intersected by more resistant doleritic intrusions which are more common in the upper catchment (Haughton, 1969). The river drops rapidly in the first 6 km (200 m km^{-1}); thereafter the gradient is less steep (3 to 13 m km^{-1}; Fig. 2.4).

Following the Köppen classification, the climate of the region is warm temperate (Cfwb in the upper catchment* and Cfbl in the lower catchment; Schülze, 1965). Snow falls occasionally in the upper catchment in winter (usually lasting no longer than four days).

The upper reaches of the river receive relatively high rainfall (2 000 mm per annum), 68% of which falls in summer, whereas the mid- and lower reaches receive considerably less (500 mm per annum; Department of Environment Affairs, South Africa, 1986).

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* Unless otherwise stated, the following terms are used in a general sense to demarcate boundaries in the Buffalo River:

upper reaches:	Sites 0 to 2c
mid-reaches:	Sites 3 to 8
lower reaches:	Sites 9 to 13

Evergreen closed-canopy [Afromontane] forest in the upper reaches gives way to dense closed-canopy vegetation dominated by the invasive black wattle, *Acacia mearnsii* de Wild, in the first 26 km of the river (Site 2b to 7). Thereafter, the river is mainly open, although dense stands of the grass *Miscanthus capensis* (Nees) are common in shallow water between Sites 6 and 8. The palm *Phoenix reclinata* Jacq. and the sedge *Cyperus textilus* Thunb. are common in the lower reaches of the river. Macrophytes and epilithic algae are rare, with the exception of *Matricaria nigellifolia* Dc., which grows in shallow, quiet pools between Sites 2b and 13. Most of the catchment consists of open savanna, termed 'Valley Bushveld' by Acocks (1975), and is used for extensive agriculture (Fig. 2.4). Relic floodplains upstream of Kingwilliamstown (Sites 6 to 7) are used for intensive market gardening.

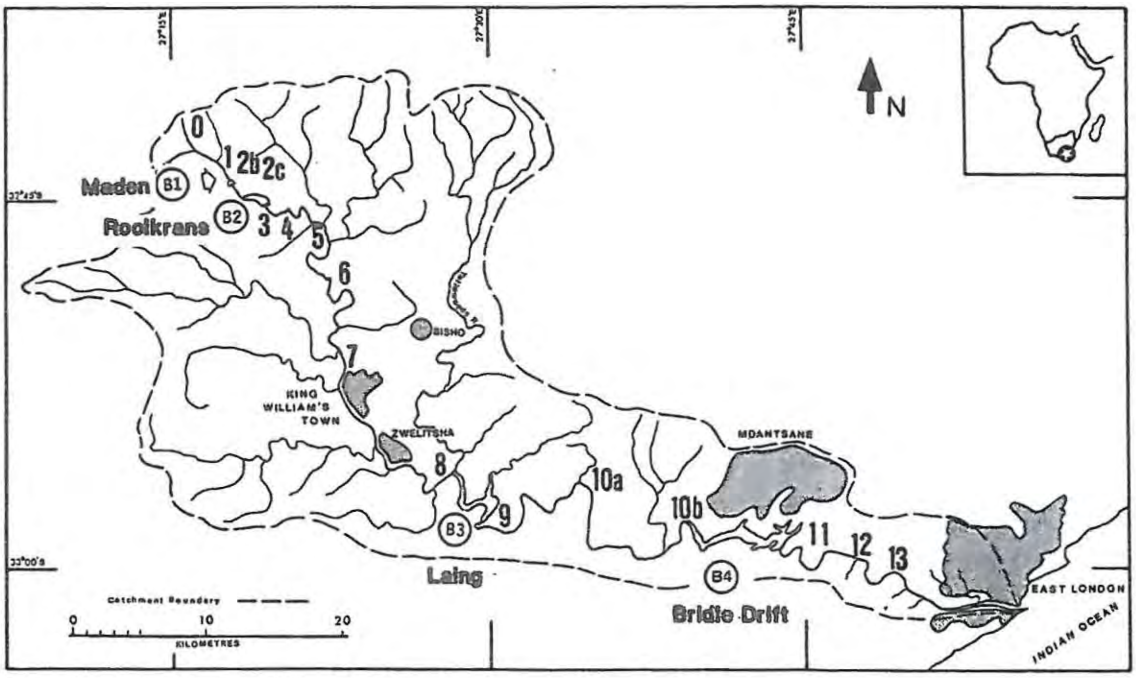

Fig. 2.2 Map of the Buffalo River showing the four impoundments (B1 to B4), the sampling sites (0 to 13), and the main sources of pollution: Kingwilliamstown, Zwelitsha and Mdantsane.

Fig. 2.3 Zonation of the Buffalo River (*sensu* Harrison & Elsworth, 1958): **a**, mountain torrent zone (Site 0). **b**, upper foothill stony run zone (Site 1). **c**, lower foothill stony run zone, closed canopy (Site 6). **d**, lower foothill stony run zone, open canopy (Site 10a).

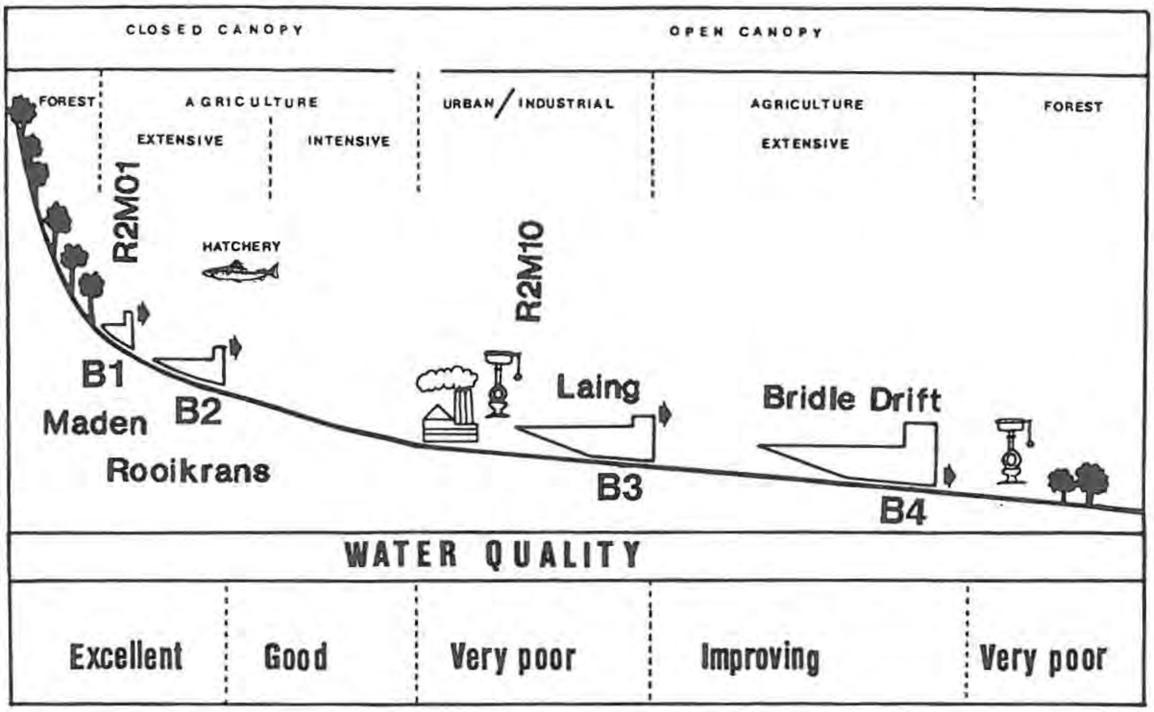

Fig. 2.4 Profile of the Buffalo River, showing catchment land-use and overall water quality. The positions of impoundments (B1 to B4) and gauging wiers (R2M01 & R2M10) are indicated.

2.3 STUDY SITES

Sixteen sites where there were stones-in- current (and water was noisy) were chosen as regular sampling sites (detailed in Appendix B). The reasons for their choice were as follows:

1. Stones-in-current represent a relatively standardised biotope (*sensu* Udvardy, 1959) so that comparisons could be made between sites.

2. Stones-in-current are typical blackfly habitat.

3. They provided a wide range of conditions, from the near-pristine headwaters to polluted reaches near the estuary, so that the

changes along the entire river could be studied.

4. They were positioned up- and downstream of impoundments, so that inferences could be made regarding the effects of impoundments.

5. They were accessible enough to allow regular sampling.

Sites were visited at roughly monthly intervals between June 1986 and April 1988. Each sampling trip took three days. Sampling sequence was not consistent between visits so as to reduce bias from regular daily variation (such as temperature and drift).

2.4 FLOW IN THE BUFFALO RIVER

Discharge data from the two gauging wiers in the river (R2M01 at Site 1, and R2M10 at Site 8) were supplied by the Department of Water Affairs, Pretoria. At an additional nine sites, discharges were calculated on each visit by means of the velocity-area method (Ward, 1975b), using an Ott^R current meter at 50 cm intervals across the river. In this thesis, 'high flow' refers to times when dams upstream of sampling sites were overflowing, and 'low flow' refers to times when they were not overflowing. Flow during the study period followed the typical seasonal pattern, with low flow in winter (June to August; median of 0.012 m^3s^{-1} at Site 1 and 0.125 m^3s^{-1} at Site 8) and high flow in summer (December to February; 1.0 m^3s^{-1} at Site 1 and 3.9 m^3s^{-1} at Site 8; Figs. 2.5 & 2.6). In November 1985 (just before this study began), there was a flood during which flows exceeded 9 m^3s^{-1} at Site 1, and 50 m^3s^{-1} at Site 8.

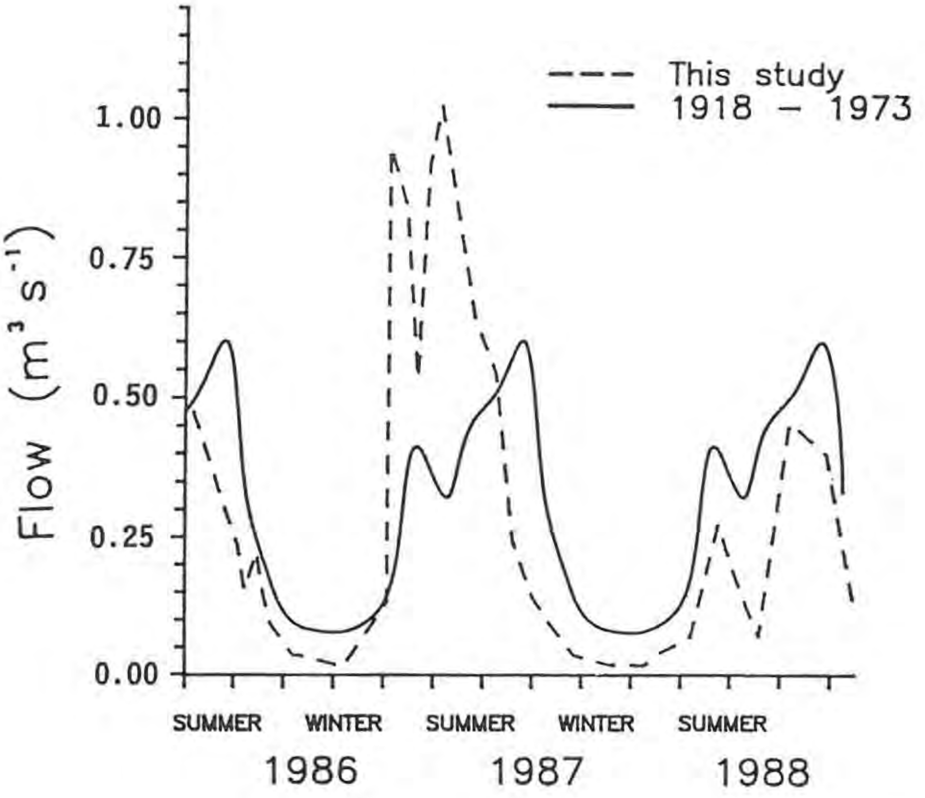

Fig. 2.5 Mean discharge at gauging weir R2M01 (Site 1) in the Buffalo River measured between 1918 and 1973 (———), and during the study period 1986 to 1988 (- - -).

2.5 IMPOUNDMENTS IN THE BUFFALO RIVER

Specifications of the four mainstream impoundments in the Buffalo River are shown in Table 2.1. Maden and Rooikrans (referred to as B1 & B2 respectively), are surface-releasing impoundments in the foothills of the Amatola Mountains (Figs. 1.1a & b). Maden (B1) receives runoff from a near-pristine, forest catchment. A distance of 1.4 river km separates Maden (B1) from the upper reaches of Rooikrans (B2). Forty-five river km separates Rooikrans (B2) from the upper reaches of Laing (B3), providing the longest stretch of unimpounded river in which to detect recovery distances. Laing (B3) (Fig. 1.1c) is a surface-releasing impoundment which receives treated sewage and industrial effluent from the urban and industrial complex of Kingwilliamstown and Zwelitsha (Fig. 2.4). The largest tributary in the catchment, the Yellowwoods River, joins the Buffalo River at Laing (B3) (Fig. 2.2). The largest impoundment, Bridle Drift (B4; Fig. 1.1d), is situated 37 river km downstream of Laing (B3). The river between Laing (B3) and Bridle Drift (B4) is bordered by steep hills and was accessible in three places only (Sites 9, 10a & 10b; Fig. 2.2).

Table 2.1 Specifications of the four impoundments (**B1** to **B4**) in the Buffalo River.

Impoundment	Maden (**B1**)	Rooikrans (**B2**)	Laing (**B3**)	Bridle Drift (**B4**)
Distance from sea (km)	137	134	65	24
Altitude (m)	525	518	310	109
Capacity $10^6 m^3$	0.32	5.43	22.08	75.47
M.A.R. $10^6 m^3$	8	11	51	114
Median discharge ($m^3 s^{-1}$)	0.06	0.05	0.3	1.0
Compensation flow ($m^3 s^{-1}$)	0	0.04	0	0.5
Catchment area (km^2)	31	48	913	1176
Height of wall (m)	10	13	25	47
Release type (Surface or Bottom)	S	S	S	S/B
Year built	1910	1953	1951	1968

Water from Maden (B1) was in great demand in the populated middle catchment because of its high quality, with the result that Maden (B1) was often reduced to low levels during dry winter months. A trout hatchery situated directly downstream of Rooikrans (B2) received water from the the surface of Rooikrans (B2) and discharged it to the river downstream of Rooikrans (B2) (Fig. 2.4).

When Rooikrans (B2) overflowed, water was discharged from a spillway in addition to the trout hatchery, but when Rooikrans (B2) was not overflowing, the trout hatchery ensured a continuous flow of 0.04 m^3s^{-1} (0.02 to 0.06 m^3s^{-1}) to the river.

Bridle Drift (B4) received overspill from Laing (B3), and differed from the other three impoundments in that it released water from a low-level outlet (situated 47 m below the top of the wall) when not overflowing. A continuous flow of at least 0.5 m^3s^{-1} was discharged from Bridle Drift (B4), and flowed to a weir 7 km downstream (Site 12), from where it was pumped to provide water for the towns of Mdantsane and East London. The river downstream of the weir at Site 12 was maintained by a leak which ensured a continuous flow of at least 0.003 m^3s^{-1}. Further downstream (Site 13), the river flowed more strongly because of inflow from the Mdantsane sewage works (Fig. 2.4).

The river remained perennial for most of its length, with the exceptions of Site 0, which dried up in winter, and immediately downstream of Maden (B1) and Laing (B3), when these impoundments stopped overflowing. This occurred when the inflow to Maden (B1) and Laing (B3) dropped below 0.1 and 0.5 m^3s^{-1} respectively (Fig. 2.6). Under these conditions, the river directly downstream of these impoundments was maintained by seepage (<0.005 m^3s^{-1}) from the impoundments. By contrast, the river downstream of Rooikrans (B2) and Bridle Drift (B4) experienced unaturally stable flow conditions because of compensatory releases (Fig. 2.6). Likewise, industrial and urban effluent from the Kingwilliamstown/Zwelitsha area ensured a continuous flow at Site 8.

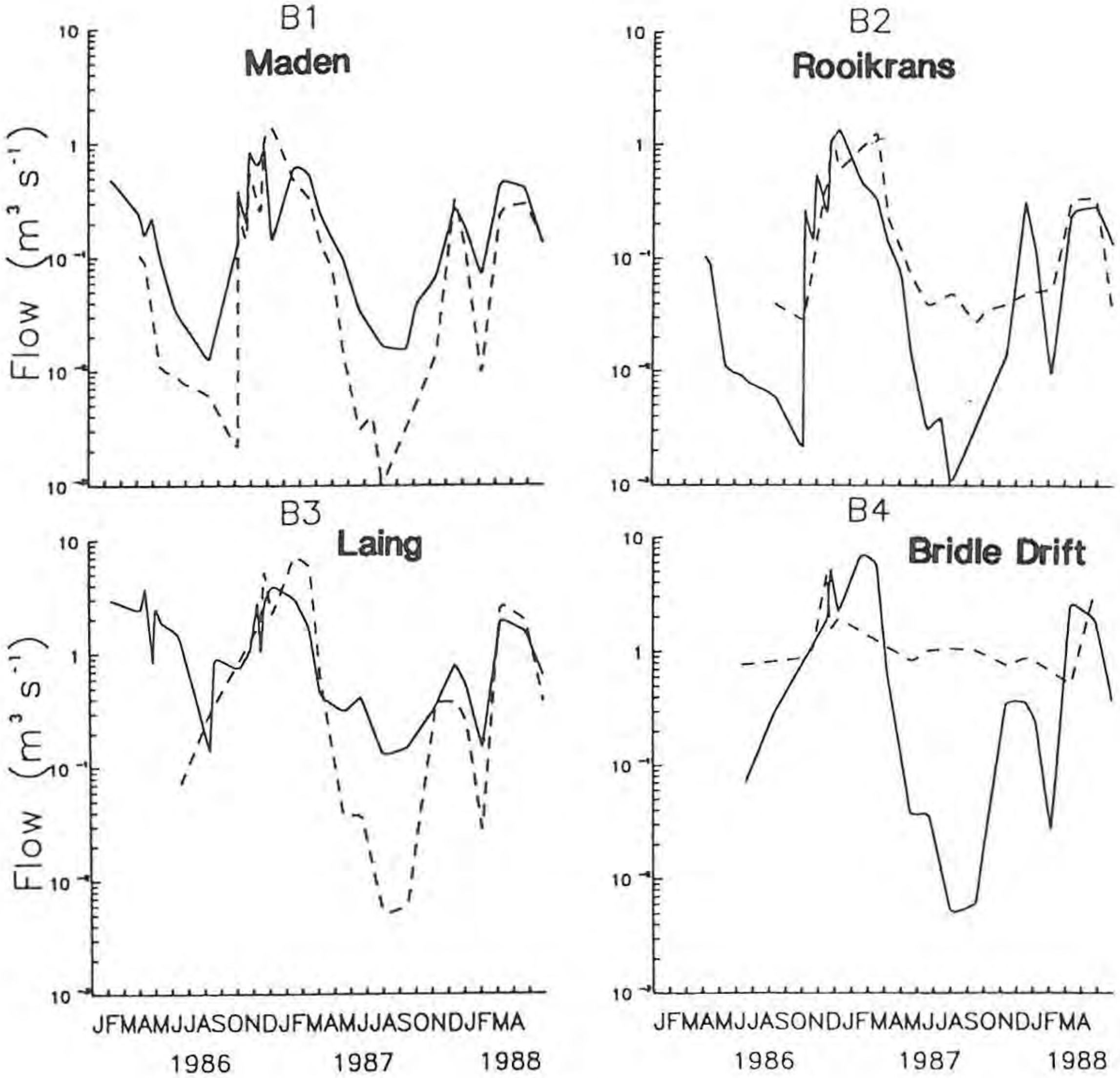

Fig. 2.6 Discharge upstream (————) and downstream (- - -) of the four impoundments in the Buffalo River measured monthly between January 1986 and April 1988. Impoundments B2 and B4 (Rooikrans and Bridle Drift) released compensatory flow throughout the year, whereas B1 and B3 (Maden and Laing) did not release water during low-flow periods.

3 WATER TEMPERATURE

3.1 INTRODUCTION

Seasonal and spatial changes in river water temperature are important determinants of the distributions and abundances of aquatic biota (Macan, 1961, 1974; Stuckenberg, 1969; Hynes, 1970a & b; Moss, 1980; Merritt et al., 1982; Vannote & Sweeney, 1980; Sweeney, et al., 1986). Despite the importance of water temperature to the ecology of river systems, very little information is available on river temperatures in southern Africa (Ward, 1985). This is surprising considering the ease by which temperature can be recorded. Air temperatures measured at meteorological stations have been successfully used to predict average river temperatures (Nishizawa & Yamabe, 1970; Crisp & Howson, 1982), and have correlated well with the distribution of certain species [e.g., schistosome species (Pitchford, 1981), frogs (Poynton, 1962, 1964), and shelduck (Geldenhuys, 1981)]. However, inaccuracies arise with this method when the meteorological station is some distance from the river, or when the river is predominantly spring fed, or when the river is impounded (Crisp, 1988). In addition, air temperatures do not provide information on the extremes in river temperature, which are likely to be more important than average temperatures in determining the distribution of animals. Accurate assessment of spatial and seasonal changes in temperature along rivers therefore depends on continuous instream temperature measurements.

Impoundment-induced alterations to river temperatures can be considerable (Neel, 1963; Pearson et al., 1968; Lehmkuhl, 1972; Lavis & Smith, 1972; Pitchford & Visser, 1975; Crisp, 1977; 1988; Fraley, 1979; Cowx et al., 1987) and have been implicated as one of the main factors leading to altered aquatic invertebrate populations in impoundment tailwaters (Ward, 1974; Lake & Burger, 1983; Bass & Armitage, 1987; Perry et al., 1987). Artificial temperature manipulation therefore provides a possible method for selecting, or eliminating, species from downstream reaches (Hubbs, 1972).

In southern Africa, every major river has been impounded, although the effects of impoundment on downstream temperatures have only been measured in the Orange River (Pitchford & Visser, 1975) and the Pongola River (Rogers, 1978). Neither of these studies looked at the downstream recovery of these alterations in temperature. Studies elsewhere have shown that it may take up to 100 km downstream of an impoundment for the altered temperatures to recover (Lehmkuhl, 1972; Walker et al., 1978). To measure the recovery distance, it is necessary to know the thermal conditions of the river in the absence of impoundment (the reference conditions - see 3.3). Because this is often not possible, it becomes necessary to use a theoretical framework to determine the reference conditions. A primary factor affecting the temperature characteristics of a water body is its size (and therefore stream order) (Ward, 1985). In a naturally flowing, unimpounded river, maximum temperatures usually increase downstream (Ward 1985), whereas the maximum range in temperature is usually found in the mid-reaches of a river (Vannote & Sweeney, 1980). The temperature range usually increases from the headwaters to the mid-reaches because of decreasing altitude, more open water and decreasing groundwater effects. Between the mid-reaches and the sea, however, the range usually decreases because of greater flow volume and coastal atmospheric effects. Impounding a river causes localized temperature changes which are superimposed on these natural fluctuations. The nature of these changes depend on the position of an impoundment along the river continuum (*sensu* Vannote & Sweeney, 1980), the size of the impoundment, and whether water is released over or from the bottom of the dam wall. Ward and Stanford (1983) postulated that a deep-release impoundment in the headwaters of a river would have little effect on the annual temperature range downstream, whereas such an impoundment in the mid- or lower reaches would cause a significant reduction in the annual temperature range. By contrast, small surface-release impoundments in the upper reaches of a river would be expected to increase the annual temperature range downstream. This is because of inflow of thermally buffered groundwater and shading, and increased contact with the atmosphere of surface water in the impoundment. In the more open mid- and lower reaches of a river, larger surface-release impoundments would be expected to reduce the annual temperature range downstream because of the thermal inertia of large water-bodies.

The aim of this chapter was to measure the effects of impoundments on the seasonal and spatial temperature changes along the entire length of the Buffalo River. The need to quantify the thermal effects of impoundments, and subsequent recovery, is a priority so that the ecological consequences of water resource developments may be predicted.

3.2 METHODS

Maximum-minimum mercury thermometers were placed in concrete blocks in pools, roughly at 0.5 m depth. The blocks were covered with camouflage fibreglass lids to prevent theft. Temperatures were recorded bimonthly from six sites between June 1986 and March 1987. The frequency was increased to monthly sampling at these six and a further nine sites until April 1988. Fluctuations in daily temperature were measured on 13 occasions at six sites. Low flows at Site 0 exposed this thermometer to air on all except five visits in summer. In March 1988 high flows swept seven thermometers away, but these were not replaced since the study period was nearly at an end.

3.3 MEASUREMENT OF RECOVERY DISTANCE

The following discussion of recovery distances has been taken from O'Keeffe et al. (1990), which deals with the physico-chemical effects of impoundments in the Buffalo and Palmiet Rivers.

> They [Ward & Stanford (1983)] referred to the 'discontinuity distance' as '...the longitudinal shift of a given parameter by stream regulation...'. For the purposes of the research reported here, we interpret 'discontinuity distance' as *that length of stream which is required for any parameter to recover from disruption by impoundment*, and accordingly we shall refer to *recovery distance* as a better description of the processes that occur in the receiving reaches downstream of impoundments.
>
> Ideally, to measure recovery distances, pre-impoundment conditions should be known so that natural changes along the stream may be taken into account. If such data are available then the recovery distance is the length of stream required for a particular parameter to recover to levels which prevailed in the unregulated system. Usually no such pre-impoundment data exists, and our definition has to be modified such that recovery distance becomes *that length of stream which is required for any parameter to return to values close to those measured at the inflow to an impoundment, or to achieve a new dynamic equilibrium.*

For the purposes of this thesis, data from sampling sites which were upstream of or remote from impoundments were used to define the 'natural' conditions in the river. The following sites were used:

Sites 0 and 1 - upstream of all impoundments
Sites 6, 7 and 8 - > 18 km downstream of Rooikrans (B2)
Sites 10a and 10b - > 15 km downstream of Laing (B3)
Site 12 - 7 km downstream of Bridle Drift (B4)

Conditions at all other sites were considered to be potentially affected by impoundment.

3.4 RESULTS

GENERAL TRENDS IN TEMPERATURE

Annual maximum temperatures increased from 20°C at the uppermost site (Site 0) to 35°C in the mid-reaches (Site 10a), but then decreased to 30°C in the lower reaches (Site 12; Table 3.1; Fig. 3.1). Annual minimum temperatures showed a general linear increase from 6°C in the upper reaches (Site 1) to 11°C in the lower reaches (Site 12; Table 3.1; Fig. 3.1). In winter, cold waters typical of the upper reaches extended further downstream (Fig. 3.2). For example, maximum summer temperatures exceeded 26°C at all sites except Sites 0 and 1, whereas in winter, maximum temperatures in the entire river never exceeded 22°C (Table 3.1). Changes in annual temperature range showed a trend similar to the annual maxima, increasing from 16°C in the upper reaches (Site 1) to 25°C in the mid-reaches (Sites 8 & 10a), and decreasing to 19°C in the lower reaches (Site 12; Table 3.1).

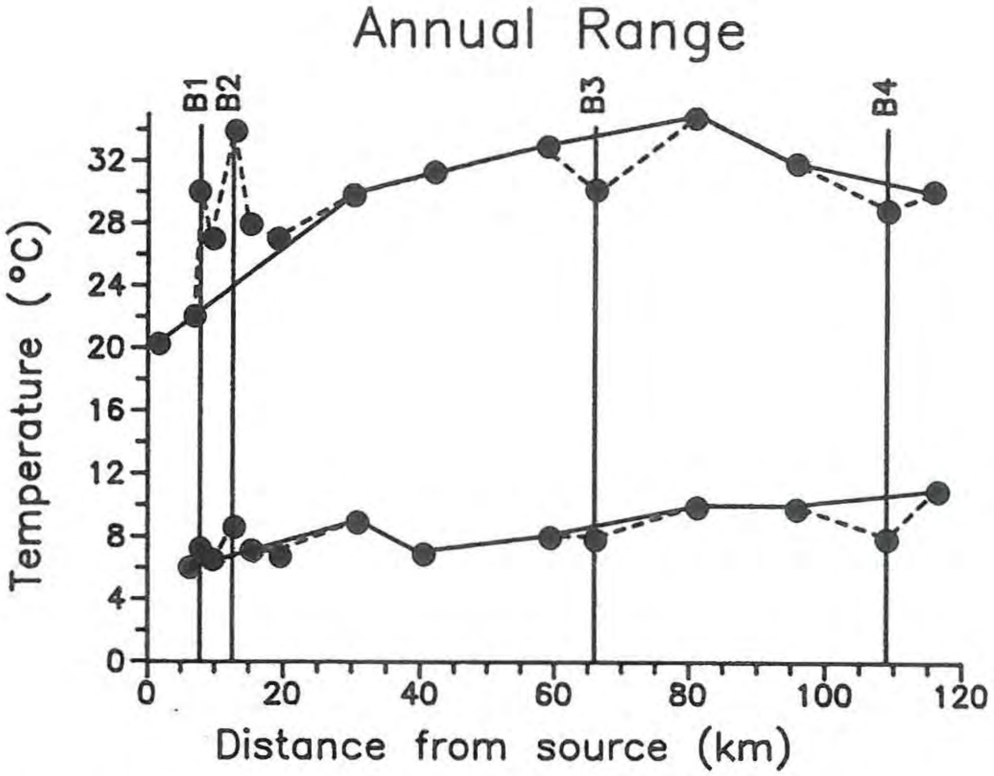

Fig. 3.1 Maximum and minimum temperatures recorded along the length of the Buffalo River. The lines (————) define natural downstream temperatures (recorded at sites which were upstream of, or sufficiently remote from, impoundments), whereas the dashes (- - -) indicate the effects of impoundments (see methods section 3.3 for a full explanation).

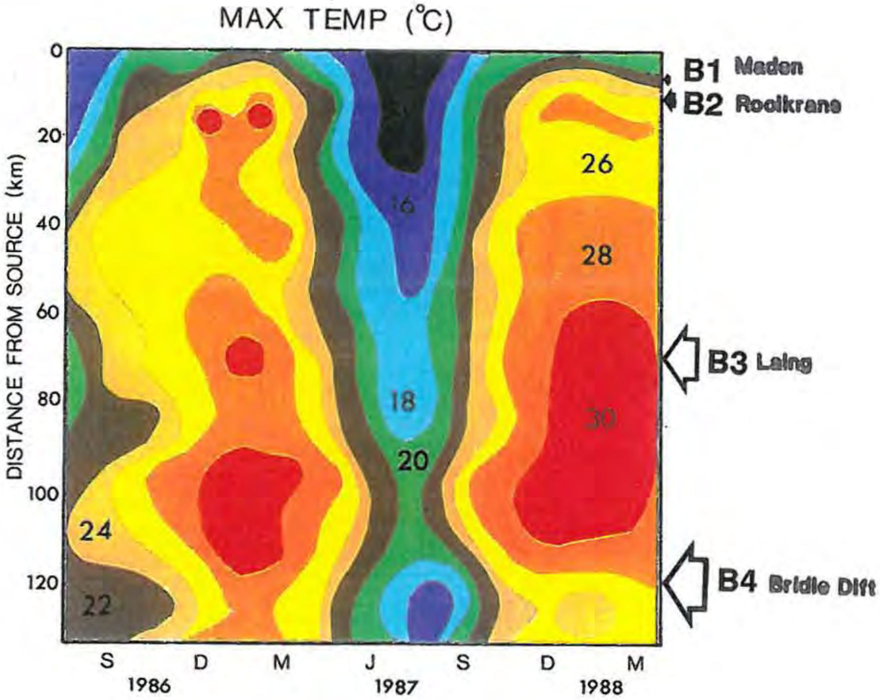

Fig. 3.2 Contour map of the maximum temperatures measured in the Buffalo River between July 1986 and April 1988. The positions of the impoundments (**B1** to **B4**) are indicated.

Figures 3.1 and 3.3 show these trends based on sampling sites least affected by impoundment as described in the methods above. The maximum spatial temperature change measured during any one month was 16°C (the difference between monthly maxima at Site 1 (15°C) and Site 10a (31°C) in May 1987 (Fig. 3.3c). This was considerably lower than the maximum seasonal temperature change at any one site (25°C at Sites 8 & 10a; Table 3.1). Seasonal temperature changes were therefore greater than downstream changes.

Table 3.1 Maximum and minimum temperatures (°C) recorded in the Buffalo River during winter and summer, together with the annual and daily temperature fluctuations (ΔT). Daily ranges were measured during summer months. The positions of the impoundments (**B1** to **B4**) are indicated, as well as the distances between each site and upstream impoundment. The type of release from Bridle Drift (B4; Site 11) is indicated in brackets (B - Bottom; S - Surface).

Site	Distance from wall (km)	Winter		Summer		Annual Range	ΔT	
		min	max	min	max			
0	-	?	?	12	20	?	-	
1	-	6	13	15	22	16	1	
								(B1)
2b	0.2	7	14	19	30	23	3	
2c	1.4	6	16	19	27	21	3	
								(B2)
3	0.3	9	15	19	34	25	2	
4	2.6	7	15	19	28	21	-	
5	6.4	7	15	19	27	20	-	
6	18.4	9	18	21	30	21	-	
7	27.1	7	16	20	31	24	-	
8	44.6	8	19	20	33	25	-	
								(B3)
9	0.5	8	19	20	30	22	-	
10a	15.5	10	22	21	35	25	-	
10b	29.0	10	21	20	32	22	-	
								(B4)
11	0.1	8(B)	15(B)	23(S)	29(S)	21	1	
12	7.0	11	20	22	30	19	5	
13	omitted							

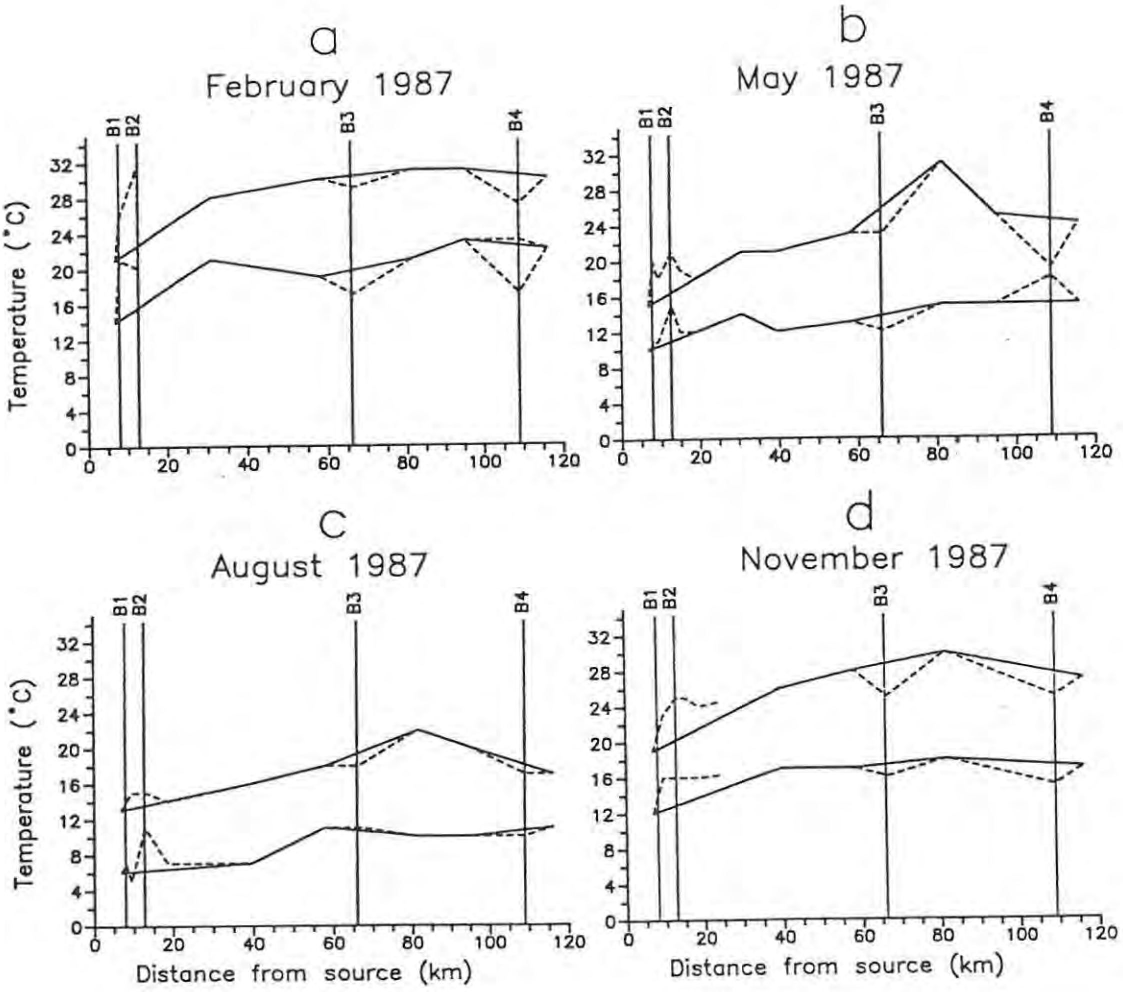

Fig. 3.3 Monthly maximum and minimum temperatures (^{o}C) recorded along the length of the Buffalo River during representative months: **a** February, **b** May, **c** August and **d** November. The positions of the impoundments (**B1** to **B4**) are indicated. The lines (______) indicate temperatures least affected by impoundments, whereas the dashes (- - -) show the effects of the impoundments (see methods section 3.3 for a full explanation). Two dashed lines in **a** are shown for minimum temperature at Bridle Drift (B4); The upper dashed line represents the temperature of water released from the surface, whereas the lower dashed line represents that of water released from the bottom of the reservoir.

Apart from temperature measurements upstream and downstream of impoundments, spot readings were also taken monthly at the inlet and outlet of the trout hatchery, downstream of Rooikrans (B2). The hatchery ponds had no significant effect on temperature (Wilcoxon matched-pairs signed-rank test, n=17, $P>0.05$). Likewise, urban and Industrial effluent from Kingwilliamstown and Zwelitsha (between Sites 7 & 8) did not cause any discontinuities in the general trends of temperature changes along the river (Table 3.1).

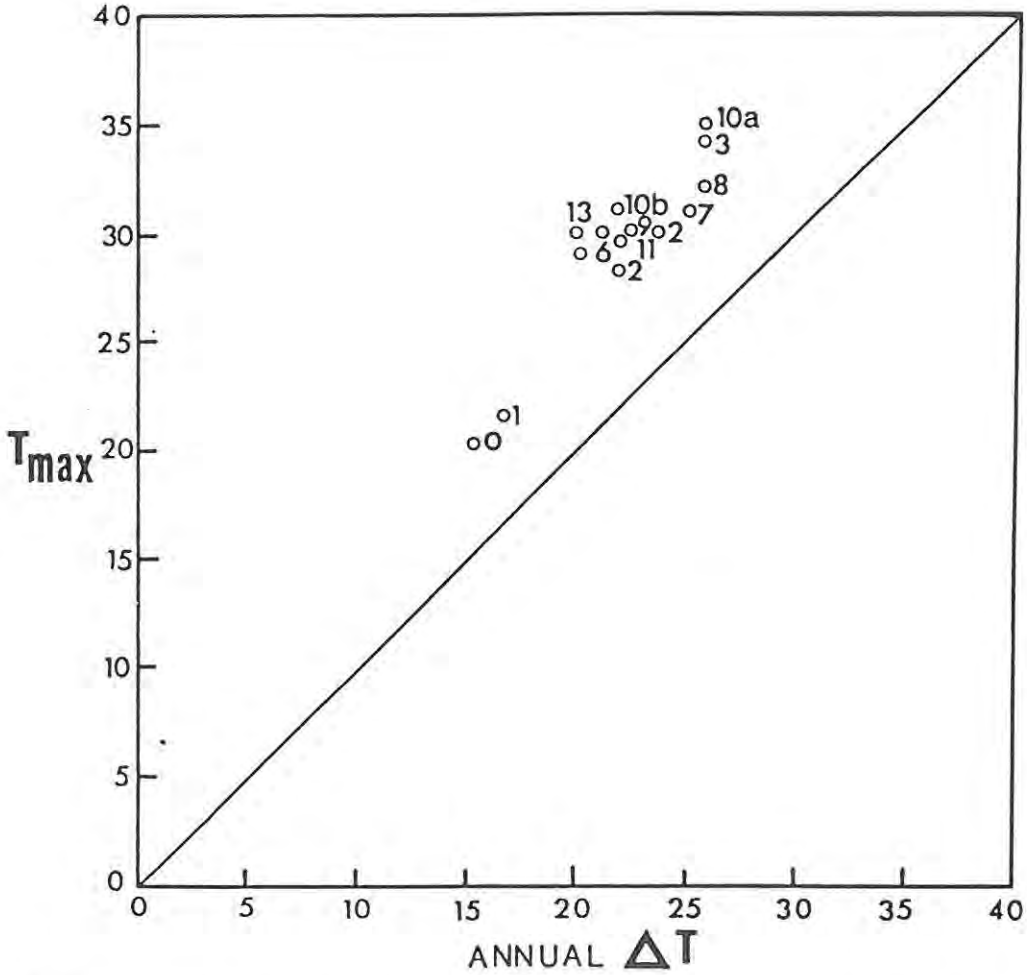

Fig. 3.4 Maximum annual temperature (T_{max}) plotted as a function of the annual temperature range (ΔT) at 14 sites in the Buffalo River. Cool headwaters (Sites 0 & 1) are separated from the rest of the river by Maden (B1), the smallest mainstream impoundment in the Buffalo River.

Twenty-four hour temperature changes were measured at six sites, but only at one site at any one time, and downstream comparisons are therefore difficult. Daily temperature fluctuations ranged from 1°C (Site 1) to 5°C (Site 13; Table 3.1).

EFFECTS OF IMPOUNDMENTS ON WATER TEMPERATURE

The Buffalo River can be divided into two thermal zones based on the annual temperature range and maximum temperature: stable and cool headwaters (Sites 0 & 1), where the annual range was less than 17°C and temperatures never exceeded 23°C, and variable and warm water in the rest of the river (Sites 2-13), where the annual range exceeded 18°C, and temperatures exceeded 26°C (Fig. 3.4). Separating these two thermal zones was Maden (B1), the smallest impoundment in the river. Temperatures downstream of Maden (B1) and Rooikrans (B2) were as much as 8 and 6°C [respectively] warmer compared to upstream (Table 3.2). Maximum temperatures downstream of Laing (B3) were either the same, or somewhat lower (0 to -5°C), compared to upstream, whereas downstream of Bridle Drift (B4) temperatures were as much as 16°C colder than at the upstream site (Table 3.2).

Table 3.2 The change in maximum temperatures directly downstream of the four impoundments (**B1** to **B4**) in the Buffalo River during overflow, and when the impoundments were not overflowing. Temperatures downstream of the impoundments were compared to those measured at the inflow. The severe reduction downstream of Bridle Drift (B4) (16°C) was a consequence of water being released from a low-level outlet.

	Overflowing	Not Overflowing
Maden (B1)	3 to 8	1 to 3
Rooikrans (B2)	1 to 6	0 to 3
Laing (B3)	0 to -5	0
Bridle Drift (B4)	-3 to -6	-3 to -16

Annual temperature ranges downstream of Maden (B1) and Rooikrans (B2) were increased by 7 and 4°C respectively, mainly as a result of the raised maximum temperatures (Table 3.1). Downstream of Laing (B3), the range was reduced by 3°C as a result of lower maximum temperatures, whereas downstream of Bridle Drift (B4), the annual temperature range was hardly affected, since both the annual maximum and minimum temperatures were reduced (Table 3.1). The results in Table 3.1 are based on summer and winter extremes, but an examination of individual monthly data sets (Fig. 3.3) confirms the consistency of the changes caused by the impoundments. The one exception was Bridle Drift (B4), which discharged water either from the surface or from the bottom of the dam wall into separate channels which joined 500 m downstream. Maximum-minimum thermometers were placed in both channels. In February 1987 (Fig. 3.3a), both surface and bottom water was released from Bridle Drift (B4). Maximum temperatures were the same in the two channels (27°C), but the minimum temperature was reduced to 17°C by bottom water, and to 23°C by surface water. In May 1987 (Fig. 3.3b), during which only bottom water was released from Bridle Drift (B4), the temperature range was reduced to 1°C (18 to 19°C) compared to a monthly range of 10°C (15 to 25°C) upstream of the impoundment (Site 10b). Figure 3.3 also provides a cross-section of seasonal temperature changes, indicating that the effects of the impoundments in winter (Fig. 3.3c) were less intense than in summer, autumn or spring (Figs. 3.3a, b & d).

DOWNSTREAM RECOVERY

Rapid equilibration of temperature occurred downstream of all four impoundments (Fig. 3.3). In the 1.4 km that separates Maden (B1) from the upper reaches of Rooikrans (B2), summer maximum temperatures dropped from 30 to 27°C (Table 3.1). Elevated temperatures downstream of Rooikrans (B2) equilibrated by Site 5 (6.4 km downstream of the dam; Fig. 3.3). The slight alterations in temperature downstream of

Laing (B3) were not detected at the next sampling site (Site 10a), 15 km downstream of the dam (Fig. 3.3). The temperature alterations caused by Bridle Drift (B4) also re-equilibrated rapidly (within 7 km: Site 12; Fig. 3.3). The daily temperature fluctuation directly downstream of Bridle Drift (B4) (Site 11) in June 1987 was 1.0°C during the release of 1 m^3s^{-1} from a low-level outlet (Table 3.1). At a site 1.6 km downstream, the daily fluctuation increased to 2.3°C, indicating very rapid equilibration.

Within the limited resolution provided by the number of available sampling sites in the Buffalo River, higher flows did not cause a detectable delay in thermal recovery (Fig. 3.3). However, flow volumes during the course of this project were low (never exceeding 7 m^3s^{-1}). The flow downstream of Laing (B3) ranged from 0.03 m^3s^{-1} (in May 1987; Fig. 3.3b) to 5.7 m^3s^{-1} (in February 1987: Fig. 3.3a), yet recovery always complete within 15 km.

3.5 DISCUSSION

Spatial changes of temperature in the Buffalo River were not as pronounced as seasonal changes, as a result of the relatively short length of the river (133 km), and the fact that it rises at a modest altitude of 1 300 amsl. The effects of impoundments on downstream temperatures at any one time were considerable, but were localized to no more than 15 km downstream of the dams.

The direction of temperature change (increase or decrease) caused by impoundment appears to be governed by the position of the impoundment along the river: Impoundments in the upper catchment, Maden (B1) and Rooikrans (B2) consistently increased downstream temperatures, whereas those in the mid- and lower reaches, Laing and Bridle Drift (B3 & B4), usually decreased temperatures (Fig. 3.3). Water temperatures immediately upstream of Maden (B1) were buffered and kept cool by shading from a dense forest canopy and inflow from thermally stable groundwater. Maden (B1) is relatively shallow (10 m at the wall), and presents a large, open surface area for solar heating. The river upstream of Laing and Bridle Drift (B3 & B4), by contrast, is open and receives little groundwater inflow. Laing (B3) and Bridle Drift (B4) are relatively large and deep (25 and 47 m at the walls respectively). Water temperatures downstream of Laing (B3), and particularly Bridle Drift (B4), were colder in summer (Fig. 3.3a), most likely as a result of the thermal inertia of a large body of water, and thermal stratification of Bridle Drift Dam (B4). In winter, river temperatures were little affected by Laing (B3), but remained cooler downstream of Bridle Drift (B4) during deep-release (Fig. 3.3c). This differs from many published studies which have shown winter-warming downstream of deep-release impoundments (e.g., Spence & Hynes, 1971; Lavis & Smith, 1972; Lehmkuhl, 1972; Hannan & Young, 1974; Ward, 1974, 1976a & b). A possible reason for this difference is that many European and North American rivers (on which much of the research into thermal effects of impoundments has been carried out), freeze over in winter (Boon & Shires, 1976; Ward & Stanford, 1979; Webb & Walling 1986, 1988; Crisp et al., 1982; Crisp, 1988). Water released from low-level outlets on such rivers during winter is therefore warmer than the surroundings. In southern Africa, river temperatures seldom fall below 6°C (Harrison & Elsworth, 1958; Allanson, 1961; Appleton, 1976), and so the phenomenon of 'winter-warming' downstream of impoundments is less likely to occur, although it has been reported by Pitchford & Visser (1975) in the Orange River.

In the Buffalo River, the size of the impoundment had very little influence on the intensity of downstream temperature changes: The smallest impoundment, Maden (B1), caused changes of 3 to 8°C in maximum temperature, whereas Laing (B3), with 70 times the capacity of Maden (B1), caused changes of 0 to -5°C in maximum temperature (Table 3.2). Although the largest impoundment (Bridle Drift: B4) caused the greatest changes in temperature (up to 16°C), this was a result of cold deep-released water (Fig. 3.3b). Continuous release of bottom water from Bridle Drift (B4) (May 1987; Fig. 3.3b) demonstrates the thermal buffering effect of a large water body: The monthly temperature fluctuation downstream of Bridle Drift (B4) during bottom-release was only 1°C (Fig. 3.3b). However, the *annual* temperature range downstream of Bridle Drift (B4) was no different from typical riverine temperature fluctuations (Table 3.1). Maden (B1), on the other hand, despite its small size, caused the greatest increase in annual temperature range in its tailwaters compared to the other impoundments in the Buffalo River. This differs from many other studies (e.g., Lavis & Smith, 1972; Pitchford & Visser, 1975; Ward & Stanford, 1979), which have shown that reservoirs tend to reduce downstream temperature fluctuations. Shading and groundwater influences upstream of, and solar heating in the impoundment, are likely to have been the causes, as explained above.

By increasing river temperatures, Maden (B1) effectively shifted the river thermal conditions upstream, and in doing so, caused a situation in which there is less habitat available for 'cold water' species, a finding similar to that of Fraley (1979). Bridle Drift (B4), on the other hand, caused a local downstream shift. The upper reach of the Buffalo River is one of the few remaining areas where the endangered minnow, *Barbus trevelyani*, may be found (Skelton, 1987). Habitat destruction caused by impoundment has been deemed as one of the factors responsible for the disappearance of these fishes (Bok & Heard, 1982). Although surface-releasing reservoirs in the upper reaches of the Buffalo River, Maden (B1) and Rooikrans (B2) caused a considerable increase in maximum temperatures, these occurred predictably in summer, in contrast to the situation downstream of Bridle Drift (B4), where there were sudden and unpredictable drops in temperature because of the release of cold bottom-water. Such changes in temperature *predictability* are likely to be unfavourable to invertebrate species with rigid life histories, and would tend to favour opportunistic species, with rapid development times.

A review of thermal recovery distances reported in the literature shows that recovery distance is highly variable, ranging from less than 1 km (Petts, 1984) to hundreds of kilometres (Walker et al., 1978). When these data are plotted as a function of reservoir discharge, a logarithmic function closely describes the relationship between recovery distance and discharge (r=0.85; n=13: Fig. 3.5). A discharge of 1 m^3s^{-1} for example, affects temperatures for roughly 13 km downstream, whereas a discharge of 10 m^3s^{-1} affects temperatures for roughly 70 km downstream. Although there may be exceptions to this function (e.g., D6 in Fig. 3.5), it provides a useful tool for predicting the thermal effects of impoundments, and can therefore be used by managers in the siting of proposed impoundments.

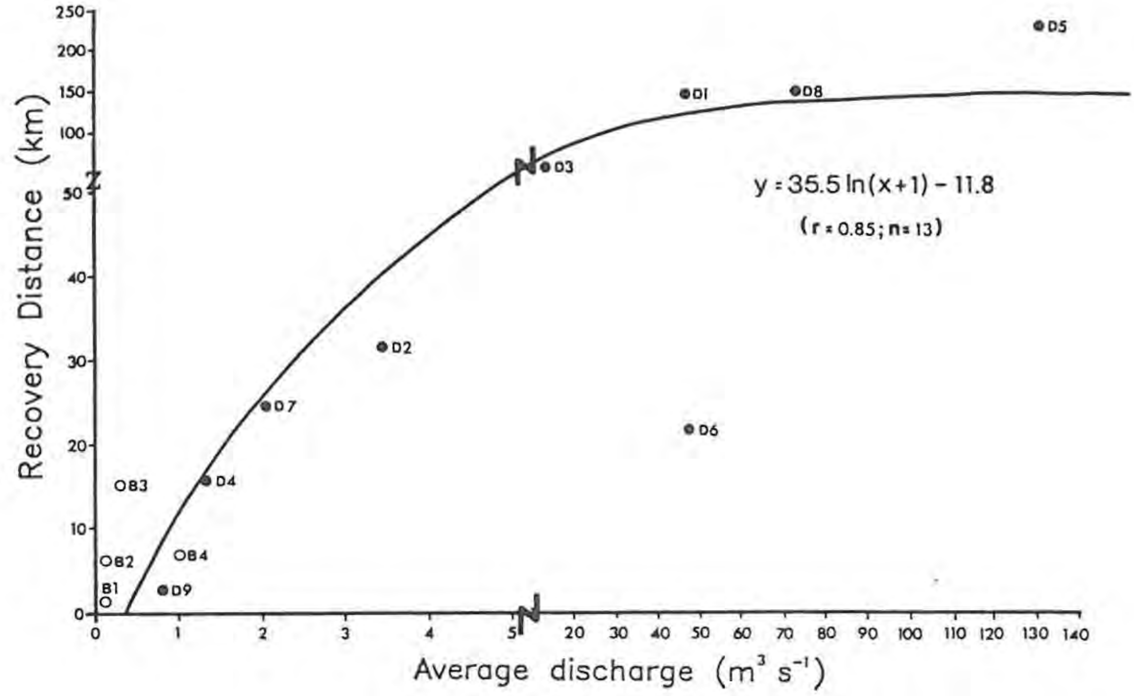

Fig. 3.5 Thermal recovery distances reported in the literature, plotted as a function of average impoundment discharge: D1 - Pearson et al., 1968; D2 - Ward, 1974; D3 - Gore, 1977; D4 - Brooker & Hemsworth, 1978, D5 - Walker et al., 1978; D6 - Fraley, 1979; D7 - Brooker, 1981; D8 - Stanford & Ward, 1984; D9 - O'Keeffe et al., 1990; B1 to B4 - This project.

4 WATER CHEMISTRY

4.1 INTRODUCTION

The Serial Discontinuity Concept (SDC; Ward & Stanford, 1983) is based on the assumption that the river is pristine in all respects, except impoundment. The Buffalo River has four mainstream storage reservoirs, two of which are situated in a near-pristine upper catchment, and two of which are situated further downstream, and receive polluted water from agricultural runoff and urban wastes. This chapter examines the changing status of the water chemistry in the Buffalo River, and compares the effects of impoundments in pristine parts of the river with those in polluted sections.

4.2 METHODS

Water samples were collected at roughly monthly intervals between April and April 1988 from 16 sites down the river (Appendix B). All sampling sites were situated in riffle zones, where the water was assumed to be mixed.

Samples for analysis of nutrients and major ions were filtered through Whatman^R (GF/C) filters into 50 ml polyethylene bottles and kept at 4°C. On return to the laboratory, samples were frozen at -18°C for later analysis. Concentrations of nitrate, nitrite, soluble reactive phosphorus and ammonium were measured using a Technicon Π autoanalyser according to the methods of Mostert (1983). Concentrations of magnesium, calcium, sodium and potassium were analysed by atomic absorption spectrophotometry as recommended by the American Public Health Association (APHA, 1980).

Turbidities were measured with a HACH model 2100A turbidimeter. Chlorophyll *a* was determined by spectrophotometry at 665 and 750 nm after extraction in methanol according to the method of Sartory and Grobbelaar (1984).

Oxygen concentrations and pH were determined in the field with a Simplair^R oxygen meter (fitted with an active-membrane electrode) and a Knick^R pH Portatest 655. Conductivities were measured with a T+C 2001 portable conductivity meter. Unfiltered water samples for the analysis of total alkalinity and chloride were titrated using hydrochloric acid and silver nitrate respectively (APHA, 1980). Site 0 was not sampled during low-flow because it was dry. Unless otherwise stated, all results are presented as medians of between 11 and 24 samples. The median provides a good reflection of typical non-drought, non-flood conditions, because it is little affected by extreme values.

The Euclidean distance was used as a measure of similarity to cluster sites (Dixon, 1985). Equal weighting was given to each of the above-mentioned variables, with the exceptions of flow and major ions, which were excluded from the analysis because of autocorrelation between conductivity and major ions, and between flow and all variables.

4.3 RESULTS

General trends in water chemistry down the river

The single most important factor affecting the chemistry of the Buffalo River was flow rate, as illustrated in Fig. 4.1. For this reason, the results for high and low flow periods are treated separately. During both low and high flow, the river was divisible into three main chemical categories (Fig. 4.2). In the upper catchment (Category 1), water quality was characterized by low chlorophyll *a* levels (<2.1 $\mu g l^{-1}$), conductivities (<17 mSm^{-1}), turbidities (<19 NTU), a slightly acidic to neutral pH (6.1 to 7.5), and low nutrients (Figs. 4.3 & 4.4). During low flow, this high quality water extended to Site 5, but during high flow, good quality water extended as far as Site 7 (Fig. 4.2). Further downstream (Sites 6 to 12, Category 2), water quality deteriorated rapidly: Chlorophyll *a* levels were higher (1.3 to 5.4 $\mu g l^{-1}$), conductivities were about 50 mSm^{-1}, turbidities were higher (3 to 66 NTU; Figs. 4.3a & d), the pH was slightly alkaline (7.4 to 8.4), and the nutrient levels (particularly nitrate levels at Site 6) were higher (Figs. 4.3 & 4.4).

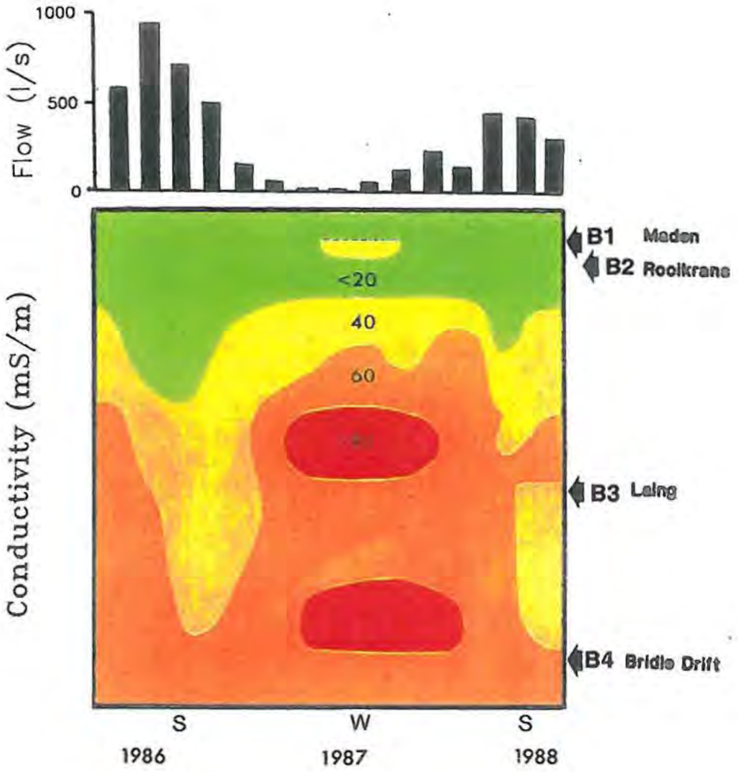

Fig. 4.1 Histogram of flow at gauging weir R2M01 (Site 1), and contour map of the conductivities in the Buffalo River between April 1986 and April 1988. The positions of the impoundments (**B1** to **B4**) are indicated.

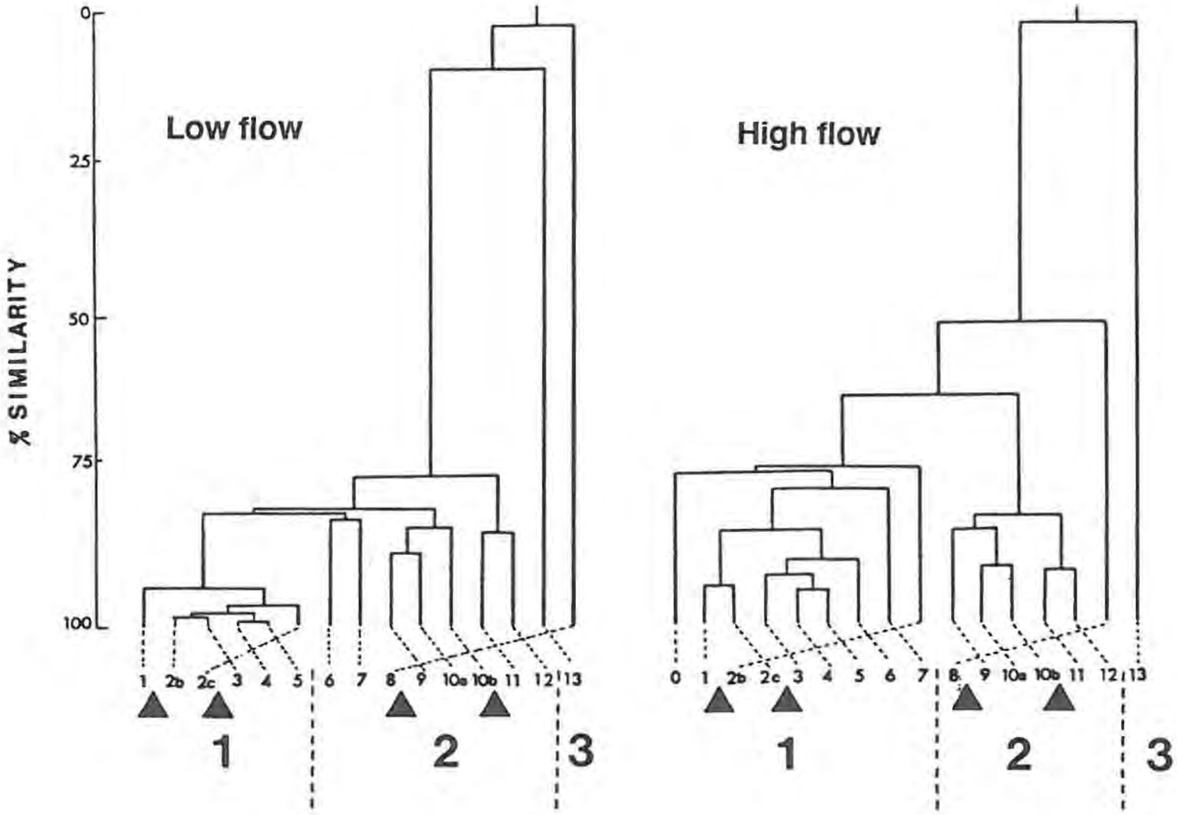

Fig. 4.2 Dendrogram of the sampling sites in the Buffalo River during low and high flow. The river was divisible into three chemical categories: a clean upper reach (Category 1), moderately eutrophic middle and lower reaches (Category 2), and highly polluted stretches at Sites 8 and 13 (Category 3). Triangles (▲) indicate the positions of impoundments.

Superimposed on this natural deterioration in water quality, was a more severe deterioration caused by inflow from urban and industrial effluents (Sites 8 & 13, Category 3). Water quality criteria in these two reaches often exceeded the maxima recommended by Kempster et al., (1980) for potable water. For example, phosphate concentrations (Fig. 4.4a) exceeded a standard of 1 mgl^{-1} (imposed by the South African Department of Water Affairs in 1985) on 70 and 80% of sampling occasions at Sites 8 and 13 respectively, and maximum soluble reactive phosphate concentrations recorded at Sites 8 and 13 were 9.3 and 27.7 mgl^{-1} respectively. On several occasions during low flow, water from Sites 8 and 13 also contained high concentrations of chloride (51% of the total molarity of major ions) and sodium (48%). During high flow, the ionic composition of the water at Sites 8 and 13 resembled that of the rest of the river, which was dominated by chloride (29 to 40%), carbonate (18 to 27%) and sodium (24 to 36%; Table 4.1). Water from the the top site (Site 0), differed from the rest of the river in that the major ion was chloride (57%), reflecting the doleritic nature of the Amatola Mountains (Kemp, 1963).

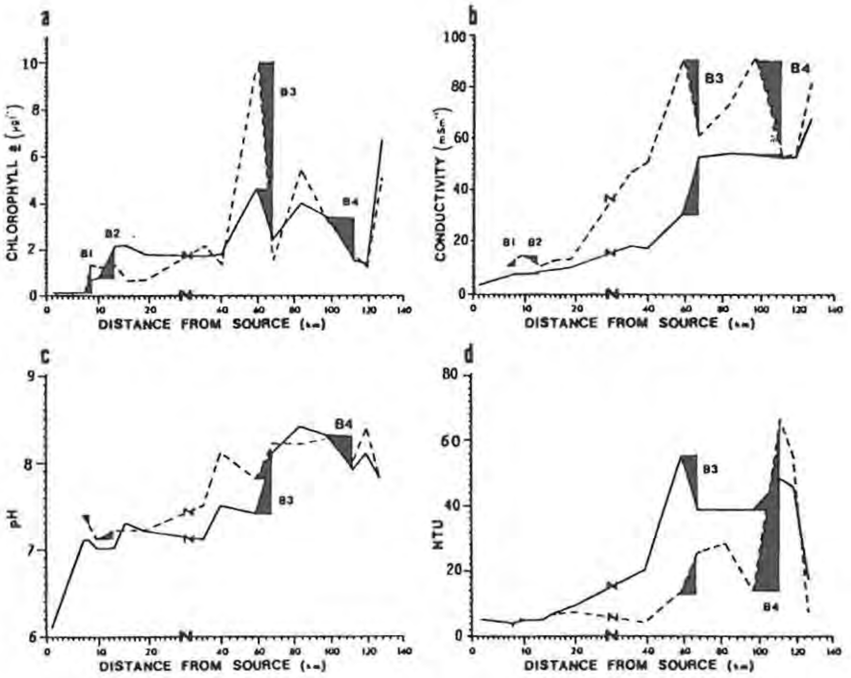

Fig. 4.3 Median values for (**a**) chlorophyll *a*, (**b**) conductivity, (**c**) pH, and (**d**) turbidity in the Buffalo River during high flow (————), when upstream dams were overflowing, and during low flow (- - -), when dams were not overflowing. The effects of the impoundments (B1 to B4) are indicated by the shaded triangles.

Table 4.1 Median composition of major ions in the Buffalo River, expressed as a percentage of their total molarities.

Ion	Site 0	Sites 1 to 13
Cl	57	29 - 40
CO_3	14	18 - 27
Na	24	24 - 36
Mg	3	5.8 - 8.5
Ca	0.5	3.5 - 5.8
K	1	0.5 - 1.1

The trout hatchery, situated downstream of Rooikrans (B2), caused significant increases in chlorophyll *a* ($p<0.1$), pH and ammonium ($p<0.025$; Student's *t*-test). When Rooikrans (B2) was overflowing, the effects of the hatchery were undetectable in the river, but during low flow, the effects of the hatchery attenuated within 2.6 km downstream (Fig. 4.3 & 4.4).

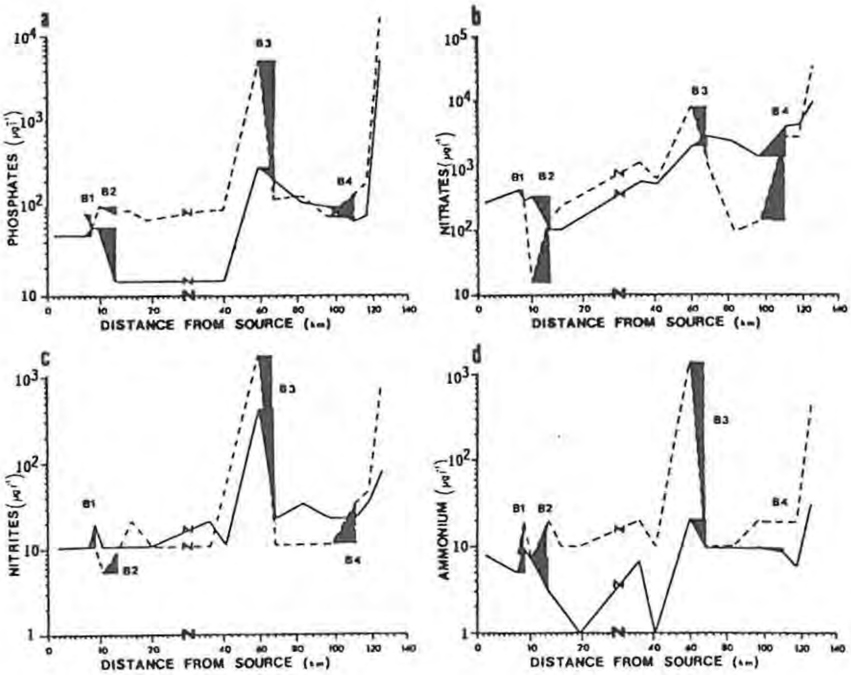

Fig. 4.4 Median values for soluble reactive phosphate (**a**), nitrate (**b**), nitrite (**c**), and ammonium (**d**) in the Buffalo River during high flow (————), when upstream dams were overflowing, and during low flow (- - -), when dams were not overflowing. The effects of the impoundments (B1 to B4) are indicated by the shaded triangles.

Effects of the dams

The most significant change in water quality influenced by Maden (B1), and to a lesser extent by Rooikrans (B2), was an increase in chlorophyll *a* levels. Chlorophyll *a* was often undetectable upstream of Maden (B1), but showed average respective increases of 600 and 330% downstream of Maden (B1) and Rooikrans (B2) during high flow (Fig. 4.3a). Although chlorophyll *a* levels downstream of these dams did not return to values measured upstream of the impoundment, attenuation was rapid. For example, recovery downstream of Rooikrans (B2) was within 2.6 km during low flow, and within 18.4 km during high flow (Fig. 4.3a). Rooikrans (B2) differed from Maden (B1) in that during the summer of 1986/87, increased chlorophyll *a* levels downstream of Rooikrans (B2) were almost entirely attributable to a single species of desmid algae, *Staurodesmus subunguiferus* (Fritsch & Rich) Thomasson, whereas downstream of Maden (B1) the increase was due to several taxa including *Volvox* sp. and *Scenedesmus* sp.. Highest chlorophyll *a* values usually occurred during summer overflow, although in the stretches of river between Maden (B1) and Rooikrans (B2) (Sites 2b & 2c), highest values occurred during low flow, when this part of the river was reduced to stagnant pools as a result of there being no compensatory release from Maden (B1).

Unlike impoundments in the upper reaches of the river, chlorophyll *a* levels downstream of Laing (B3) and Bridle Drift (B4) were usually lower than values in the river upstream of the dams (Fig. 4.3a). However, in the autumn of 1987 (April to May), and the summer of 1987/88 (November to January), the blue-green algae, *Microcystis aeruginosa* Kützing and *Anabaena* sp. *indet*, developed in Laing (B3) and Bridle Drift (B4) (Fig. 4.5). In December 1987 these algae formed a scum on the surface of Laing (B3), and surface-released water contained high concentrations of chlorophyll *a* (40 $\mu g l^{-1}$). At the same time, the pH and oxygen percentage saturation downstream of Laing (B3) was 9.5 and 168% respectively. Although nuisance algae were still evident at the next sampling site (Site 10a), 15.5 km downstream of Laing (B3), chlorophyll *a* concentrations had dropped to 4.5 $\mu g l^{-1}$, and the pH and oxygen levels had returned to typical riverine levels (8.3 & 105% respectively). A month later, the dam had stopped overflowing, and stagnant pools downstream of the dam contained senescent algae. Oxygen saturation downstream of the dam dropped to 6%, and ammonium levels rose to 3,600 $\mu g l^{-1}$, the latter showing 80% recovery after 15.5 km, and full recovery, to 23 $\mu g l^{-1}$, after 29 km.

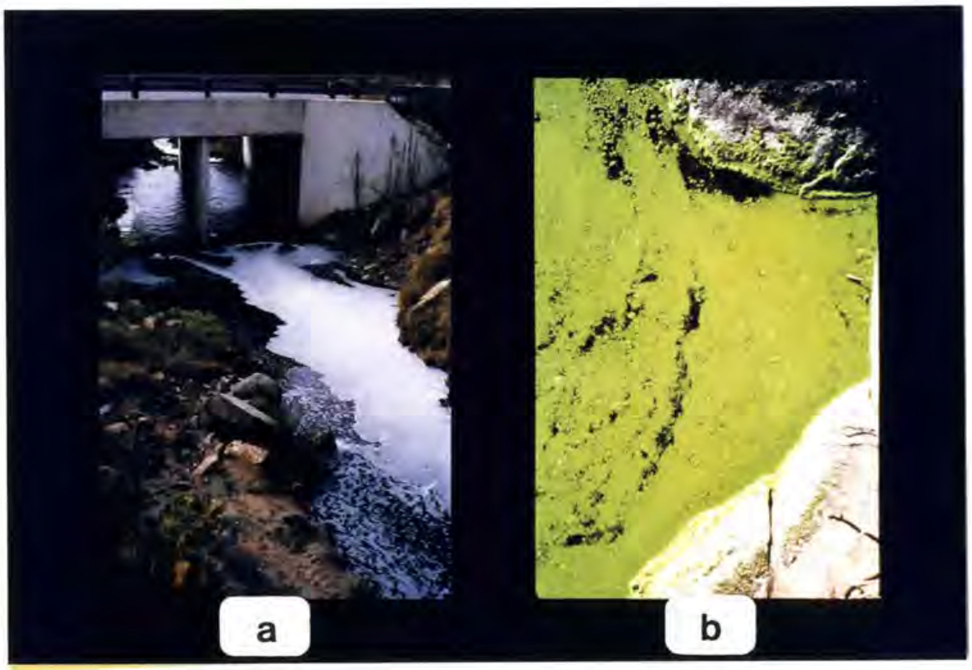

Fig. 4.5 **a** The Makalaka Stream, a polluted tributary of the Buffalo River carrying industrial effluents from Zwelitsha into the Buffalo River upstream of Laing (B3). **b** Algal bloom in Laing (B3) caused by *Microcystis aeruginosa* Kützing and *Anabaena* sp. *indet.*

During high flow, conductivities were much the same upstream and downstream of all impoundments except Laing (B3), where conductivities were higher downstream of the dam (Fig. 4.3b). This exception again reflects the poor quality of water that flows into Laing (B3), coupled to the residence time within the reservoir. With the onset of the dry season, conductivities rose steadily upstream of all four impoundments, particularly upstream of Laing (B3) and Bridle Drift (B4). There was a dampening of the seasonal range in conductivity downstream of all dams except Maden (B1), which had maximum values (up to 28 mSm^{-1}) towards the end of the dry season. Altered conductivities did not recover in the 1.4 km which separated Maden (B1) and Rooikrans (B2), whereas downstream of Rooikrans (B2), recovery was within 2.6 km (Fig. 4.3b).

Impoundments in the upper reaches of the river, Maden and Rooikrans (B1 & B2), had no detectable effect on pH, whereas the water downstream of Laing (B3) was usually more alkaline compared to upstream, with no sign of recovery. Downstream of Bridle Drift (B4), the pH was usually lower than upstream, with recovery within 7 km (Fig. 4.3c). Similarly, turbidities were unchanged downstream of Maden (B1) and Rooikrans (B2), but showed large alterations downstream of Laing (B3) and Bridle Drift (B4). The highest turbidity measured during the study period (290 NTU) was recorded at Site 8, upstream of Laing (B3). Water released from Laing (B3) had a maximum turbidity of 80 NTU, indicating considerable dampening of the turbidity within Laing (B3). During low flow, turbidities downstream of Laing (B3) were higher than upstream of the dam, and recovery was within 29 km. Bridle Drift (B4) released turbid water (66 NTU) from a low-level outlet, at a time when the rest of the river was clear (2 to 18 NTU), and there were no signs of recovery 7 km downstream of Bridle Drift (B4) (Fig. 4.3d).

Phosphate concentrations upstream and downstream of Maden (B1) were not significantly different, whereas downstream of Rooikrans (B2) they were considerably lower, with recovery within 18.4 km during high flow, and within 2.6 km during low flow (Fig. 4.4a). Phosphate concentrations downstream of Bridle Drift (B4) during low flow (110 $\mu g l^{-1}$) were higher than riverine levels upstream of the impoundment (70 $\mu g l^{-1}$) because of the release of bottom-water, but showed no signs of recovery (Fig. 4.4a).

Nitrate concentrations were consistently lower downstream of Maden (B1) and Rooikrans (B2) compared to typical riverine levels (Fig. 4.4b). Recovery was more rapid during low flow (2.6 km) compared to high flow (18.4 km). The low value at Site 2c during low flow is unexplained. Unlike Maden (B1) and Rooikrans (B2), nitrate concentrations downstream of Laing (B3) and Bridle Drift (B4) were high compared to typical riverine levels (Fig. 4.4b). During high flow, values downstream of Laing (B3) dropped by 52% in 29 km, whereas during low flow, levels had recovered within 15.5 km (Fig. 4.4b). In the 7 km of undisturbed river downstream of Bridle Drift (B4), there was no sign of recovery.

Nitrite and ammonium concentrations were low throughout most of the river (<20 $\mu g l^{-1}$), and were not consistent enough to show any impoundment-induced trends.

4.4 DISCUSSION

Anthropogenic changes in water quality in rivers are superimposed on natural changes, caused by tributary inflows, riparian vegetation, and underlying geology. The upper Buffalo River Catchment is situated primarily on doleritic intrusions, and although it constitutes only 2% of the total Buffalo River Catchment area, it contributes 40% of the total annual discharge of the river (Middleton et al., 1981). This water is of high quality, and much sought after for industrial and domestic supply in the middle reaches of the river. Tributaries draining the less resistant sedimentary rocks further downstream, carry high concentrations of suspended and dissolved material, and contribute to the natural increase in turbidity and conductivity in the middle reaches. Conductivities recorded in the middle and lower reaches of the Buffalo River have increased steadily from 20 mSm^{-1} in 1950 (Hart, 1982) to the present median of 55 mSm^{-1}. In 1970, a flood reduced conductivities in Laing (B3) from 50 mSm^{-1} to 20 mSm^{-1} (Hart, 1982), indicating that a large proportion (over 50%) of increased salinity in the Buffalo River can be attributed to human activities, rather than natural salinization.

Intensive agricultural activities (at Sites 5 to 7), caused a deterioration in water quality, mainly as a result of increased nitrate concentrations. However, the contributions to salinization caused by agriculture were small in comparison to those made by urban and industrial activities. The latter were confined to localized stretches of river (Sites 8 & 13), where water quality criteria often exceeded acceptable limits for potable water.

Given this backdrop of natural and man-made modifications to the Buffalo River, the effects of the impoundments were weak in comparison. The results reported here are consistent with the predictions of Ward and Stanford (1983): that is, the downstream effects of impoundments depended on the variables examined, and the position of the impoundment along the river profile. Impoundments situated in the upper catchment, Maden and Rooikrans (B1 & B2), caused increases in levels of chlorophyll *a* in impoundment tailwaters compared to upstream, and reductions in levels of soluble phosphates and nitrates. Recovery was within 2.6 to 18.4 km, depending on flow. Impoundments in the middle and lower reaches, Laing and Bridle Drift (B3 & B4), usually had lower chlorophyll *a* levels in the tailwater compared to upstream, whereas nitrate levels were considerably higher. Periodic algal blooms caused by *Microcystis aeruginosa* and *Anabaena* sp. occurred in Laing (B3) and Bridle Drift (B4). Several studies have ascribed increases in nitrate concentrations downstream of reservoirs to the fixation of atmospheric nitrogen by algae (e.g., Horne & Goldman, 1972; Soltero et al., 1973; Martin & Arneson, 1978; Rada & Wright, 1979). *Anabaena* sp. and *M. aeruginosa*are well known fixers of nitrogen (Toerien et al., 1975), and so it is likely that the elevated nitrate levels downstream of Laing (B3) and Bridle Drift (B4) were due to these algae.

Meaningful comparisons of recovery distances of water chemistry with studies done elsewhere are difficult, since most studies on the downstream effects of dams have paid little attention to downstream recovery (e.g., Nishizawa & Yamabe, 1970; Lavis & Smith, 1972; Hannan & Young, 1974; Pitchford & Visser, 1975; Crisp, 1977; Edwards, 1978; Bass & Armitage, 1987), and those which have, deal primarily with water temperature (e.g., Webb & Walling, 1986; Cowx, et al., 1987), benthic invertebrates (Pearson, et al., 1968; Lehmkuhl, 1972; Ward, 1974, 1976a & b; Armitage, 1976, 1977; Gore, 1977; Brooker &

Hemsworth, 1978; Fraley, 1979; Hauer & Stanford, 1982) and drift (Ward, 1975a; Armitage & Capper, 1976; Armitage, 1977; Keefer & Maughan, 1985). In general, the larger the impoundment, the longer the recovery distance. For example, recovery of water chemistry downstream of Caban Coch Reservoir, in the River Wye, during an artificial discharge of water (3.0 m^3s^{-1}) was within 16 km (Brooker & Hemsworth, 1978), whereas altered oxygen saturation downstream of Lake Hume in the much larger Murray River (with an annual average discharge of 126 m^3s^{-1}) took 100 km to recover (Walker et al., 1978). Similarly, the recovery distance downstream of Laing (B3) during an algal bloom in December 1987 was further (15.5 to 29.0 km) than the recovery distance downstream of Maden (B1) and Rooikrans (B2), and recovery downstream of the larger Bridle Drift (B4), was seldom evident in the 7 km stretch of unpolluted river downstream of the dam. The recovery distances for the Buffalo River reported here were based on results collected during base flow conditions, and may differ under different discharges.

Reservoirs with deep-release outlets, such as Bridle Drift (B4), are often reported to have elevated ammonia levels (Hannan & Young, 1974; Marcus, 1980) and decreased oxygen levels (Neel, 1963; Wright, 1967; Isom, 1971; Walker et al., 1978; Krenkel et al., 1979) in their tailwaters compared to upstream. There was little chemical difference between surface-released water (high flow) and deep-released water (low flow) from Bridle Drift (B4) for most of the year (Figs. 4.3 & 4.4). Low-level releases from Bridle Drift (B4) usually occurred in winter, when the impoundment was not thermally stratified. Conditions associated with hypolimnetic release therefore seldom occurred downstream of Bridle Drift (B4). The downstream effects of Bridle Drift (B4) therefore differ from many published studies.

Results presented here indicate that Laing (B3), and to a lesser extent Bridle Drift (B4), served to protect the downstream reaches of the river from urban effluents and agricultural runoff, a similar finding to that of Simmons and Voshell (1978). This represents a reversal of the SDC (Ward & Stanford, 1983) described for pristine rivers, since Laing (B3) and Bridle Drift (B4) were not acting as perturbations, but rather restoring the river to more natural conditions. This may only be a temporary reversal, since eventually both the impoundment and the river downstream are likely to become saturated when conditions continue to deteriorate. Impoundments in the Buffalo River are typical of many impoundments in arid regions, where compensatory flow is regarded as waste. During low flow, Laing (B3) was effectively managed as a closed loop system, because water was extracted to supply Kingwilliamstown and Zwelitsha, and returned into the river as waste upstream of Laing (B3). When these conditions persisted into summer, warmer temperatures created conditions ideal for the development of algal blooms (Fig. 4.5). The downstream effects of the four dams in the Buffalo River are therefore best understood in terms of the relative impact of other catchment disturbances. Disturbances become more severe during low flow, and it is during low flow that impoundments have the greatest effect on the river.

5 TRANSPORTED MATERIAL

5.1 INTRODUCTION

A principal ecological process in rivers, distinguishing them from other types of ecosystem, is the unidirectional transport of materials from the headwaters to the sea. The types of material which are transported can be categorized functionally as inorganic and organic, and within these categories various functional size classes can be defined. Organic material provides the food base of the river, whereas inorganic material affects the availability of food in a number of ways. Small particles act as adsorption sites for nutrients (Grobbelaar et al., 1980), and affect availability for primary production (Keulder, 1977). Sediment in transport influences light penetration for primary production (Wetzel, 1975), and affects feeding by animals relying on sight (Vinyard & O'Brien, 1976). High concentrations of sediments in transport dilute the concentration of organic material available to filter-feeders (Hart, 1986), and may clog the gills of fish (Bruton, 1984). From a management perspective, transported sediment is often increased as a result of catchment degradation and accumulates in water storage structures (such as impoundments), and reduces their life-spans (Rooseboom, 1978). In extreme cases, impoundments are converted into so-called 'sand-storage' reservoirs (Wipplinger, 1974). One way of alleviating the siltation problem is to drain the impoundment periodically. This can result in large alterations of the concentrations of suspended material in the receiving river, and affect the river biota for as much as 160 km downstream (Roux, 1982; Petts, 1986).

Many rivers in southern Africa are turbid and carry high sediment concentrations (mainly clay) because of the nature of the underlying geology, and the erosive effects of poor catchment management (Noble & Hemens, 1978; Kirk & Akhurst, 1984; Walling, 1984). Such conditions may be responsible for the ecological distinctiveness of semi-arid rivers typical of much of the southern hemisphere (Davies & Walmsley, 1984; Williams, 1989). This raises the question as to whether impoundments in turbid rivers create any special ecological conditions that differ from those of the clearer northern hemisphere rivers which have been the focus of much previous research. The questions addressed in this chapter are closely related to the predictions of the River Continuum Concept (RCC) (Vannote et al., 1980) and the derivative Serial Discontinuity Concept (SDC) of Ward & Stanford (1983), and include:

1 - Is there a change in the ratio of CPOM:FPOM in transport with increasing stream order in the Buffalo River as predicted by the SDC?

2 - How do impoundments alter the size distribution, composition and concentrations of particles in transport in the Buffalo River?

3 - Does the river recover from the effects of impoundment, and if so, can typical recovery distances be measured?

5.2 METHODS

Water samples were consistently taken from the middle of the water column, so as to exclude bed-load, and in rapids, where the water was assumed to be mixed. Sixteen sites were sampled at roughly monthly intervals for two years starting in April 1986. One sample was taken for each size fraction at each site on each sampling occasion. Total 'dissolved' solids (TDS) were determined by filtering river water through ashed Whatman^R GF/C (0.6 μm) filters, and pipetting 50 ml of the filtrate into pre-weighed plastic containers. These were kept at 60°C until evaporation was complete and then reweighed. Measurements of TDS were done in the initial stages of the study to give a rough indication of the quantities of dissolved solids present in the river. After October 1986, TDS measurements were replaced by conductivity measurements.

Fig. 5.1 **a** Cushing-Mundie drift net used in regular sampling of suspended material in the Buffalo River. **b** Diatoms, common components of ultra fine suspended material in the Buffalo River. **c** Cladocera, common components of fine suspended material in the upper reaches of the Buffalo River. **d** Copepoda, common components of fine suspended material in the lower reaches of the Buffalo River.

Particulate material was arbitrarily categorized (see Wotton, 1990) into five size classes: **(1)** ultra fine (0.6-80 μm), **(2)** very fine (80-250 μm), **(3)** fine (250-1000 μm), **(4)** coarse (1000-4000 μm), and **(5)** ultra coarse (>4000 μm; based on King et al., 1987). These size classes have been abbreviated as UFPM, VFPM, FPM, CPM and UCPM, respectively.

Concentrations of ultra fine particulate matter were determined by filtering river water through an 80 μm mesh sieve. The Buffalo River was often turbid, and the amount of water that could be sampled varied accordingly. A known volume of water (250 to 1000 ml depending on clogging) was then filtered through ashed and pre-weighed Whatman^R GF/C (0.6 μm) filters, which were kept at 4°C until returned to the laboratory. The concentration of material was determined by weighing the filters after they had been dried for 24 hrs at 60°C (to prevent loss of volatile organic compounds; Lovegrove, 1966; Beers, 1976; Minshall et al., 1983). The organic fraction was determined by difference after ashing at 490°C for 3 hours (Beers, 1976).

Larger size fractions (>80 μm) were collected with a Cushing-Mundie drift net with a mesh size of 80 μm (Fig. 5.1; Cushing, 1964; Mundie, 1964; Elliott, 1970). The volume of water passing through the net (1 to 44 m^3) was determined with an Ott^R current meter held at the entrance to the net. The net was always placed on to the stream bottom, and the top of the net was never submerged, so that the entire water column was sampled. The net remained in the water for 10 to 20 min, or until it started to clog. Each sample was preserved in 5% formaldehyde, and on return to the laboratory, was passed through a series of sieves with mesh sizes of 4000, 1000, 250 and 80 μm. Each size fraction was placed in a perspex tray and invertebrates were counted. Some samples contained large numbers of zooplankton, and these were subsampled in the following way (modified from Allanson & Kerrich, 1961). Each sample was placed in a volumetric flask (250 to 1000 ml depending on the numbers of zooplankton) which was then filled with water. The sample was decanted into an octagonal beaker and stirred vigorously. Three 5 ml replicates were removed by automatic pipette, placed into a Bogoroff tray and counted separately. Recovery distance for zooplankton was taken as the distance required for 95% of the animals discharged to disappear. The amount of material and the organic fraction in each size class was determined gravimetrically as for ultra fine material (see above).

On two occasions, the particle size distributions of ultra fine material between 2 and 18 μm equivalent spherical diameters were measured by a Coulter Counter (Model ZB). Water was collected in 250 ml polythene bottles and kept at 4°C in the dark until returned to the laboratory. The Coulter Counter was calibrated using polystyrene latex beads with a diameter of 8.4 μm. An aperture of 70 μm was used. Four replicate counts, using 0.05 to 0.5 ml of sample, were made for each of twelve logrithmically defined size classes.

5.3 RESULTS

General trends in transported material

Most of the material transported in the river was 'dissolved' (<0.6 μm), and concentrations ranged between 14 gm^{-3} (Site 1) and 872 gm^{-3} (Site 8; Table 5.1). Of the particulate material (>0.6 μm), 88.6 to 99.6% was less than 80 μm in diameter (Table 5.2). The concentration of total particulate material ranged from a median of 3 gm^{-3} (Sites 1 & 2b) to 45 gm^{-3} (Site 10a; Table 5.1). Very fine, fine, and coarse material made up no more than 11% of the total particulate material (Table 5.2), whereas ultra coarse made up less than 0.1%, and was omitted from further analysis. In the upper reaches of the river (Sites 0 to 2b), maximum POM concentrations occurred in winter, whereas the lower reaches usually had highest concentrations during spring and summer (Table 5.1).

Table 5.1 Total dissolved solids (TDS), and median values for total suspended solids (TSS), and particulate organic matter (POM) in the Buffalo River (in gm^{-3}). (Bracketed figures indicate ranges.) 'Season' refers to the time of year when concentrations of POM were at a maximum. W=Winter, Sp=Spring, Su=Summer, A=Autumn. Dashes indicate the positions of the four mainstream impoundments (**B1** to **B4**).

Site	TDS (gm^{-3})	TSS (gm^{-3})	POM (gm^{-3})	Season (Max.)	
0	-	5 (2-31)	1 (1-5)	W	
1	(14-62)	3 (1-17)	1 (0-4)	W	
					(B1)
2b	(19-200)	3 (1-12)	2 (0-7)	W	
2c	-	4 (1-14)	1 (0-8)	W	
					(B2)
3	(28-232)	4 (2-19)	2 (0-6)	Sp	
4	(81-248)	6 (1-17)	2 (0.4-4)	W	
5	(48-308)	6 (1-12)	2 (0.3-4)	W	
6	(188-389)	12 (1-88)	3(0.1-108)	Sp	
7	(184-487)	9 (1-34)	3 (2-6)	A	
8	(334-872)	33 (5-560)	10 (5-51)	Su	
					(B3)
9	(266-384)	30 (6-117)	5 (1-29)	Su	
10a	(286-385)	45 (8-104)	7 (4-61)	Sp	
10b	-	39 (15-90)	5 (0.7-10)	Su	
					(B4)
11	(174-274)	42(11-190)	5 (2-23)	Sp	
12	-	40(13-156)	5 (1-49)	Sp	
13	(314-435)	22 (5-64)	5(0.1-110)	Sp	

Table 5.2 The percentage of total transported material and percentage organic mass in each size class in the Buffalo River, showing that most of the material was ultra fine (0.6 to 80 µm), and that larger particles contained a higher organic content. Data are based on the total range at all sites throughout the study period.

	Size Classes				
	UFPM	VFPM	FPM	CPM	UCPM
	0.6	80	250	1000	4000 µm
Total %	88.6-99.6	0.2-4.7	0.1-2.5	0.1-3.8	0
% organic	12-44	22-40	31-63	37-60	72-86

There was an increase in organic fraction with increasing particle size: ultra fine material had a median organic content between 12 and 44%, whereas ultra coarse material had an organic content between 72 and 86% (Table 5.2).

Changes in particle size spectrum down the river

In the upper reaches of the river (Sites 0 to 5), total particulates did not exceed 20 gm^{-3} (Table 5.1). A sudden increase [up to 88 gm^{-3}] occurred where agricultural runoff entered the river (Site 6; Table 5.1). Particularly high values [up to 560 gm^{-3}] occurred where industrial and domestic effluents entered the river (Site 8; Table 5.1).

The organic fraction decreased from the headwaters (30-68%) to the lower reaches (10-20%), although there was an increase (to 20-30%) where domestic effluent from Mdantsane entered the river (120 km from the source; Fig. 5.2). During periods of high flow, when dams were overflowing, the organic fraction was usually lower than at times of low flow, particularly in the upper and middle reaches (Fig. 5.2).

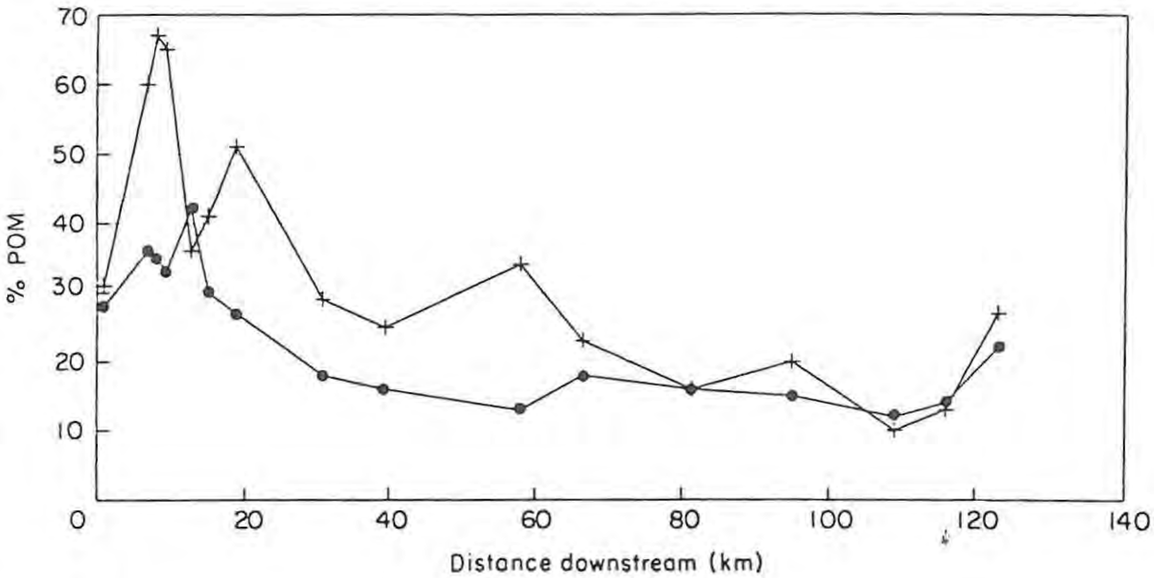

Fig. 5.2 Median organic material as a percentage of median total particulate material in the Buffalo River during high flow (·), when the dams were overflowing, and during low flow (+), plotted as a function of distance from the source.

Within the size range of 1.4 to 18 μm, the upper reaches of the river (Sites 1 & 2a) had a bimodal particle size distribution, with peaks between 2 and 5 μm, and between 10 and 18 μm (Fig. 5.3). Sites 3 and 9 (downstream of Rooikrans (B2) & Laing (B3) respectively) had peaks at 11.1 μm and 5.5 μm respectively (Fig. 5.3). Further downstream (Site 10b) an increase in the volume of small particles (less than 3 μm) was observed, whereas downstream of Bridle Drift (B4) (Site 11: during bottom release) the water was dominated by particles smaller than 3 μm (Fig. 5.3).

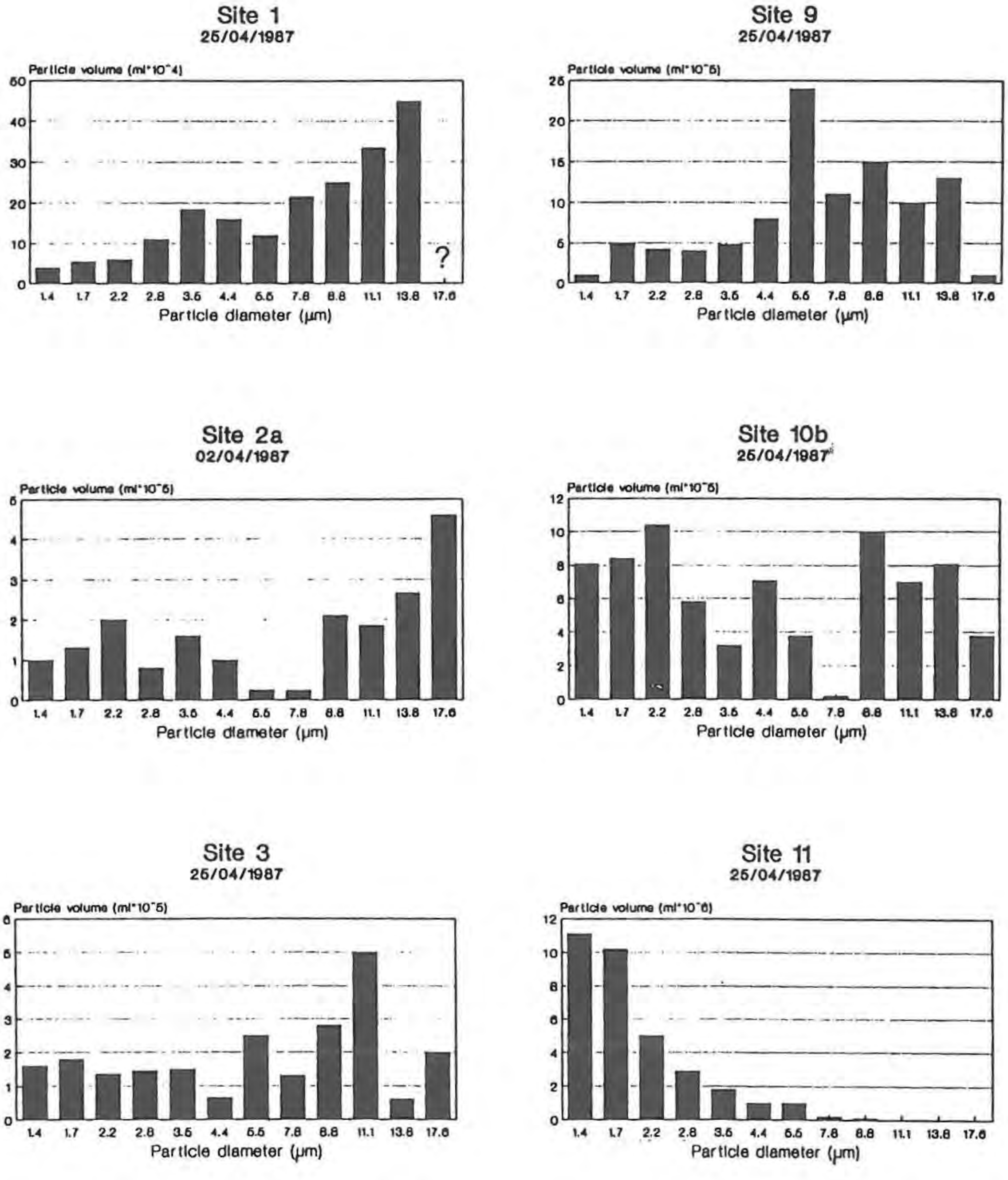

Fig. 5.3 Particle volume as a function of equivalent spherical diameter for particles between 1 and 18 μm in the Buffalo River, when B1 to B4 were overflowing, and Bridle Drift (B4) (Site 11) was releasing from a low-level outlet.

The ratio of CPOM:FPOM decreased with distance from the source of the river (Fig. 5.4). Highest values (1.5 to 1.8:1) occurred in the well-wooded first 60 km of the river (Sites 0 to 7), although local depressions occurred downstream of Maden (B1) and Rooikrans (B2) (Fig. 5.4). Further downstream, the ratio was usually below 1, with local depressions downstream of Bridle Drift (B4) and particularly Laing (B3) (Fig. 5.4).

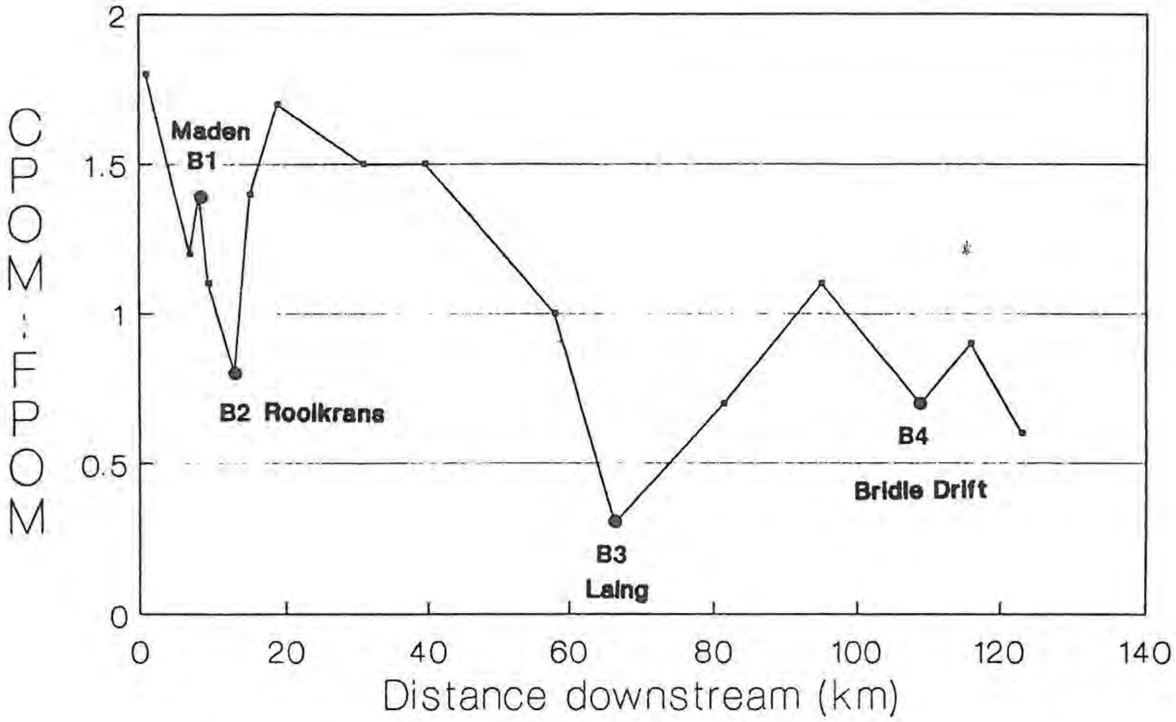

Fig. 5.4 Median ratio of CPOM:FPOM (1000-4000:250-1000 μm) as a function of distance from the source of the Buffalo River. Sites directly downstream of impoundments (**B1** to **B4**) are indicated.

Effects of impoundments

In general, small impoundments in the upper reaches, Maden (B1) and Rooikrans (B2), had the least effects on transported material (Fig. 5.5). The concentrations of all size fractions, with the exception of UFPOM, were lower downstream of Maden (B1) than upstream (Fig. 5.5). Similar trends were found downstream of Rooikrans (B2), except that concentrations of inorganic particles were usually higher downstream of Rooikrans (B2) than upstream (Fig. 5.5).

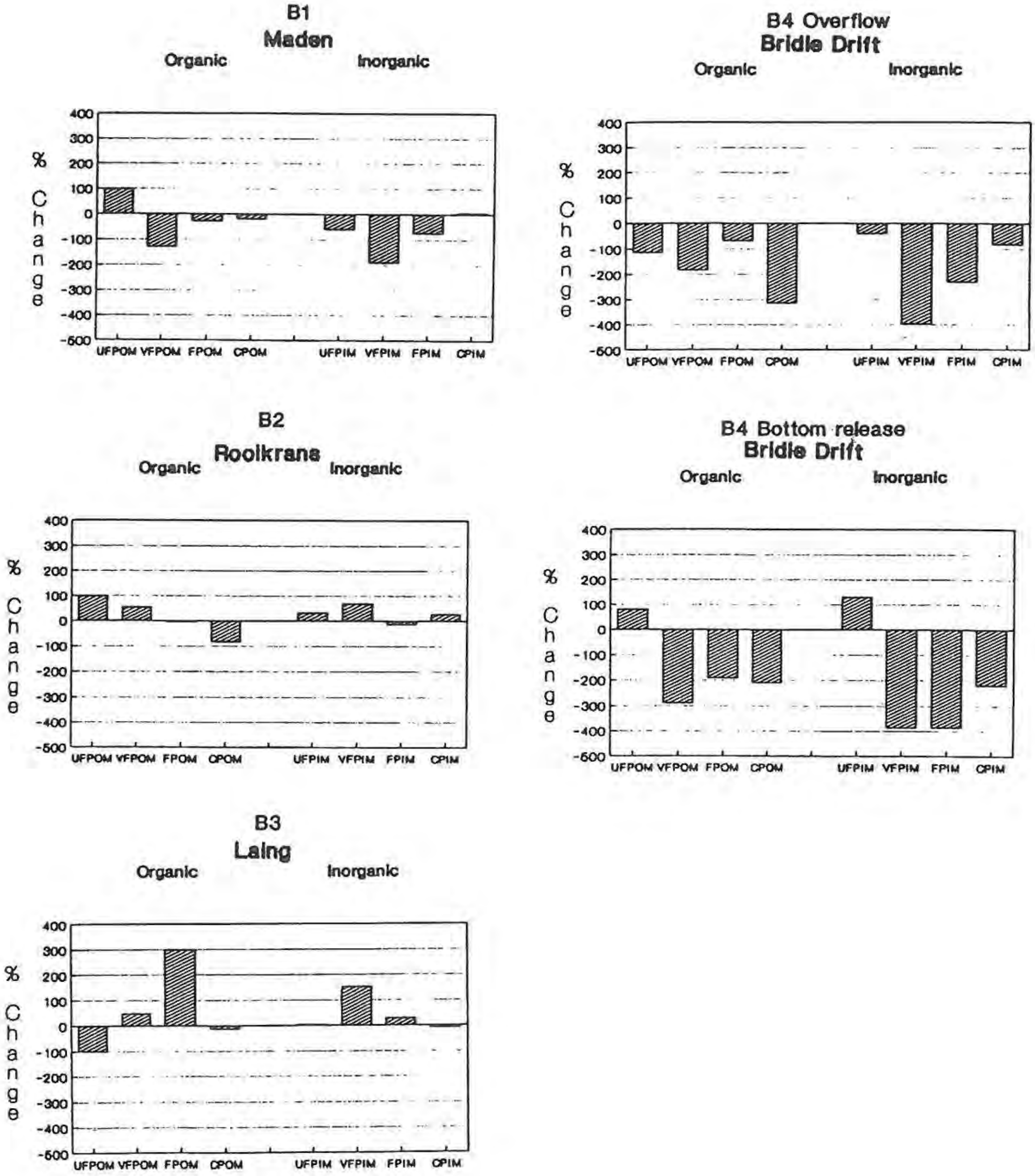

Fig. 5.5 The effects of impoundments on organic and inorganic particle size distributions in the Buffalo River, expressed as the percentage change in median concentrations upstream and downstream of each impoundment.

The most pronounced effect of Laing (B3) was the large increase in the concentration of FPOM downstream of the dam (Fig. 5.5). The concentration of UFPOM on the other hand was lower downstream of the dam (Fig. 5.5). This was true for all occasions except in December and January 1987/88 when the concentration of ultra fine material was higher downstream of Laing (B3). This was caused by a bloom of the toxic algae, *Microcystis aeruginosa*. Blooms of this algae occured in Laing (B3), and to a less extent Bridle Drift (B4), when temperatures were high (20-30°C), turbidity low (<10 NTU), and after a period of low flow (<0.125 m^3 s^{-1} inflow to Laing (B3)).

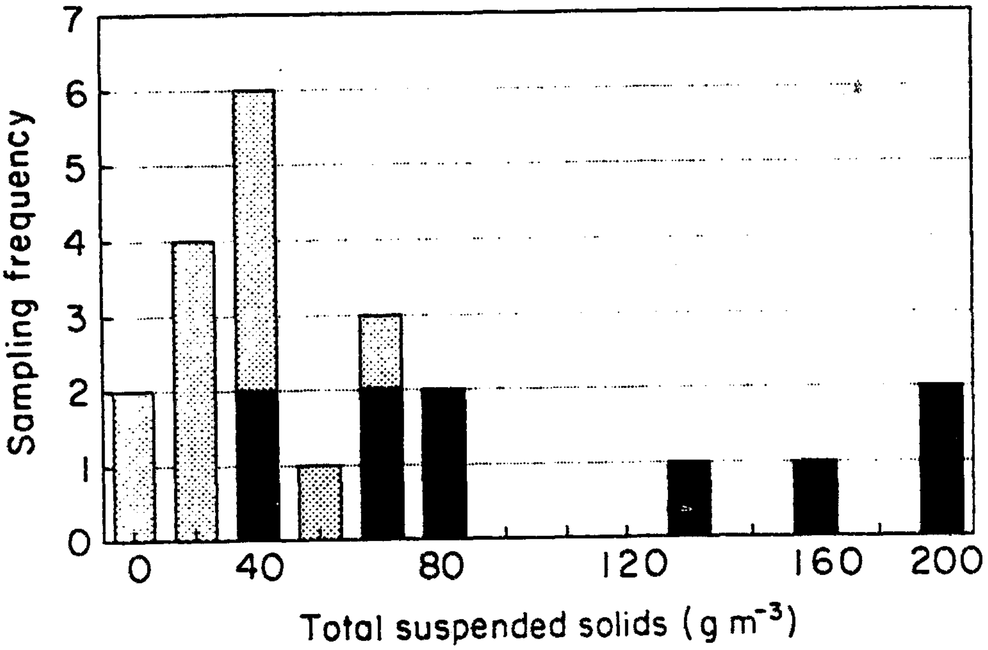

Fig. 5.6 Histogram of the sampling frequency for TSS downstream of Bridle Drift (B4) (Site 11), during overflow (▒), and when the dam was releasing water from a low-level outlet (■).

The largest impoundment, Bridle Drift (B4), had the greatest effect on material transport (Fig. 5.5). Water from Bridle Drift (B4) was discharged either from the surface (during high flow, usually in summer), or from a low-level outlet (during low flow in winter). Surface-released water carried a relatively low concentration of suspended material (11 to 66 gm^{-3}), compared to bottom-released water, which was usually sediment-laden (36 to 190 gm^{-3})(Fig. 5.6).

The concentrations of all sized particles were lower downstream of Bridle Drift (B4) than upstream, except for bottom-released water, which consisted largely of ultra fine inorganic particles (86 to 93%) (Figs. 5.3 & 5.5).

Zooplankton

In the upper reaches of the Buffalo River, Cladocera were the most numerous zooplankters, particularly downstream of Maden (B1) and Rooikrans (B2) during summer and autumn (Table 5.3). Maximum population densities (80 000 m^{-3}) occurred downstream of Laing (B3) in spring. Taxa included *Daphnia pulex*, *D. barbarta*, and *Moina sp.*. The lower reaches of the river, by contrast, were dominated by Copepoda (Table 5.3). Highest numbers of Copepoda occurred downstream of Laing (B3) in summer (108 700 m^{-3}), and downstream of Bridle Drift (B4) in winter (89 500 m^{-3}; Table 5.3). Copepod taxa included *Metadiaptomus meridianus*, *M. purcelli*, *Mesocyclops major*, and *Thermocyclops* sp.. Zooplankters were also present in small numbers at Site 0, upstream of any impoundment. (Taxa included *M. meridianus* & *Paracyclops poppei*.) Chaoboridae were occasionally found downstream of all four impoundments (usually mid to late summer), but were few in number (up to 4 700 m^{-3} downstream of Laing (B3)) compared to Cladocera and Copepoda. Release of zooplankton was greatest from Laing (B3), with an annual total of about 18 700 × 10^{6} Copepoda and 10,400 × 10^{6} Cladocera (Table 5.3).

Table 5.3 Annual number ($\times 10^6$) and maximum concentrations (per m^3) of zooplankters passing each site in the Buffalo River. Stars (*) indicate recovery to less than 5% of the numbers discharged from impoundment. The positions of the impondments (**B1** to **B4**) are indicated. 'Distance' refers to the distance from upstream impoundment, and 'Season' refers to the time of year when zooplankton densities were at a maximum. W=Winter, Sp=Spring, Su=Summer, A=Autumn.

Site	Copepoda			Cladocera			Distance (km)
	number ($\times 10^6$)	max (m^{-3})	Season	number ($\times 10^6$)	max (m^{-3})	Season	
0	0.1	146	Su	0.4	438	Su	-
1	0.4	35	Su	0.2	17	Su	-
(B1)							
2b	67	3,940	Su	279	14,400	Su	0.2
2c	108	27,200	Su	509	38,800	Su	1.4
(B2)							
3	91	9,722	Su	782	58,300	A	0.3
4	28	2,543	Su	4*	300*	W	2.6
5	3*	240*	Su	4	650	Sp	6.4
6	25	380	Sp	14	2,800	W	18.4
7	12	455	W	3	280	W	27.1
8	226	29,400	W	54	1,000	W	44.1
(B3)							
9	18,777	108,700	Su	10,398	80,200	Sp	0.5
10a	5,913	48,000	Su	2,220	14,400	Su	15.5
10b	465*	1,400*	W	855*	3,800*	Su	29.0
(B4)							
11	3,365	89,500	W	333	11,400	Sp	0.1
12	16*	279*	W	8*	704	Su	7.0
13	5	160	W	5	65*	A	14.5

The distance downstream of an impoundment for 95% of the zooplankton to fall out of suspension usually ranged between 4 km (for Cladocera downstream of Rooikrans (B2)) and 8 km (downstream of Bridle Drift (B4)). Recovery distance downstream of Laing (B3) was particularly long (35 km for Copepoda and 32 km for Cladocera; Table 5.4). A review of zooplankton recovery distances reported in the literature shows that nearly all zooplankton are eliminated after 10 km, irrespective of the flow (Table 5.4). The recovery data obtained downstream of Rooikrans (B2) and Bridle Drift (B4) are therefore comparable to those found in studies elsewhere, whereas recovery distance downstream of Laing (B3) was unusually long (Table 5.5).

Table 5.4 Recovery distances (km) for Copepoda and Cladocera downstream of impoundments (**B2** to **B4**) in the Buffalo River. Recovery distance is the distance downstream of impoundment taken for densities to reduce by 95%. Data are based on fitting a logarithmic curve to the number of zooplankters passing each site annually (presented in Table 5.3). Maden (B1) is ommitted because of the short distance (1.4 km) separating it from the upper reaches of Rooikrans (B2).

Dams	Copepoda	Cladocera
Rooikrans (B2)	6	4
Laing (B3)	35	32
Bridle Drift (B4)	8	8

Table 5.5 Recovery distances for zooplankton reported in the literature at various river discharges. Recovery distance is the distance downstream of a lake or impoundment for 95% of the zooplankton discharged to fall out of suspension.

River discharge (m^3 s^{-1})	Recovery distance (km)	Reference
9.0	5.5	(Elliott & Corlet, 1972)
7.2	7.2	(Chandler, 1937)
3.9	6.5	(Armitage & Capper, 1976)
3.5	6.5	(Armitage & Capper, 1976)
3.3	6.5	(Armitage & Capper, 1976)
3.0	8.5	(Ward, 1975a)
2.7	3.9	(Armitage & Capper, 1976)
1.1	1.4	(Armitage & Capper, 1976)
1.0	8.0	Bridle Drift **(B4)** - This study
0.6	0.2	(Illies, 1956)
0.4	4.0	(Armitage & Capper, 1976)
0.4	1.8	(Chandler, 1937)
0.3	32 to 35	Laing **(B3)** - This study
0.05	4 to 6	Rooikrans **(B2)** - This study

5.4 DISCUSSION

The River Continuum Concept (RCC; Vannote et al., 1980) suggests that leaves are broken by physical abrasion and the feeding activity of stream invertebrates, with the result that lower reaches of rivers receive organic material in the form of fine particulate material from upstream degradation (Short & Maslin, 1977; Wallace & Merritt, 1980; Wallace et al., 1982). The upper reaches of the Buffalo River are characterised by clean water which receives a high proportion of organic material in the form of fallen leaves. Further downstream, the river becomes more sediment-laden, and organic material is introduced mainly from impoundment discharge (particularly in summer), and point sources of pollution. Most transported material is very small, and in this regard the Buffalo River is typical of rivers worldwide (Sedell et al., 1978; Voshell & Parker, 1985; Meybeck, 1987). The ratio of transported CPOM:FPOM decreases with distance downstream, but the absolute amount of CPOM does not decrease downstream. Since CPOM makes up no more than 3.8% of the transported material in the river (Table 5.2), and because the highest concentrations of organic matter occur in polluted stretches of the river and downstream of impoundments (Table 5.1), there is strong evidence to suggest that the fine, very fine and ultra fine organic material in the Buffalo River is mainly from anthropogenic sources, rather than the breakdown of CPOM. Since most rivers today are in some way disturbed (particularly in their middle and lower reaches), it is likely that major sources of organic material in rivers throughout the world are anthropogenic. The RCC tends to overemphasise the role of coarse particulate matter because of an emphasis on small forested streams, and many studies clump the ultra fine material (0.6 to 80 μm) into a single category.

Since most transported material occurs within the ultra fine fraction (Table 5.2), clumping this size class not only underestimates the importance of ultra fine material, but may also mask important changes. For example, impoundments in this study had major effects on the 1.4-18 μm particle size spectrum of the receiving stream (Fig. 5.3), although the total amount of suspended material upstream and downstream of the dams was similar in three of the four cases (Table 5.1).

Part of the difficulty in assessing the degree of recovery from impoundment lies in the difficulty in separating natural changes down the river from other anthropogenic effects, such as catchment degradation and diffuse pollution. For example, the sudden increase in TSS at Site 6 (Table 5.1) was a consequence of the inflow of two large tributaries (the Cwengcwe and the Iseleni streams) which drain an overgrazed grassland catchment, in contrast to the well-wooded upper catchment of the main Buffalo River. Despite these tributaries, flow volume in the main channel did not increase because of abstraction of water for irrigation. Further downstream, urban and industrial effluent from Kingwilliamstown and Zwelitsha increased the flow and the concentration of ultra fine inorganic and organic particles.

The most obvious impoundment-induced change to transported material in the Buffalo River was the addition of plankton. Impoundments acted as generating 'nodes' of autochthonous production, shifting the river continuum (*sensu* Ward & Stanford, 1983) upstream by releasing (from the surface) plankton, which is normally associated with high order rivers. For most of the year, impoundments acted as 'transducers', swopping incoming inorganic material for outflowing organic material, and 'converting' the particle size spectrum from small to large. (Low-level releases from Bridle Drift (B4) usually had the opposite effect.) Comparison with studies elsewhere show that the magnitude of the shift is usually localised to no more than 10 km, even at flows of up to 9 m^3 s^{-1} (Table 5.5). The one exception to this occurred downstream of Laing (B3) in the Buffalo River, where particularly high numbers of zooplankton (up to 189 900 m^{-3}) were discharged, and these took 32 to 35 km to recover. High population densities of zooplankton in Laing (B3) are attributed to the enriched conditions within the impoundment, since it is situated directly downstream of the urban centres of Kingwilliamstown, Zwelitsha and Bisho, and receives urban and industrial wastes from these towns.

The change in dominance from Cladocera in the upper reaches of the Buffalo River, to Copepoda in the middle and lower reaches, is likely to be linked to changes in turbidity down the river. Evidence for this suggestion comes from Hart (1986), who found that reduced turbidities in the P. K. Le Roux impoundment in the Orange River, South Africa, favoured an increase in cladoceran biomass over copepod biomass. Similarly, clear water discharged from Gebel Aulyia Dam in the Nile River was dominated by Cladocera, whereas in more turbid influent water, Copepoda were dominant (Brook & Rzòska, 1954). The fact that reservoirs in the Buffalo River did not greatly change the Cladocera:Copepoda ratio suggests that natural changes in turbidity down the river were more important than changes induced by impoundment.

6 TAXONOMY OF BLACKFLIES IN SOUTHERN AFRICA

6.1 INTRODUCTION

This chapter examines the use of cephalic fan structure as a potential diagnostic character, describes the larvae of seven blackfly species for the first time, and provides keys and illustrations for the identification of southern African blackflies.

Blackflies are considered a relatively old group of flies (Rubtsov, 1937, 1956; Dumbleton, 1963). Although not easily preserved, their origins can be traced back about 100 to 180 million years to fossils from Australia (Riek, 1970; Crosskey, 1990). Fossil blackflies have also been reported from Baltic amber (Rubtsov, 1937) estimated at about 30 million years old (Oligocene), Pleistocene interglacial deposits from England, estimated at 130 000-120 000 years BP (Crosskey & Taylor, 1986), and deposits from Ontario, estimated at 50,000+ years BP (Williams et al., 1981). What were previously thought to be blackfly remains from Jurassic rocks in England (195 to 135 million years old) have proved, on re-examination, to have been misidentified (Craig, 1977b).

Although there are no fossil records of blackflies from Africa, Rubtsov (1937) proposed that early blackflies evolved on the African-Brazilian mainland. The absence of fossils means that theories of blackfly evolution have to be inferred from morphometric, ecological and cytological data. The most closely related flies to blackflies are Ceratopogonidae and Chironomidae (Peterson, 1989). Shared characters include the prothoracic proleg of the larva, features of the genitalia (including the formation of a spermatophore and its method of transfer), and details of wing venation (Wood, 1978). The three families are considered the sister-group to Dixidae and Culicidae on account of the larval cephalic fans (Wood, 1978).

At the turn of the centuary, no more than 6 species of blackflies where known in Africa south of the Sahara Desert (the Afrotropical Region *sensu* Crosskey & White, 1977). Today, this number has risen to 191, most of which are endemic to Africa, its islands, and the Saudi Arabian Peninsula (Crosskey, 1987a). A further 24 species are found in Africa north of the Sahara (Morroco, Algeria, Tunisia, Lybia), all of which have affinities with the Palaearctic fauna, with the exception of *S. ruficorne*, which is widespread in the Afrotropical region and Iberian Peninsula (Beaucournu-Saguez & Braverman, 1987a & b; Gagneur & Clergue-Gazeau, 1988). In southern Africa south of (and including) the Limpopo and Orange River catchments, 39 species of Simuliidae are known (Appendix A). They fall into two genera: *Prosimulium* (6 species) and *Simulium* (33 species). The former are generally restricted to cool mountain streams, particularly in the southwestern Cape, whereas the latter are common throughout the Afrotropical region.

Blackflies are easily distinguished from other flies on account of their uniform morphology, although this often makes species identification difficult (Rubtsov, 1956; Crosskey, 1981). Southern African blackflies are particularly difficult to identify because descriptions are widely dispersed in the literature, and available keys do not include all species or life-history stages. As a result, records of several species from southern Africa are now believed to be mistaken (Appendix A).

The taxonomy of blackflies has been complicated by the widespread occurrence of species complexes* within the family Simuliidae

(Crosskey, 1987b; Rothfels, 1956; 1987; Bedo, 1977; 1989a; Adler, 1986, 1987; Conn et al., 1989). Blackfly larvae have giant polytene chromosomes which are useful in identifying sibling species (Vajime & Dunbar, 1975). However, external morphological characters have often been linked to cytotypes* (Garms, 1978; Quillevere et al., 1976; Quillevere & Sechan, 1978; Dang & Peterson, 1980; Elsen & Post, 1989), implying that morphological criteria may be found to differentiate blackfly sibling species, provided one looks hard enough. Natural hybridization within the *S. damnosum* complex (Post, 1984; Boakye & Mosha, 1988) and intraspecific polymorphism (Post, 1986) suggest that species status inferred from chromosomal banding patterns suffers similar problems to those associated with traditional morpho-taxonomy. Furthermore, rearrangements with similar breakpoints may be overlooked, and identical inversions may arise independantly (Bedo, 1989a & b). Although chromosomes are useful taxonomic tools, and may provide useful information on ecological seggregation (Adler & Kim, 1986; Adler, 1986; Ciborowski & Adler, 1990), they are time-consuming to examine, and fall beyond the scope of this work. For practical reasons, this project is concerned with morphospecies**.

Ideally, taxonomic characters should be chosen on the basis of biologically meaningful content (Oliver, 1979). A taxonomic hierarchy based on arbitary characters does not infer information about evolutionary processes, and is therefore of limited use. Cephalic fan microtrichia are considered to increase surface area for food capture

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* Species complexes comprise species which are not separable morphologically (Crosskey, 1981: 6). Members of a complex are often refered to as sibling, cryptic, isomorphic or aphanic species (Steyskal, 1972). Chromosomes are commonly used to distinguish between members of species complexes, and these are refered to as 'cytospecies'. A species complex may be suspected wherever a morphospecies occupies divers (Adler, 1987) or isolated habitats.

(Ross & Craig, 1980; Braimah, 1987a & b), and therefore have direct biological meaning. Their use in the identification of southern African blackflies was therefore examined in this thesis.

Nomenclature and diagnostic characters used in the keys are based on those used by Crosskey (1960b; 1969). Additional characters include the pilous plate of the pupae (du Jardin & Fain, 1980), the number and lengths of spines at the base of the proleg circlet, the pigmentation of the postgena and the structure of the microtrichia of the larval cephalic fan.

6.2 METHODS

Primary fans of mature (those with visible gill-spots/respiratory histoblasts) larvae of 26 taxa of southern African blackflies, and a single species of *Prosimulium* from Zambia (*P. morotoense*) were examined under light and scanning electron microscopes. Descriptions of primary rays were based on median rays midway along their length. The area of a single cephalic fan was calculated by means of a gridded occular micrometer. Head-capsule lengths were measured on the postgena, between the mandibular phragma and the post-occiput (Fredeen, 1976). Drawings of mouthparts were made from slide material (mounted in Canada Balsam), with the aid of a camera lucida. First

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** Biological species are defined by Mayr (1942: 120) as 'groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups'. Blackflies are difficult to rear and mate in captivity, and species status is usually *infered* from morphological differences, and such species are termed 'morphospecies'. Morphological differences often, however, indicate *reproductive isolation* (*sensu* Mayr, 1942) or dissimilar *specific mate recognition systems* (*sensu* Paterson, 1985).

instar larvae of *S. chutteri* were examined to indicate developmental changes.

Apart from specimens of *P. morotoense* (which were obtained from the South African Institute for Medical Research, Johannesburg), and unless otherwise stated, all material used in this study was collected by the author, and is housed in the Albany Museum, Grahamstown. Specimens collected during regular sampling of benthic invertebrates in the Buffalo River (Cat. BRS) could not be used for taxonomic purposes because they were often damaged. Separate taxonomic collections (Cat. BRSO for the Buffalo River, and Cat. RPS for a regional collection) were made from larvae and pupae collected with fine forceps and placed directly in 80% ethanol, or pupae which were reared out to adults to confirm identification. Slides bear the same catalogue numbers as wet material.

Keys were constructed with the aid of the computer programme DELTA (DEscription Language for TAxonomy; Dallwitz & Paine, 1986).

6.3 ABBREVIATIONS

INSTITUTIONS

AM ..... Albany Museum, Grahamstown.
NEC .... Department of Nature and Environmental Conservation, Stellenbosch.
SAIMR .. South African Institute for Medical Research, Johannesburg.
VRI .... Veterinary Research Institute, Pretoria.
WSM .... Windhoek State Museum, Namibia.

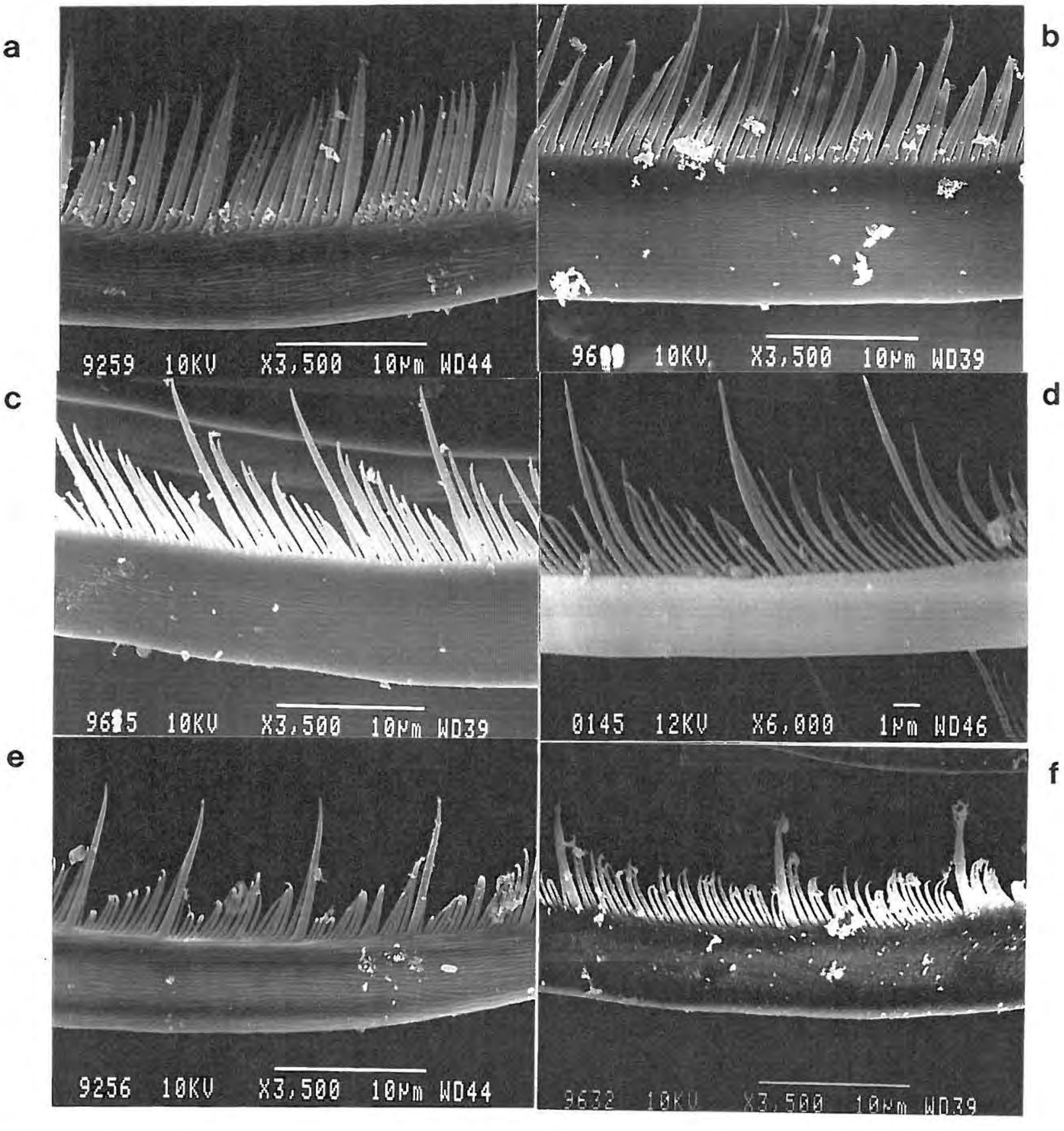

Fig. 6.2 One row, moderately differentiated microtrichial pattern of larval cephalic fan rays: **a**, *S. letabum*. **b**, *S. dentulosum*. **c**, *S. vorax*. **d**, *S. adersi*. **e**, *S. damnosum* s.l.. **f**, *S. hargreavesi*.

2. One row, moderately differentiated (Figs. 6.2 & 6.3)

Moderately differentiated microtrichia were defined as those with every 10-35th microtrichium no more than 6 times the length of the shortest microtrichium. Microtrichia in this category were grouped into repeating series. Each series, or group, consisted of 6 to 32 microtrichia of increasing length; They closely resembled those of the so-called 'primitive' *P. morotoense*, and included a wide range of species, from those with strong rays and small fans relative to body size (*S. dentulosum*, *S. vorax* and *S. letabum*), to those with delicate rays and large fans relative to body size (*S. adersi*, *S. nigritarse* and *S. ruficorne*). The former were found in fast-flowing water, including waterfalls, whereas the latter were found in slow to fast-flowing water (Table 6.1). With the exception of *S. brachium*, all blackfly taxa found in impoundment outlets in southern Africa had cephalic fans of this type (Table 6.1).

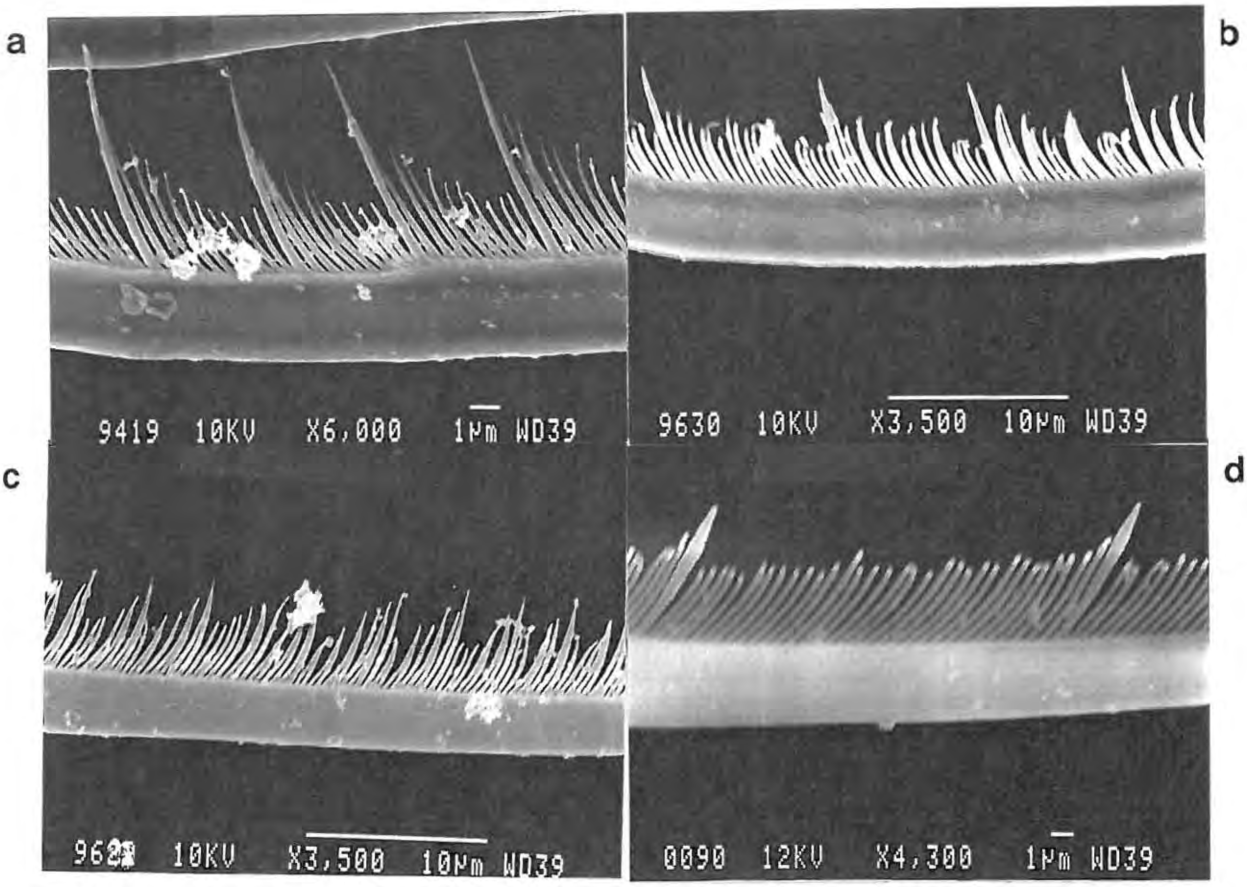

Fig. 6.3 One row, moderately differentiated microtrichial pattern of larval cephalic fan rays: **a**, *S. bovis.* **b**, *S. nigritarse.* **c**, *S. mcmahoni.* **d**, *S. ruficorne.*

3. **One row, highly differentiated** (Figs. 6.4 & 6.5)

Highly differentiated microtrichia were defined as those with every 6-12th microtrichium at least 6 times longer than the shortest microtrichium. Microtrichia in this category were grouped into repeating series. Each series, or group, consisted of 7 to 12 microtrichia of increasing length. Included in this category were most southern African members of the Subgenus *Pomeroyellum*. Under light microscope (at 400 × magnification), microtrichia on these fans appeared peg-like and of equal length (similar to *P. morotoense*). Closer examination (under oil immersion at 1000 × magnification) showed that each 'peg' consisted of a group of 6-12 highly differentiated microtrichia. All members within this category were found in slow-flowing, clear streams (Table 6.1).

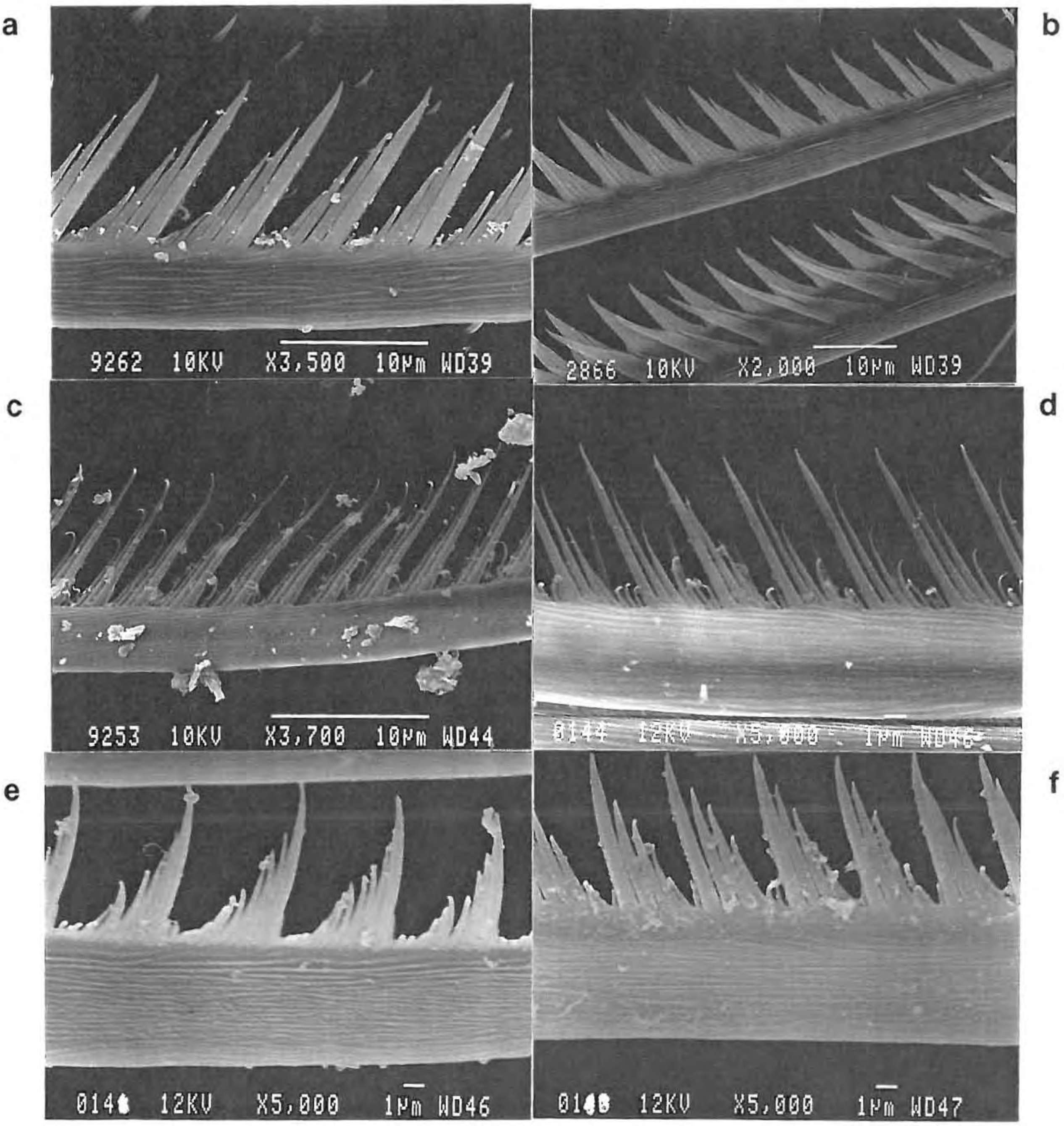

Fig. 6.4 One row, highly differentiated microtrichial pattern of larval cephalic fan rays: **a**, *S. rutherfoordi*. **b**, *S. brachium*. **c**, *S. cervicornutum*. **d**, *S. hirsutum*. **e**, *S. harrisoni*. **f**, *S. katangae*.

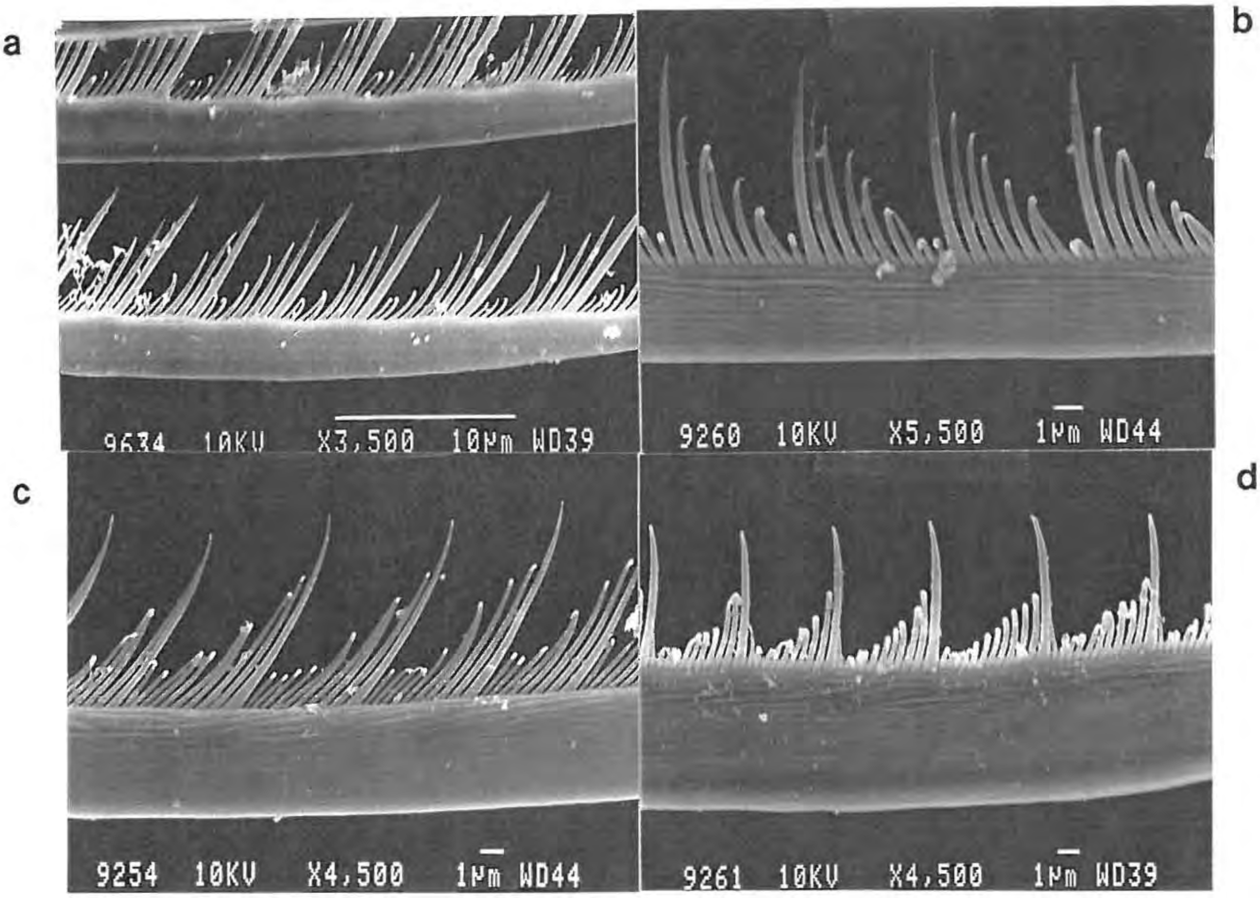

Fig. 6.5 One row, highly differentiated microtrichial pattern of larval cephalic fan rays: **a**, *S. bequaerti*. **b**, *S. impukane*. **c**, *S. rotundum*. **d**, *S. merops*.

4. **One row, reduced** (Fig. 6.6)

Fans characterised by delicate rays (3 µm width) carrying a single row of microtrichia, consisting of a few long (15 µm) and flexible microtrichia interspersed by 13 to 17 short (1 µm) microtrichia. One species, *S. griseicolle*, found in slow-flowing, turbid reaches of the Orange River, belonged to this category (Table 6.1).

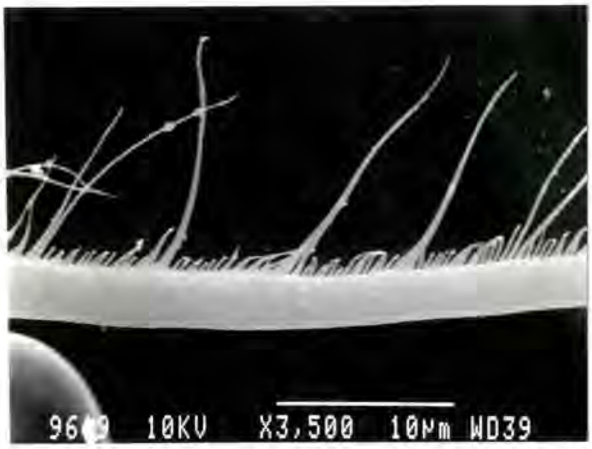

Fig. 6.6 Reduced microtrichial pattern of larval cephalic fan ray of *S. griseicolle*.

5. Two rows, highly differentiated, without lateral fringe (Fig. 6.7)

A complex fan structure, with each ray carrying two rows of microtrichia, consisting of long microtrichia (14 μm) interspersed by short microtrichia (Fig. 6.7b). Long microtrichia were flexible and bore curved tips which hooked around the base of microtrichia on adjacent rays. One species, *S. chutteri*, belonged to this catergory. The cephalic fan rays of first instar larvae of *S. chutteri* bore one row of moderately differentiated microtrichia, resembiling the fans in Category 2 (Fig. 6.7a). *Simulium chutteri* is found in fast-flowing reaches of turbid rivers (Chutter, 1968; de Moor, 1982a; de Moor et al., 1986).

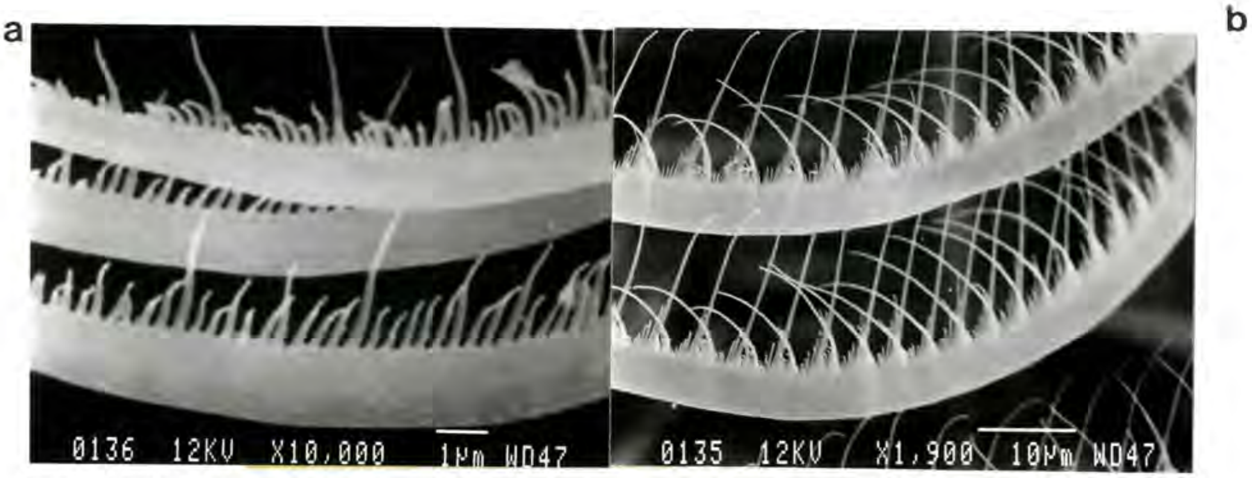

Fig. 6.7 *Simulium chutteri* microtrichial pattern of larval cephalic fan rays: **a**, first instar (Category 2). **b**, final instar (Category 5).

6. Two rows, highly differentiated, with lateral fringe (Figs. 6.8 & 6.9)

Similar to *S. chutteri*, but rays were stronger and microtrichia more complex. Each ray bore two rows of unusually long and flexible microtrichia with curved tips (Fig. 6.8b). The tips hooked around the base of microtrichia on adjacent rays, and appeared to be held in place by a lateral fringe of short microtrichia which were curved to the rear. The microtrichia formed a coupling network in much the same way as a bird's feather, or hymenoptera wing. A strong peg-like microtrichium, and two smaller peg-like microtrichia, occurred between long microtrichia (Fig. 6.9. Members of the Subgenus *Freemanellum* (*S. debegene* and *S. hessei*), which are restricted to fast-flowing, mountain streams, were included in this category (Table 6.1).

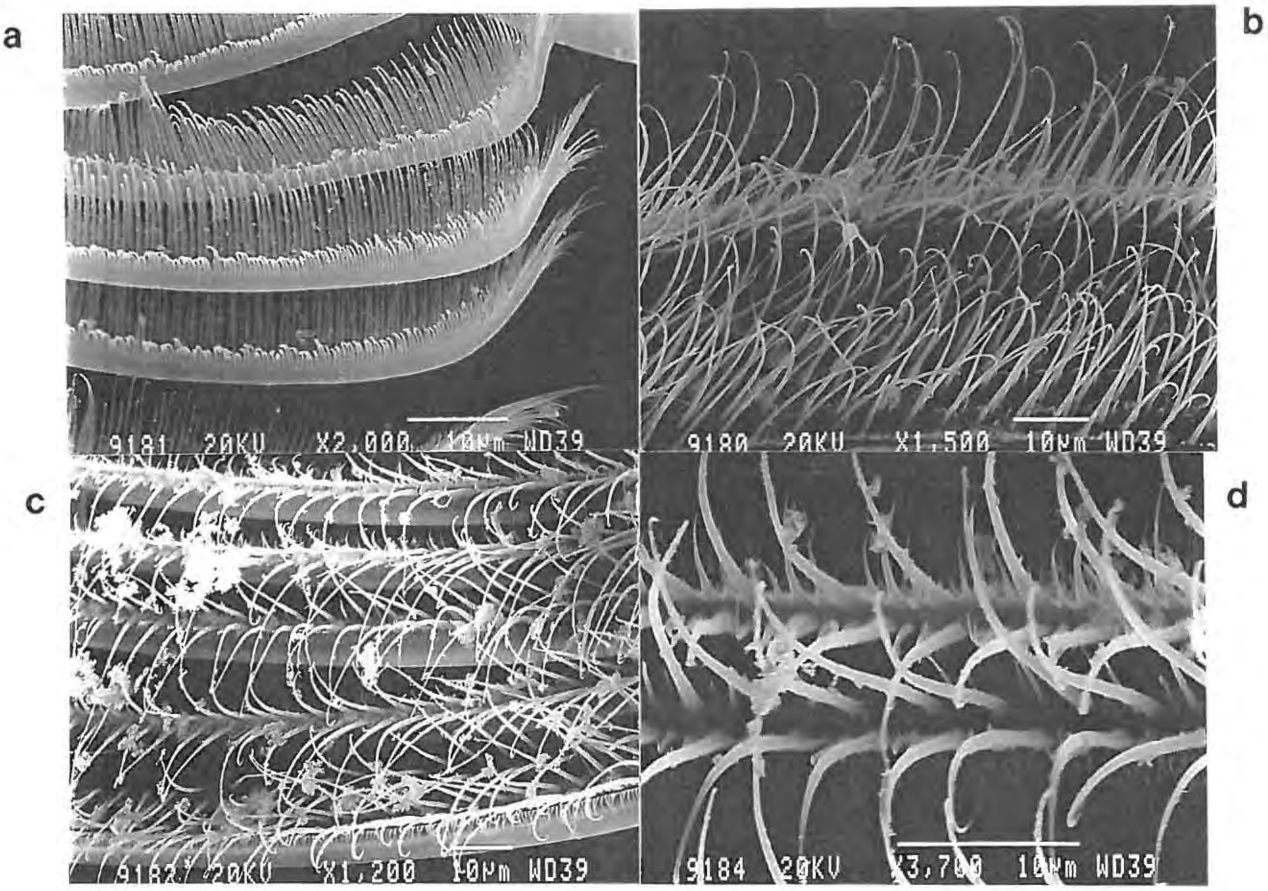

Fig. 6.8 Two rows, highly differentiated microtrichial pattern of larval cephalic fans rays of *Simulium hessei*. - **a**, lateral aspect of fan apex. **b**, lateral aspect showing long microtrichia with curved tips. **c**, ventral aspect of fan rays. **d**, close-up of ventral aspect of two fan rays.

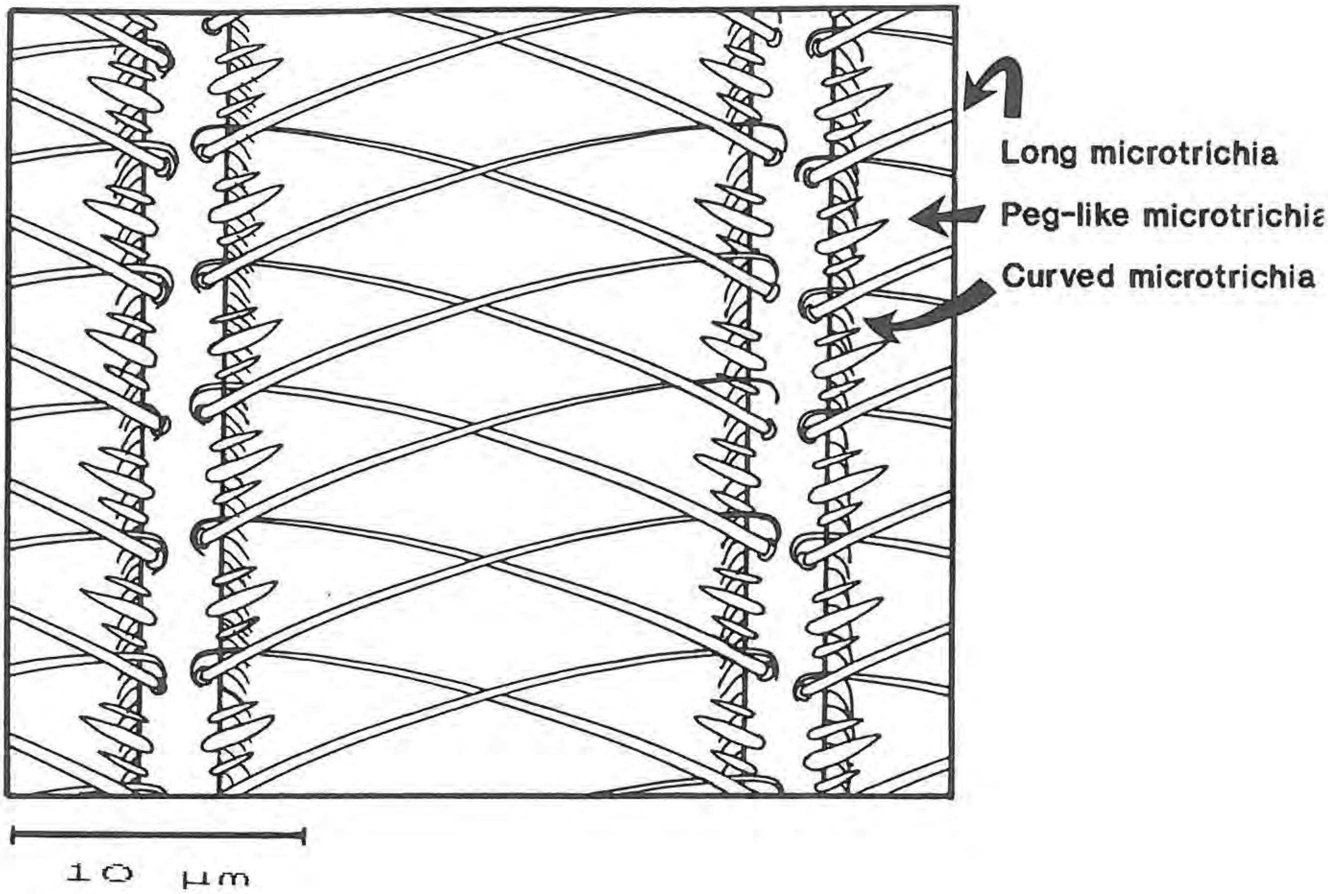

Fig. 6.9 Diagramatic view of the ventral aspect of two cephalic fan rays of *S. hessei* (Category 6: Two rows, highly differentiated). Each ray bears two rows of long microtrichia with curved tips which hook around the base of microtrichia on adjacent rays. Long microtrichia are flanked by short microtrichia which curve to the rear, and hold tips of microtrichia from adjacent rays in position to form a coupling network. [Scale is in µm.]

Table 6.1 Specifications of cephalic fan structure of final instar blackfly larvae, grouped into 6 categories of increasing complexity. Subgenus status is indicated in brackets (see Appendix A). 'Microtrichia length' refers to the length of the longest microtrichia, and 'grouping' refers to the number of microtrichia in a group.

Microtrichia type Species	Fan area (mm^2)	Ray length (mm)	Ray width (μm)	Microtrichia length (μm)	Microtrichia grouping	Larval habitat
1. One row, undifferentiated						
P. (Pro) morotoense	0.9	1.0	27	20	-	Fast-flowing, mountain streams
2. One row, moderately differentiated						
STRONG RAYS						
S. (Ana) dentulosum	0.9	0.7	10	11	17-22	Waterfalls
S. (Met) letabum	0.4	0.6	9	13	12	Mountain streams
S. (") vorax	0.6	0.5	9	12	6-11	Fast-flowing rivers
WEAK RAYS						
S. (Edw) damnosum s.l.	0.5	0.5	6	9	17	Impoundment outlets
S. (Mei) adersi	0.7	0.5	4	4	16	" "
S. (Met) med/harg.	0.3	0.5	7	7	13-25	" "
S. (") bovis	?	?	5	7	11	" " "
S. (Nev) nigritarse s.s	0.7	0.9	5	9	20	" "
S. (") ruficorne	0.9	0.6	7	9	32	Temporary streams & trickles
S. (Pom) mcmahoni	?	0.4	3	5	10	Slow-flowing, turbid rivers
3. One row, highly differentiated						
S. (Mei) hirsutum	0.5	0.5	5	6	8	Slow-flowing, clear streams
S. (Nev) brachium	0.6	?	6	8	8	" " " "
S. (") rutherfoordi	0.5	0.7	6	10	7-10	" " " "
S. (Pom) alcocki	0.9	0.6	4	6	8	" " " "
S. (") bequaerti	0.5	0.6	3	8	10	" " " "
S. (") cervicornutum	0.7	0.5	5	11	10	" " " "
S. (") harrisoni	0.4	?	7	10	12	" " " "
S. (") katangae	0.5	?	8	10	6	" " " "
S. (") merops	0.4	0.7	6	8	8	" " " "
S. (") rotundum	0.6	0.5	5	7	10	" " " "
S. (") unicornutum	0.6	0.4	5	6	10	" " " "
S. (") impukane	0.8	0.6	4	7	9	Slow to fast-flowing, clear streams
4. One row, reduced						
S. (Bys) griseicolle	?	?	3	15	13-17	Slow-flowing, turbid rivers
5. Two rows, highly differentiated, without lateral fringe						
S. (Met) chutteri	0.4	0.4	4	14	-	Fast-flowing, turbid rivers
6. Two rows, highly differentiated, with lateral fringe						
S. (Fre) debegene	0.7	0.8	16	40	-	Waterfalls
S. (") hessei	0.7	0.8	16	43	-	"

6.5 DISCUSSION

Trophic relations play an important part in ecological theory, influencing energy flow and material cycling between biotic and abiotic components, and linking biotic components (Odum, 1968). Stream invertebrates have been classified into functional feeding groups (FFG's), which appears to be an appealing classification because it uses *biologically meaningful* characters, and obviates the need for 'time-consuming' and skilled taxonomic identifications (Cummins, 1973, 1974). Although a classification based on functional characters alone is limited because it does not infer information about evolutionary processes, and may lead to tautological arguments about adaptation, it can be useful in conjunction with a phylogenetic classification. For example, feeding structures may provide useful ecological information, but are of little use in a phylogenetic analysis (because it is the adults which mate). By contrast, behavioural and morphological characters associated with reproduction may provide useful phylogenetic information (Oliver, 1979).

Microtrichial patterns of cephalic fans of southern African blackfly larvae generally corresponded with subgeneric taxonomic groupings (Table 6.1). However, microtrichia of the following three pairs of closely related species (which were formerly indistinguishable, or difficult to distinguish, as larvae), are very different:

S. (Mei) adersi (Cat. 2: Fig. 6.2d) and *S. (Mei) hirsutum* (Cat. 3: Fig. 6.4d).

S. (Nev) nigritarse (Cat. 2: Fig. 6.3b) and *S. (Nev) brachium* (Cat. 3: Fig. 6.4b).

S. (Met) bovis (Cat. 2: Fig. 6.3a) and *S. (Met) chutteri* (Cat. 5: Fig. 6.7).

These species are found in different habitats (Table 6.1), and are likely to have different feeding ecologies, despite their close [phylogenetic] relationship. Even within species, cephalic fan structures differ (Fig. 6.7), which suggests that blackfly cephalic fan microtrichia are evolutionary flexible characters, closely adapted to performing specific tasks. These observations, together with the fact that blackfly larvae do not always filter-feed (see Burton, 1971, 1973; Craig, 1987; Currie & Craig, 1987), suggests that a great deal of information is lost by lumping blackfly larvae into a single taxonomic or functional group.

One of the most widespread blackflies in Africa is *S. ruficorne*, which is often found where current speeds are negligible. This species is therefore likely to supplement its feeding by scraping epilithic algae. The hypostomial teeth of *S. ruficorne* are unusually prominent (Fig. 6.27), but it is not known whether they are used for scraping. Craig (1977a) shows a clear relationship between the shape of mandibular teeth and hypostomial teeth, and it has been suggested that the two are used in cutting silk strands (Crosskey, 1973; Craig, 1977a). The feeding behaviour of *S. ruficorne* under different environmental conditions needs to be observed in detail, and compared to that of *Simulium* with typical hypostomia before any conclusions may be drawn. Hypostomial teeth are useful taxonomic characters, and an understanding of their function among blackfly larvae may be useful in distinguishing between facultative and obligative filterers. Furthermore, the functional responses of blackfly larvae with different fan structures under different feeding conditions (flow velocity, particle sizes and particle concentrations), may be useful in fine-tuning the FFG concept for blackfly larvae.

Food is a limiting resource for blackfly larvae at times (Morin et al., 1988b), and ways to mitigate food limitation are likely to evolve. Kurtak (1978) attributed the high filtration efficiency of *Cnephia dacotensis* feeding on small particles (5 to 10 μm) to the presence of two rows of microtrichia. Similarly, the success of *S. chutteri* in the Great Fish River, South Africa, following the introduction of Orange River water by canal, has been attributed to their ability to feed more efficiently at high Reynolds number (>1,300) compared to the previously dominant *S. nigritarse* (Barber, 1985). Cephalic fan microtrichia of *Freemanellum* larvae, found in upper-reach, food-poor waterfalls, are highly evolved (Figs. 6.8 & 6.9). By contrast, the microtrichia of *S. griseicolle* larvae, found in large, turbid rivers, are reduced (Fig. 6.6). An implication of these observations is that particle concentration and water velocity are important environmental constraints in the evolution of cephalic fan structure among blackfly larvae: There has been a trend towards a more complex fan among species inhabiting fast-flowing, clear water (usually found in low order streams), and a simplification among species inhabiting slow-flowing, turbid water (usually found in high order streams and rivers). The cephalic fan of *S. fulvinotum*, found in clear-water streams in the Amazon Basin (Lacey & Lacey, 1983), is typical of *Pomeroyellum* larvae found in clear-water streams in southern Africa, which suggests that the proposed classsification of cephalic fan structures (Table 6.1), is widely applicable. The lack of structural differences among cephalic fans of species examined by Chance (1970) and Nübel (1984) is most likely because the species examined were from similar hydrodynamic and/or trophic conditions.

6.6 DESCRIPTIONS OF SEVEN SPECIES OF LARVAL BLACKFLIES PREVIOUSLY ONLY KNOWN AS ADULTS AND PUPAE

Simulium (Freemanellum) hessei, Fig. 6.15.

DESCRIPTIONS: Gibbins (1941, male, female, pupa), Freeman & de Meillon (1953, male, female, pupa), Crosskey (1969, pupa).

Length: of mature larvae 8-10 mm (n=6).

Head: Head-capsule length 0.46-0.54 mm (n=6). Head-capsule dark brown. Head-spots with positive pigmentation pattern consisting of 4-9 discrete anteromedian spots, more diffuse and broader posteromedian spots, a single anterolateral spot in line with the eye-spots on either side, and diffuse posteromedian dark patches (Fig. 6.15b). Lateral aspect of head with a clear round patch surrounding the eye-spots, and three rather indistinct darker pigmented spots below the eye-spots (Fig. 6.15c). Eye-spots fully developed. Gena with a pigmented mid-lateral stripe and a small posterior tentorial pit on either side of the postgenal cleft (Fig. 6.15d). Postgenal cleft large; pointed apically and parallel-sided basally (Fig. 6.15d). Postgenal bridge equal in length to hypostomium; with a pale median stripe (Fig. 6.15d). Hypostomium with 9 apical teeth, median and lateral teeth slightly produced; lateral serrations present but small and embedded in hypostomium so that they appear absent (Fig. 6.15e). Hypostomium with 9-12 setae in each row; rows divergent from lateral margin of hypostomium (Fig. 6.15e). Antenna weakly pigmented except for third segment which is strongly pigmented (Fig. 6.15h); antenna longer (600 μm) than the stem of the cephalic fan (450 μm). Ratio of first antennal segment length:breadth at base 5:1; length ratio of first three segments 1:1.6:0.6. Mandible with large comb-teeth; first comb tooth smaller than second, and second smaller than third (Fig. 6.15f). Mandibular serrations consisting of 2-3 large teeth of equal size, followed by 2-4 smaller serrations (Fig. 6.15g). Maxillary palp darkly pigmented except for the tip, which is clear; length 190 μm; with a conspicuous tuft of hairs at the base of the palp (Fig. 6.15i). Ratio of maxillary palp length:width at base 3.2:1. Cephalic fan with 55-66 primary rays (n=5); width of single fan ray 8-13 µm; length 0.73-0.87 mm (n=3). Area of single cephalic fan 0.67 mm^2 (0.57-0.82 mm^2; n=5). Microtrichia unusual: consisting of two rows of very long (30-35 µm) and flexible microtrichia with curved tips, evenly spaced between three short (2-3 µm), peg-like microtrichia, of which the median one is the longest (Fig. 6.8). The two rows are flanked by a fringe of short (2-3 µm) microtrichia which are curved to the rear (Fig. 6.8).

Thorax and abdomen: Abdomen bulbous posteriorly; integument dark in colour (Fig. 6.15a). Gill-spot dissected composed of four short and stout filaments and a short basal projection (Figs. 6.15j & k). Proleg circlet with 8-13 hooks in each row. Base of proleg bears laterally and dorsally a row of long (up to 40 µm), basally paired spines. Thoracic and abdominal cuticle with a few scattered simple setae (30 µm long). Ventral papillae absent. Accessory sclerites absent. Rectal gill with 9-10 secondary lobules on each lobe. Posterior circlet with 260-280 rows of 34-40 hooks. Anal sclerite extends to 46-55th row.

MATERIAL EXAMINED: 32 larvae and 9 pupae were collected from Blindekloof River (32° 41'S, 25° 16'E), a tributary of the Swartkops River near Port Elizabeth, 21.xi.1988, at an altitude of 150 m (Cat. GEN 830a). Pupae were reared to confirm adult identification (Cat. RPS 2).

TAXONOMIC NOTES: Larvae of *S. hessei* are distinguished from other members of the Subgenus *Freemanellum* by the presence of 2-3 large and 2-4 small mandibular serrations (Fig. 6.15g), smaller body length (8-10 mm), the basal structure of the gill-spot (Figs. 6.15j & k), a dark pigmented pigmented stripe on either side of the postgenal cleft (Fig. 6.15d), and the postgenal cleft with parallel sides (Fig. 6.15d). In Crosskey's (1960b) key they key out to couplet 19.

Longer microtrichia have curved tips which hook around the base of microtrichia on adjacent rays, in much the same way as the rays of bird's feathers, or coupling mechanism of a hymenoptera wing, forming a network. The short, curved mictrotrichia which flank the two rows of long microtrichia help to hold the tips of microtrichia from adjacent rays in place. This unusual feature is most likely related to their preference for fast-flowing, shallow mountain torrents, where particulate material (food) is scarce.

Simulium (Metomphalus) letabum, Fig. 6.21.

DESCRIPTIONS: de Meillon (1935, male, female, pupa), Freeman & de Meillon (1953, male, female, pupa).

Length: of mature larvae 5.8-6.4 mm (n=5).

Head: Head-capsule length 0.45-0.48 mm (n=4). Head-capsule amber-brown in colour. Head-spots with positive pigmentation pattern, sometimes very pale (Fig. 6.21b). Lateral spect of head with a row of three pigmented spots below and behind eye-spots (Fig. 6.21c). Eye-spots fully developed. Gena with a pigmented mid-lateral stripe and a posterior tentorial pit on each side of the postgenal cleft (Fig. 6.21d). Postgenal cleft large; pointed apically; constricted basally (Fig. 6.21d). Postgenal bridge equal in length to hypostomium (Fig. 6.21d). Hypostomium with 9 rather blunt apical teeth: only the median tooth produced (Fig. 6.21e). 3-5 lateral serrations; hindmost serration level to first hypostomial seta (Fig. 6.21e). Hypostomium with 5-7 setae in each row; rows divergent from lateral margin of hypostomium (Fig. 6.21e). Distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.21e). Antennae longer (400 μm) than stem of cephalic fan (300 μm); weakly pigmented. Ratio of first antennal segment length:breadth at base 3.8-5.5:1; length ratio of first three segments 1:1:0.5. Mandible with outer margin not strongly arched; first three comb-teeth sub-equal in size (Fig. 6.21i). Mandible with a long, thin posterior serration followed by a very small serration (Fig. 6.21f). Maxillary palp length 0.14-0.15 mm (n=5), darkly pigmented except for pale apex (Fig. 6.21j); an inconspicuous tuft of hair at the base of the palp. Ratio of maxillary palp length:width at base 2.8-3.7:1 (n=5). Cephalic fan with roughly 50-53 primary rays; width of single ray 7-9 μm (Fig. 6.2a); length 0.52-0.65 mm. Area of single cephalic fan 0.39-0.48 mm^2. Microtrichia strong: consisting of equally spaced groups of 12 microtrichia arranged in size from short (6 μm) to long (13 μm) (Fig. 6.2a).

Thorax and abdomen: Body shape normal; integument dark in colour (white ventrally, grey dorsally; Fig. 6.21a). Gill-spot composed of two large and semi-transparent basal filaments, each bearing a short secondary filament at the apex, and 14 median filaments arising basally (Figs. 6.21k & l). Proleg circlet with 10 hooks in each row, the base of which bears a row of long (40 μm) simple spines. Thoracic cuticle with a few minute colourless setae dorsally. Abdominal cuticle with a few, scattered simple setae (Fig. 6.21h). Ventral papillae absent. Accessory sclerites absent. Rectal gill simple, trifid shape. Posterior circlet with 180 rows of 27-34 hooks. Anal sclerite extends to 35th row.

MATERIAL EXAMINED: 3 larvae and 12 pupae were collected from the upper reaches of the Buffalo River, eastern Cape (32°44'S, 27°17'E), 14.i.1989, at an altitude of 530 m (Cat. BRSO 334d). 87 larvae and 14 pupae were collected from the same site on the 3.iii.1989 (Cat. BRSO 351c). Pupae were reared to confirm adult identification (Cat. BRSO 341).

TAXONOMIC NOTES: Larvae of *S. letabum* are easily confused with *S. vorax*, *S. medusaeforme* and *S. hargreavesi*. They are distinguished from these three species by a longer postgenal bridge (equal in length to the hypostomium) and the structure of the gill (Figs. 6.21k & l). They differ from larvae of *S. vorax* by their smaller size (up to 6.5 mm), and the absence of a pale median stripe on the postgenal bridge. They differ from *S. medusaeforme* and *S. hargreavesi* by the postgenal bridge which is equal in length to the hypostomium (Fig. 6.21d), simple rectal gill, elongated anterior mandibular serration (Fig. 6.21f) and the shape of the postgenal cleft (Fig. 6.21d). In Crosskey's (1960b) key they key out to couplet 20.

Simulium (Nevermannia) rutherfoordi, Fig. 6.23.

DESCRIPTIONS: de Meillon (1937, male, female, pupa), Wanson & Henrard (1944, pupa), Freeman & de Meillon (1953, male, female, pupa), Crosskey (1969, male, pupa). Rivosecchi & Merighi (1970) describe larvae and pupae of S. ?rutherfoordi from Yemen.

Length: of mature larvae 6-7 mm.

Head: Head-capsule length 0.48 mm. Head-capsule pale in colour. Head-spots with positive pigmentation pattern (sometimes very pale) in the form of an arrow-head, consisting of an anteromedian row of four spots followed by a posteromedian row which broadens posteriorly, and 2 anterolateral rows directed obliquely posterolaterally from the mid-line (Fig. 6.23b). Lateral aspect of head without distinctive pattern (Fig. 6.23c). Eye-spots fully developed. Postgenal cleft small; quadrate; not constricted basally (Fig. 6.23d). Postgenal bridge longer than hypostomium (Fig. 6.23d). Hypostomium with 9 apical teeth, only the median tooth produced (Fig. 6.23e). Lateral serrations 4-5 in number, with at least two strongly developed; hindmost serration posterior to first hypostomial seta (Fig. 6.23e). Hypostomium with 4-6 setae in each row, nearly parallel to lateral margin of hypostomium (Fig. 6.23e). Distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.23e). Antennae longer (560 μm) than stem of cephalic fan (330 μm). Ratio of first antennal segment length:breadth at base 5.5-6.7:1; length ratio of first three segments 1:0.9:0.5. Mandible with outer margin not strongly arched; first comb-tooth larger than second and third, second larger than third (Fig. 6.23g). Mandible with a large and small posterior serration (Fig. 6.23h). Maxillary palp 0.14-0.15 mm long; distinctly pigmented (basal $^{7}/_{10}$ dark; apex transparent); with a few inconspicuous hairs at the base of the palp. Ratio of maxillary palp length:width at base 3.5-3.8:1 (Fig. 6.23f). Cephalic fan with 38-52 primary rays (n=4); width of single fan ray 6 μm (Fig. 6.4a); length 0.6-0.8 mm (n=3). Area of single cephalic fan 0.54 mm^2 (0.4-0.7 mm^2; n=12). Microtrichia stiff and thick (1 μm at base); strongly unequal in length: consisting of evenly spaced groups of 7-10 microtrichia arranged in size from short (1.3 μm) to long (10-13 μm)(Fig. 6.4a).

Thorax and abdomen: Body shape normal; integument pale in colour (Fig. 6.23a). Gill-spot composed of 4 thin, tightly coiled filaments (Fig. 6.23l). Proleg circlet with about 37 rows of 8 hooks in each row. Base of proleg bears a row of lateral spines. Thoracic cuticle with a few, scattered simple setae dorsally (Fig. 6.23i). Abdominal cuticle with a few, scattered simple setae. Ventral papillae large and conspicuous. Accessory sclerites absent. Rectal gill with 7-9 secondary lobules on each lobe. Posterior circlet with 79-88 rows of 11 hooks. Anal sclerite extends to 16th row.

MATERIAL EXAMINED: 12 larvae and 3 pupae were collected from the source of the Buffalo River, eastern Cape (32°43'S, 27°14'E), 3.iii.1989 at an altitude of 1120 m (Cat. BRSO 350h). 40 larvae and 3 pupae were collected from the same river further downstream (32°44'S, 27°17'E), 15.x.1988 at an altitude of 530 m. (Cat. BRS 324c). Pupae were reared out to confirm adult identification.

TAXONOMIC NOTES: Larvae of *S. rutherfoordi* resemble those of *S. nigritarse* and *S. brachium*, from which they are distinguished by the distinctive pigmentation of the cephalic apotome (Fig. 6.23b), absence of pigmented spots below the eye-spots (Fig. 6.23c) and the compound rectal gill. In Crosskey's (1960b) key they key out to couplet 6.

Simulium (Nevermannia) katangae, Fig. 6.25.

DESCRIPTIONS: Fain (1951, male, female, pupa), Freeman & de Meillon (1953, male, female, pupa).

Length: of mature larvae 0.55-0.58 mm (n=2).

Head: Head-capsule length 0.40-0.42 mm (n=2). Head-capsule brown in colour. Head-spots absent or with slight positive pigmentation pattern (Fig. 6.25b). Lateral aspect of head without distinctive pattern (Fig. 6.25c). Eye-spots fully developed. Postgenal cleft small; quadrate; not constricted basally (Fig. 6.25d). Postgenal bridge longer than hypostomium (Fig. 6.25d). Hypostomium with 9 apical teeth, median and lateral teeth moderately produced (Fig. 6.25g). Lateral serrations 6-7 in number, hindmost serration posterior to first hypostomial seta (Fig. 6.25g). Hypostomium with 4-5 setae in each row, nearly parallel to lateral margin of hypostomium (Fig. 6.25g). Distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.25g). Antennae slightly longer (430 μm) than stem of cephalic fan (330 μm); weakly pigmented. Ratio of first antennal segment length:breadth at base 5.4:1; length ratio of first three segments 1:1.2:0.7. Mandible with outer margin not strongly arched; first comb-tooth larger than second, second larger than third (Fig. 6.25h). Mandible with a large and small posterior serration (Fig. 6.25h). Maxillary palp 0.14 mm long (basal $^7/_{10}$ brown; apex transparent); a few inconspicuous hairs at the base of the palp. Ratio of maxillary palp length:width at base 3.6:1 (Fig. 6.25f). Cephalic fan with 53 primary rays. Width of single fan ray 7-10 μm; Area of single cephalic fan 0.49-0.52 mm^2 (n=2). Microtrichia stiff and thick; strongly unequal in length: consisting of groups of 6 microtrichia arranged in size from short (1.0 μm) to long (8-10 μm) (Fig. 6.4f).

Thorax and abdomen: Body shape normal; integument dark in colour (Fig. 6.25a). Gill-spot composed of four tubular filaments. Base of proleg bears a row of 15-17 lateral spines, bifid at base. Thoracic and abdominal cuticle with a few, scattered simple setae dorsally (up to 50 μm long). Ventral papillae present, but not large. Accessory sclerites absent. Posterior circlet with 77 rows of 12-14 hooks. Anal sclerite extends to 12th row.

MATERIAL EXAMINED: 2 mature larvae collected from the Bulolo River, Port St. Johns, Transkei (31°38'S, 29°31'E), 3.xii.1989 at an altitude of 10 m (Cat. RPS 46f). Pupal gills were dissected to confirm identification.

TAXONOMIC NOTES: Larvae of *S. katangae* are distinguished by the absence of compound abdominal setae, absence of pigmented stripes on the gena (lateral and ventral: Figs. 6.25c & d), and the pigmentation of the cephalic apotome (Fig. 6.25b). In Crosskey's (1960b) key *S. katangae* key out as *S. aureosimile*, a tropical species (Cameroon, Kenya, Nigeria: Crosskey, 1987a), from which they are distinguished by head pigmentation and fewer (4-5) hypostomial setae.

Simulium (Pomeroyellum) bequaerti, Fig. 6.29.

DESCRIPTIONS: Gibbins (1936b, male, female, pupa), Bequaert (1938, pupa), Freeman & de Meillon (1953, male, female, pupa), Crosskey (1969, male, pupa).

S. phoroniforme de Meillon (1937, male, female, pupa).

Length: of mature larvae 3.8-5.2 mm (n=5).

Head: Head-capsule length 0.36-0.4 mm (n=12). Head-capsule pale in colour. Head-spots with negative pigmentation pattern, very pale in some specimens (Fig. 6.29b). Specimens in which the head-capsule is pigmented have a diagnostic white stripe above a pale circular area surrounding the eye-spot, and an M-shaped pigmented region on the side of the head (Fig. 6.29c). Eye-spots fully developed. Postgenal cleft small, (approximately the same length as hypostomium); rounded (or slightly pointed) apically; parallel-sided basally (Fig. 6.29d). Postgenal bridge longer than hypostomium (Fig. 6.29d). Hypostomium with 9 apical teeth and 6-8 lateral serrations. Median and corner teeth strongly produced; lateral serrations prominent; hindmost serration well posterior to first hypostomial seta (Fig. 6.29e). Hypostomium with 5-6 setae in each row (n=4), rows parallel to lateral margin of hypostomium (Fig. 6.29e). Antennae lightly and evenly pigmented and much longer (490-510 μm) than the stem of the cephalic fan (300 μm). Ratio of first antennal segment length:breadth at base 6.9-7.4 :1 (n=3); length ratio of first three segments 1:0.7-1.0:0.6 (Fig. 6.29h). Mandible with outer margin not strongly arched; first and third comb-teeth larger than second (Figs. 6.29f & k). Mandibular serrations consisting of a single large serration followed by a smaller serration (Fig. 6.29g). Maxillary palp length 107-115 μm (n=5); basal $^2/_3$ lightly pigmented (Fig. 6.29i); with an inconspicuous tuft of hairs at the base of the palp. Ratio of maxillary palp length:width at base 3.0-3.7 :1 (Fig. 6.29i). Cephalic fan with 43-52 primary rays (n=4); width of single fan ray 3.4 μm (Fig. 6.5a); length 580-630 μm (n=5). Area of single cephalic fan 0.50-0.58 mm^2 (n=3). Microtrichia long and thin; strongly unequal in length: consisting of groups of 10 microtrichia arranged in size from short (1.3 μm) to long (8 μm) (Fig. 6.5a)

Thorax and abdomen: Body shape normal; integument pale in colour with grey segments (Fig. 6.29a). Gill-spot composed of a single long filament (Figs. 6.29l & m). Proleg circlet with 7-8 hooks in each row. Base of proleg bears a row of simple and bifid spines laterally and dorsally. Thoracic cuticle with a few scattered simple setae (12 μm long). Abdominal cuticle with simple and numerous compound setae (Fig. 6.29j). Ventral papillae large. Accessory sclerites absent. Rectal gill with 5-7 secondary lobules on each lobe. Posterior circlet with 80-90 rows of 10-12 (n=3) hooks. Anal sclerite extends to 13-14th row.

MATERIAL EXAMINED: 13 larvae and 16 pupae were collected from the Wewe River near Tonga, Natal (29° 32'S, 31° 06'E), 17.vi.1989 at an altitude of 100 m (Cat. RPS 20). Pupae were reared to confirm adult identification. 3 larvae were collected in the Tyusha River, a tributary of the Buffalo River, eastern Cape (32° 44'S, 27° 18'E), 5.x.1986, at an altitude of 500 m, (Cat. BRS 13.3).

TAXONOMIC NOTES: Larvae of *S. bequaerti* are distinguished from other members of the Subgenus *Pomeroyellum* by the compound abdominal setae (Fig. 6.29j), the negative head pattern (Fig. 6.29b), the shape of the postgenal cleft (Fig. 6.29d), the hypostomium with prominent lateral serrations (Fig. 6.29e), and the unequal size of the first three comb-teeth (Fig. 6.29f). In Crosskey's (1960b) key they key out to couplet 13.

Simulium (Nevermannia) harrisoni, Fig. 6.31.

DESCRIPTIONS: Freeman & de Meillon (1953, male, female, pupa).

Length: of mature larvae 4.0-5.0 mm (n=4).

Head: Head-capsule length 0.38-0.40 mm (n=6). Head-capsule brown colour. Head-spots with positive pigmentation pattern, consisting of a single broad, median dark stripe with fused posterolateral pigmentation (Fig. 6.31b). Lateral aspect of head with dark pigmentation posterior and anterodorsally to eye-spots (Fig. 6.31c). Eye-spots fully developed. Postgenal cleft small; rounded, parallel-sided to slightly constricted basally (Fig. 6.31d). Postgenal bridge longer than hypostomium (Fig. 6.31d). Hypostomium with 9 apical teeth; median tooth strongly produced, lateral teeth moderately produced (Fig. 6.31g). Lateral serrations 6-8 in number, with at least two strongly developed; hindmost serration posterior to first hypostomial seta (Fig. 6.31g). Hypostomium with 5-7 setae in each row, nearly parallel to lateral margin of hypostomium (Fig. 6.31g). Distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.31g). Antennae longer (470 μm) than stem of cephalic fan (300 μm). Ratio of first antennal segment length:breadth at base 7.0-7.7:1; length ratio of first three segments 1:0.88-0.9:0.7-0.8 (Fig. 6.31e). First and third segments weakly pigmented: second segment unpigmented. Mandible with outer margin not strongly arched; first comb-tooth larger than second; second smaller than third (Fig. 6.31h). Mandible with a large and small posterior serration (Fig. 6.31h). Maxillary palp 0.12 mm long; weakly pigmented (basal $^{8}/_{10}$ yellow; apex transparent); with a few inconspicuous hairs at the base of the palp. Ratio of maxillary palp length:width at base 3.4:1 (Fig. 6.31f). Cephalic fan with about 50 primary rays; width of single fan ray 7.5 μm. Area of single cephalic fan 0.4 mm^2. Microtrichia strongly unequal in length: consisting of groups of 12 microtrichia arranged in size from short (1 μm) to long (7-10 μm)(Fig. 6.4e).

Thorax and abdomen: Body shape normal (Fig. 6.31a); integument grey in colour. Gill-spot composed of a long, single, tubular filament. Base of proleg bears a row of about 22 simple and bifid lateral spines (25 μm long). Thoracic cuticle with a few, scattered simple setae dorsally. Abdominal cuticle with numerous short (10 μm), compound setae and a few long (50 μm), simple setae . Ventral papillae present, but not large. Accessory sclerites absent.

MATERIAL EXAMINED: 5 mature larvae collected by A. H. Coetzer from the Molenaars River, a tributary of the Breede River, south-western Cape ($33^{o}42$'S, $19^{o}15$'E), 17.vii.1989. One mature larvae was collected by the same person in the Breede River ($33^{o}34$'S, $19^{o}15$'E), 17.vii.1989. Specimens are housed at the Department of Nature and Environmental Conservation, Stellenbosch. Pupal gills were dissected to confirm identification.

TAXONOMIC NOTES: Larvae of *S. harrisoni* resemble those of *S. merops*, but are distinguished by the absence of pigmented stripes on the gena (Fig. 6.31d), the pigmentation of the cephalic apotome (Fig. 6.31b), and the long median hypostomial tooth (Fig. 6.31g). In Crosskey's (1960b) key they key out to couplet 5.

Simulium (Pomeroyellum) merops, Fig. 6.34.

DESCRIPTIONS: de Meillon (1950, male, female, pupa), Freeman & de Meillon (1953, male, female, pupa), Crosskey (1969, male).

Length: of mature larvae 4.0-5.5 mm.

Head: Head-capsule length 0.38-0.4 mm (n=4). Head-capsule dark in colour. Head-spots with positive pigmentation pattern (sometimes very pale), consisting of an anteromedian row of 2-5 distinct spots and less distinct posteromedian, anterolateral and posterolateral spots (Fig. 6.34b). Lateral aspect of head with a pale round patch surrounding the eye-spots and a row of three pigmented spots (sometimes very pale) below and posterior to the eye-spots (Fig. 6.34c). Eye-spots fully developed. Gena with a pigmented mid-lateral stripe on either side of the postgenal cleft (Fig. 6.34d). Postgenal cleft small; quadrate; not constricted basally (Fig. 6.34d). Postgenal bridge longer than hypostomium (Fig. 6.34d). Hypostomium with 9 apical teeth; median and lateral teeth strongly produced (Fig. 6.34f). Hypostomium with 4-5 lateral serrations; hindmost serration posterior to first hypostomial seta (Fig. 6.34f). Hypostomium with 4-5 setae in each row, rows nearly parallel to lateral margin of hypostomium (Fig. 6.34f). Distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.34f). Antennae unpigmented to slightly pigmented; longer (540 μm) than stem of cephalic fan (380 μm)(Fig. 6.34e). Ratio of first antennal segment length:breadth at base 6.5-10:1; length ratio of first three segments 1:0.9:0.8 (Fig. 6.34e). Mandible with outer margin not strongly arched; first comb-tooth larger than second and third (Fig. 6.34g). Mandibular serrations consisiting of a single large serration followed by a smaller serration (Figs. 6.34g & h). Maxillary palp length 0.12 mm (n=3); without tuft of hair at the base of the palp (Fig. 6.34i). Ratio of maxillary palp length:width at base 3.5-4.0:1. Cephalic fan with 50-56 primary rays; width of single fan ray 5-6 μm (Fig. 6.5d); length 0.6-0.8 mm. Area of single cephalic fan 0.45 mm^2 (0.37-0.54 mm^2; n=6). Microtrichia long and thin (0.4-0.6 μm at base); strongly unequal in size: consisting of groups of 8 microtrichia arranged in size from short (to 1.0 μm) to long (6-8 μm) (Fig. 6.5d).

Thorax and abdomen: Body shape normal; integument pale in colour (Fig. 6.34a). Gill-spot dissected composed of 18 thin, long and flexible filaments (Fig. 6.34k). The base of the proleg circlet with a row of simple and bifid spines laterally and dorsally. Thoracic cuticle with a few minute colourless simple setae dorsally. Abdominal cuticle with numerous simple and compound setae (Fig. 6.34j). Ventral papillae large. Accessory sclerites forming two rows: an anterior row of 4-5 large sclerites followed by about 6 small sclerites in posterior row. Rectal gill with 0-3 secondary lobules on each lobe. Posterior circlet with 80 rows of 8-14 hooks. Anal sclerite extends to 13th row.

MATERIAL EXAMINED: 20 larvae and 29 pupae were collected from Witelsbos, Tsitsikamma

Forest ($34^{o}00$'S, $24^{o}05$'E), 1.i.1990 (Cat. RPS 59) at an altitude of 250 m.

TAXONOMIC NOTES: Larvae of *S. merops* are recognised by the numerous simple and compound abdominal setae (Fig. 6.34j), the lateral aspect of the head with three dark pigmented spots below the eye-spots (Fig. 6.34c), the gena with a mid-lateral pigmented stripe on either side of the postgenal cleft (Fig. 6.34d), the gill-spot which is composed of 18 flexible filaments (Fig. 6.34k), and the pattern of the cephalic apotome (Fig. 6.34b). *Simulium merops* shows characters typical of the Subgenus *Nevermannia* (female abdomen thickly covered with silvery scales; spermatheca with surface reticulations; larva with small, quadrate postgenal cleft and positive head pattern) as well as the Subgenus *Pomeroyellum* (details of the male genitalia, pupa with numerous gill filaments which are shorter than the pupal body). Although these two Subgenera are closely related (Crosskey, 1969: 67), the present evidence, as well as a study by Lewis & Raybould (1974a), suggests that a re-classification of these subgenera is needed. Until such a time, *S. merops* should remain in the *alcocki*-group (Subgenus *Pomeroyellum*), although it should be viewed as an intermediate between the two subgenera (a position it probably shares with *S. evillense*).

6.7 KEY TO THE GENUS PROSIMULIUM IN SOUTHERN AFRICA

[*Prosimulium* in southern Africa are poorly collected, and descriptions are incomplete. This key uses larval, pupal and adult characters, and forms part of a joint paper on *Prosimulium* being written together with Dr F. C. de Moor of the Albany Museum, Grahamstown. The key includes a new species from the south-western Cape (**sp. nov.**), collected by Dr J. King. Illustrations and full descriptions are being prepared by Dr. F. C. de Moor. The key to the three Subgenera is based on Crosskey (1969: 19) with minor alterations, but the key to species is original. The subgeneric status of each species is indicated in brackets. *Prosimulium* larvae are distinguished from those of *Simulium* by the hypostomial teeth which are aggregated into three main groups, and the enlarged third comb-tooth of mandible; Pupae are distinguished by a pair of strong terminal hooks, and adults are distinguished by the absence of a pedisulcus, and the katepisternum which is about as deep as its length (Crosskey, 1969: 14).]

1(0). Costa with hair-like macrotrichia only, at most some slightly stouter setae in male; calcipala absent or small; parameral hooks absent or if present small and inconspicuous; pupal gill with 6 or 7 tapered filaments intertwining apically; larval hypostomial teeth aggregated into three main groups .... PROCNEPHIA **2**

\- Costa with well developed spiniform macrotrichia as well as hair-like macrotrichia; without the above combination of characters .... PARACNEPHIA **4**

2(1). Pupal gill with 7 filaments; female scutum with three broad dark longitudinal lines; female claw with small basal tooth; calcipala absent; parameral hooks absent; basal arms and median section of ventral plate M-shaped; hind leg with banding pattern; style exceeds length of coxite; female mouthparts reduced; terminal hooks of pupae long and slender; (Southern Africa) .... **P. (Pro) damarense**

\- Pupal gill with 6 filaments; female scutum with or without pattern; female claw with large basal tooth; calcipala present but small; parameral hooks small, pale and inconspicuous; basal arms and median section of ventral plate round in shape; Hind leg uniformly pale **3**

3(2). Parameral hooks numerous; style exceeding length of coxite; apical spines 3; ventral plate quadrate and longer than broad; larval head spots negative or unclear; ventral papillae hemispherical (Uganda) .... **P. (Pro) morotoense**

\- Parameral hooks few; style subequal in length to coxite; apical spines 4; ventral plate with unique pair of horn-like processes; larval head-spots positive and clearly defined; Ventral papillae absent; Female with 10 to 20 inner mandibular teeth; female scutum with faint pale median line (Zimbabwe) .... **P. (Pro) rhodesianum**

4(1). [Female only]. Ground colour of thorax black; antenna dark; fourth and fifth palpal segments subequal in length; legs yellow except for apex of tibia which is brown; legs covered with pale and dark hairs; abdomen dark greyish brown, thinly clothed with pale scales and some darker hairs apically (Namibia) .... **P. (Par) herero**

\- Ground colour of thorax yellow to brown; antenna light brown; fourth palpal segment about half the length of the fifth segment; legs yellow with hind tibia and tarsi 4 and 5 slightly darker; legs covered with yellow hairs; abdomen dark brown with black hairs only and no scales; maxilla with 12 to 16 teeth on either side; mandible with 24 inner and 10 outer teeth; pupal gill with 6 strongly divergent, subequal, tapering and weakly furrowed filaments; fourth abdominal segment of pupae with only one hook on each side; terminal hooks of pupae relatively short and spine-like; pupal cephalothorax with small colourless nodules; trichomes small thickish spines; male with one or two large and prominent parameral hooks and a variable number of small ones; apical spines 6; larval hypostomium with teeth aggregated into three groups (South western Cape) .... **P. (Par) brincki**

\- Pupal gill with 10 to 22 filaments; without the above combination of characters (South western Cape) **5**

5(4). [Female only]. Calcipala large; ground colour of thorax black; scutum without pattern; abdomen with pale setae only at the base, the remainder with dark setae; hind leg uniformly dark; antenna uniform in colour; maxilla with 18 inner and 10 outer teeth; mandible with 35 inner and 13 outer teeth; vein R_1 with spiniform as well as hair-like setae .... **P. (Par) turneri**

\- Calcipala small; without the above combination of characters **6**

6(5). Pupal gill with 10 to 12 deeply furrowed, non-tapered filaments; pupal cephalothorax without nodules; apical spines

4 to 5; parameral hooks 6 to 20; ventral plate quadrate, about as wide as long; female mouthparts reduced or developed **7**

\- Pupal gill with 13 to 22 filaments; pupal cephalothorax with or without nodules; apical spines 5 to 9; parameral hooks 2 to 9, sometimes weak; female mouthparts reduced **8**

7(6). Pupal gill with 12 filaments not equal in length; parameral hooks 6 to 14, dark in colour; apical spines 4 to 5 in a single row; ground colour of thorax reddish; female maxillary and mandibular teeth reduced; female abdomen with dark setae throughout; larval hypostomium teeth not aggregated into three groups; hypostomium with only the median tooth produced; female scutum with three fine longitudinal lines; hind leg with banding pattern .... **P. (Par) sp. nov**

\- Pupal gill with 10 filaments equal or subequal in length; parameral hooks numerous; apical spines 4; ground colour of thorax black; female maxillary and mandibular teeth not reduced; mandibles with 30 inner and 15 outer teeth, maxilla with 18 outer teeth and 13 inner teeth; abdomen black, clothed with pale scales, basal fringe pale; larval hypostomium teeth divided into three groups ... . **P. (Par) thornei**

8(6). Pupal gill with 20 to 22 tapered filaments; pupal cephalothorax with nodules; parameral hooks weak and about 4 in number; apical spines 9 in single row; style shorter than coxite; ventral plate tongue-shaped; ground colour of thorax dark brown with paler legs; larval hypostomium with teeth not aggregated into three groups; hypostomium with only the median tooth produced .... **P. (Par) muspratti**

\- Pupal gill with 13 to 17 non-tapered filaments equal or subequal in length; pupal cephalothorax without nodules; apical spines 5 to 6 in two rows **9**

9(8). Pupal gill with 13 to 15 shallowly furrowed filaments; parameral hooks small, 2 to 3 in number; ventral plate strongly arched in profile; ventral plate quadrate, wider than long .... **P. (Par) barnardi**

\- Pupal gill with 16 to 17 filaments; trichomes simple and hair-like; parameral hooks 9 and colourless; ventral plate quadrate, as wide as long .... **P. (Par) harrisoni**

6.8 KEY TO LARVAE OF THE GENUS SIMULIUM IN SOUTHERN AFRICA

[This key is based on mature (final instar) larvae. Identification may require the dissection of the gill-spot. Not all *Simulium* larvae in southern Africa are separable to species, and positive identification may require pupae or adults. For practical purposes, species which are difficult to identify as larvae are refered to by their combined names (e.g., *S. medusaeforme/hargreavesi*). Larvae with hypostomial teeth aggregated into three main groups belong to the genus *Prosimulium*, and are not included in this key (see Crosskey, 1969: 15). *Simulium empopomae*, *S. hirsutilateris*, *S. natalense* and *S. narcaeum* have been omitted because they are not known as larvae.]

1(0). Abdominal cuticle with large, black, spatulate scales 30 to 50 µm long (Figs. 6.13i & 6.35k); body with two rows of dorsal conical tubercles, sometimes not well-defined (Fig. 6.13a) **2**

Abdominal cuticle without large, black, spatulate scales; body without two rows of dorsal conical tubercles **4**

2(1). Thoracic cuticle, including proleg, with numerous setae (Fig. 6.13a); ventral papillae absent; head-spots positive or unclear (Fig. 6.13b); hypostomial setae divergent from margin of hypostomium (Fig. 6.13e); hypostomial teeth short and blunt (Fig. 6.13e); postgenal cleft large and subcircular, constricted basally (Fig. 6.13d) .... **S. (Edw) damnosum** s.l. *

Thoracic cuticle completely bare, or with a few minute hairs; ventral papillae present; head-spots negative or unclear

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* There are at least 3 cytologically distinct members of the *S. damnosum* complex in southern Africa (Car, unpubl. data). In the Buffalo River, leg colouration of adults was either light or dark, suggesting two sympatric members, but larvae and pupae of these forms were indistinguishable.

(e.g., Fig. 6.35b); hypostomial setae parallel or nearly parallel to margin of hypostomium (e.g., Fig. 6.35f); hypostomium with median and lateral teeth moderately to strongly produced; postegenal cleft large and slightly pointed apically; parallel-sided or slightly constricted basally ... **3**

3(2). Hypostomium and postgenal bridge with numerous scattered hairs (Fig. 6.35d); gill-spot composed of barrel-shaped tubular filament (Fig. 6.35i) .... **S. (Pom) rotundum**

Hypostomium and postgenal bridge without scattered hairs; gill-spot composed of two tubular filaments, usually with anterior arm longer than posterior arm (Fig. 6.35l) .... **S. (Pom) unicornutum**

4(1). Ventral papillae present (e.g., Fig. 6.16a); body colouration and cephalic apotome usually pale **5**

Ventral papillae absent (e.g., Fig. 6.11a); body colouration and cephalic apotome usually dark **17**

5(4). Head-spots positive (sometimes unclear, as in *S. katangae*); postgenal cleft small and usually quadrate; postgenal bridge longer than hypostomium (Figs. 6.23, 6.25, 6.26; 6.27) **6**

Head-spots negative; postgenal cleft small or large, but not quadrate (Figs. 6.16, 6.17, 6.28, 6.29, 6.30, 6.32, 6.33) **11**

6(5). Abdominal cuticle with a few, scattered, simple setae (Figs. 6.23i, 6.27i) **7**

Abdominal cuticle with numerous setae, both simple and compound (Figs.9.32i, 9.35j); found in small and usually acidic streams of the southern and south-western Cape **10**

7(6). Gena with pigmented mid-lateral stripe on either side of the postgenal cleft (Figs. 6.26d, 6.27d) **8**

Gena without pigmented mid-lateral stripe on either side of the postgenal cleft (Figs. 6.23d, 6.25d) **9**

8(7). Head with well defined anterolateral pigmented spots (Fig. 6.26b); mandible with 2 or 3 serrations which are unequal in size (Fig. 6.26f); lateral aspect of head without a row of three pigmented spots below and behind eye-spots (Fig. 6.26c); spines on proleg circlet short (less than 25 μm); gill-spot composed of long, thin and tightly coiled filaments; hypostomium with median and corner teeth moderately produced (Fig. 6.26e) **28**

Head without anterolateral pigmented spots (Fig. 6.27b); mandible with 2 large and characteristic serrations which are equal in size (Fig. 6.27g); lateral aspect of head with a row of three pigmented spots below and behind eye-spots (Fig. 6.27c); spines on proleg circlet long (exceeding 25 μm); respiratory histoblast composed of large, wrinkled, tubular filaments (Fig. 6.27j); hypostomium with very prominent, and sharp, median and corner teeth (Fig. 6.27e); found in pristine to polluted water, often where flow is negligible .. .. **S. (Nev) ruficorne**

9(7). Head capsule and overall body colour dark; head-spots absent or with slight positive pigmentation (Fig. 6.25b); lateral serrations 6-7 in number (Fig. 6.25g); antenna slightly longer (4300 µm) than stem of cephalic fan (330 µm)(Fig. 6.25e); gill-spot composed of large, wrinkled tubular filaments (Fig. 6.25i); proleg circlet with 15-17 bifid spines on each side; spines 25 µm long .... **S. (Nev) katangae**

Head capsule and overall body colour pale; head-spots positive, widening posteriorly to form arrow-shape (Fig. 6.23b); hypostomium with 4-5 lateral serrations (Fig. 6.23e); antenna longer (560 µm) than stem of cephalic fan (330 µm)(Fig. 6.23j); gill-spot composed of thin tightly coiled filaments (Fig. 6.23m); proleg circlet with more than 20 spines on each side; spines less than 25 µm long; usually found in pristine streams .... **S. (Nev) rutherfoordi**

10(6). Head-spots consisting of an anteromedian row of 2-5 distinct spots and less distinct posteromedian, anterolateral and posterolateral spots (sometimes very pale) (Fig. 6.34b); gena with pigmented mid-lateral stripe on either side of the postgenal cleft (Fig. 6.34d); postgenal cleft quadrate (Fig. 6.34d); head capsule and body pale; lateral aspect of head with three dark spots below eye-spots (Fig. 6.34c); gill-spot composed of 18 thin, flexible filaments (Fig. 6.34k) .... **S. (Pom) merops**

Head-spots consisting of a single broad, median, dark stripe with fused posterolateral pigmentation (Fig. 6.31b); gena without pigmented mid-lateral stripe on either side of the postgenal cleft (Fig. 6.31d); postgenal cleft round (Fig. 6.31d); head capsule and body dark; lateral aspect of head without three dark spots below eye-spots (Fig. 6.31c); gill-spot composed of single tubular filament (Fig. 6.31j) .. .. **S. (Pom) harrisoni**

11(5). Posgenal cleft small and rounded, sometimes slightly pointed apically (Figs. 6.29d, 6.32d); postgenal bridge longer than hypostomium (Figs. 6.29d, 6.32d) **12**

Postgenal cleft not as above **13**

12(11). Abdominal cuticle with a few, scattered, simple and compound setae (Fig. 6.29j); gill-spot composed of a single crenulated filament bearing thread-like apical filaments (Fig. 6.29l) ... . **S. (Pom) bequaerti**

Abdominal cuticle with numerous fan-shaped setae (Fig. 6.32i); gill-spot composed of 10 thin filaments (Fig. 6.32j) .... **S. (Pom) impukane**

13(11). Postgenal cleft large (Figs. 6.16d, 6.17d, 6.30d, 6.33d); postgenal bridge shorter than hypostomium; spines on proleg circlet less than 25 µm **14**

Postgenal cleft small and rounded (Fig. 6.28d); postgenal bridge equal in length to hypostomium (Fig. 6.28d); abdominal setae complex (Fig. 6.28h); spines on proleg circlet exceeding 25 µm .... **S. (Pom) alcocki**

14(13). Abdominal cuticle with two distinct types of setae (Figs. 6.30i, 6.16h); head-spots clearly defined **15**

Abdominal cuticle with one type of setae only (Figs. 6.16i, 6.17i); head-spots pale and poorly defined **16**

15(14). Postgenal cleft rounded and slightly pointed apically (Fig. 6.30d); gena with lateral pigmented stripes on either side of postgenal cleft (Fig. 6.30d); lateral serrations with hindmost serration posterior to first hypostomial seta (Fig. 6.30e); distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.30e); antenna short, equal in length or slightly longer than stem of cephalic fan; gill-spot composed of large, wrinkled tubular filaments (Fig. 6.30j) .... **S. (Pom) cervicornutum**

Postgenal cleft mitre-shaped (Fig. 6.33d); gena without lateral pigmented stripes on either side of postgenal cleft (Fig. 6.33d); lateral serrations with hindmost serration level to first hypostomial seta (Fig. 6.33f); distance between apex of corner tooth and first hypostomial seta equal to that between corner teeth (Fig. 6.33f); antenna long, much longer than stem of cephalic fan; resipiratory histoblast composed of long and slender filaments (Fig. 6.33j); usually found in large rivers .... **S. (Pom) mcmahoni**

16(14). Head-pigmentation usually well-defined (Fig. 6.16b); lateral serrations with hindmost serration posterior to first hypostomial seta (Fig. 6.16f); distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.16f); antenna short, equal in length or slightly longer than stem of cephalic fan; ventral papillae small; cephalic fans with moderately differentiated microtrichia (Fig. 6.2d); found in small streams to large rivers; often in impoundment outlets......... **S. (Meil) adersi**

Head-pigmentation poorly defined (Fig. 6.17b); lateral serrations with hindmost serration level to first hypostomial seta (Fig. 6.17e); distance between apex of corner tooth and first hypostomial seta equal to that between corner teeth (Fig. 6.17e); antenna long, much longer than stem of cephalic fan; ventral papillae large; cephalic fans with microtrichia strongly unequal in length (Fig. 6.4d); found in small streams; never in impoundment outlets ..... **S. (Meil) hirsutum**

17(4). Postgenal cleft very large (Figs. 6.10d, 6.12d, 6.18d); head-capsule and body pale; body length usually shorter than 6 mm; usually found in large rivers **18**

Postegenal cleft rectangular or apically pointed (Figs. 6.11d, 6.14d, 6.15d, 6.20d, 6.21d, 6.22d); head-capsule and body dark; body length usually longer than 6 mm; found in mountain streams to large rivers **21**

18(17). Hypostomial setae parallel or nearly parallel to margin of hypostomium (Figs. 6.10c, 6.12e); abdominal cuticle with two distinct types of setae (Figs. 6.10e, 6.12i); distance between apex of corner tooth and first hypostomial seta equal to that between corner teeth (Figs. 6.10c, 6.12e); mandible with one elongate posterior serration (Figs. 6.10f, 6.12f); gill-spot composed of 3 large and wrinkled tubular filaments (Figs. 6.10g, 6.12j) **19**

Hypostomial setae divergent from margin of hypostomium (Fig. 6.18e); abdominal cuticle with small, spatulate setae (Fig. 6.18j); distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.18e); mandible with 2 or 3 serrations which are unequal in size (Fig. 6.18g); gill-spot composed of several thin filaments (Figs. 6.18l, 6.19l) **20**

19(18). Postgenal cleft rounded, with posterior width more than half its length (Fig. 6.12d); postgenal bridge present (Fig. 6.12d); abdominal cuticle with numerous simple and fan-shaped setae (Fig. 6.12i); hypostomium less than twice as high as distance between corner teeth (Fig. 6.12e) .... **S. (By) griseicolle**

Postgenal cleft pointed apically (Fig. 6.10d); postgenal cleft with posterior width less than half its length (Fig. 6.10c); postgenal bridge very narrow or incomplete (Fig. 6.10d); abdominal cuticle with scattered, simple setae and numerous spatulate scales (not fan-shaped); hypostomium narrow: more than twice as high as distance between corner teeth (Fig. 6.10c) .... **S. (Afr) gariepense**

20(18). Antenna long, much longer than stem of cephalic fan; apical teeth short and blunt (Fig. 6.18e); head-spots pale (Fig. 6.18b); gill filaments consisting of one or more stout primary filaments branching into thin secondary filaments (Fig. 6.18l) **26**

Antenna short, equal in length or slightly longer than stem of cephalic fan; apical teeth with median and lateral teeth moderately produced; head-spots clearly defined; gill filaments consisting of primary filaments bearing thin secondary filaments; filaments not consisting of one or more stout primary filaments branching into thin secondary filaments (Fig. 6.19l) .... **S. (Met) wellmanni**

21(17). Postgenal cleft small and rectangular (Fig. 6.11d); postgenal bridge longer than hypostomium (Fig. 6.11d); gill-spot composed of 14 short and stout filaments with sharp-pointed blackened tips (Figs. 6.11m & o); found in fast-flowing water including waterfalls .... **S. (Ana) dentulosum** *

Postgenal cleft large (Figs. 6.14d, 6.15d, 6.20d, 6.21d, 6.22d); postgenal bridge shorter than, or equal in length to, hypostomium; gill filaments without sharp-pointed blackened tips **22**

22(21). Postgenal bridge shorter than hypostomium (Figs. 6.20d, 6.22d); found in large rivers; common in impoundment tailwaters **23**

Postgenal bridge equal in length to hypostomium (Figs. 6.14d, 6.22d, 6.28d); not found in large rivers; seldom found in impoundment tailwaters **24**

23(22). Hypostomium with lateral serrations present with at least one strongly developed (Fig. 6.20f); antenna weakly pigmented; first three comb teeth unequal in length; mandible with apical teeth with median and lateral teeth moderately produced (Fig. 6.20f); head-spots clearly defined (Fig. 6.20b); accessory sclerite absent; common in impoundment tailwaters **27**

Hypostomium with lateral serrations present but small and blunt; antenna distinctly pigmented (Fig. 6.22e); first three comb teeth equal or subequal in length; mandible with apical teeth with only the median tooth produced; head-spots obscured by dark infuscation of head-capsule (Fig. 6.22b); accessory sclerite present .... **S. (Met) vorax**

24(22). Body length less than 7 mm; mandible typical form (Fig. 6.29k); lateral serrations with hindmost serration level to first hypostomial seta (Fig. 6.21e); distance between apex of corner tooth and first hypostomial seta shorter than that between corner teeth (Fig. 6.21e); mandibular serration elongate (Fig. 6.21f); antenna long, much longer than stem of cephalic fan; usually found in pristine streams .... **S. (Met) letabum**

Body length 7 mm or longer; mandible unusually broad, with outer margin strongly arched (Fig. 6.14i); lateral serrations absent, or embedded in lateral margin of hypostomium so that they appear absent (Figs. 6.14f, 6.15e); distance between apex of corner tooth and first hypostomial seta equal to that between corner teeth (Figs. 6.14f, 6.15e); antenna short, equal in length or slightly longer than stem of cephalic fan; usually found in waterfalls **25**

25(24). Gena with lateral pigmented stripes on either side of postgenal cleft (Fig. 6.15d); postgenal cleft parallel-sided (Fig. 6.15d); lateral head with a row of three pigmented spots below and behind eye-spots .... **S. (Fre) hessei**

Gena without lateral pigmented stripes on either side of postgenal cleft; postgenal cleft divergent basally; lateral head with a single pigmented spot below eye-spots .... **S. (Fre) debegene**

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* *Simulium dentulosum* larvae from the Buffalo River, eastern Cape, differ from those described by Crosskey (1960b) by having shorter and broader antennae and maxillary palps, and fewer hypostomial setae.

26(20). Cephalic fan microtrichia in two rows, and strongly unequal in length when veiwed under 1000 × oil immersion (Fig. 6.7b); larvae usually found in fast-flowing water .... **S. (Met) chutteri**

Cephalic fan microtrichia in one row, moderately differentiated when veiwed under 1000 × oil immersion (Fig. 6.3a); larvae usually found in slow-flowing water .... **S. (Met) bovis**

27(23). Gill-spot with central primary filament simple (Fig. 6.20g) .... **S. (Met) medusaeforme**

Gill-spot with central primary filament forked (Fig. 6.20h) .... **S. (Met) hargreavesi**

28(8). Cephalic fan microtrichia moderately differentiated when veiwed under 1000 × oil immersion (Fig. 6.3b); larvae usually found in slow-flowing water; tolerates polluted conditions; often found in impoundment outlets.. **S. (Nev) nigritarse**

Cephalic fan microtrichia strongly unequal in length when veiwed under 1000 × oil immersion (Fig. 6.4b); larvae usually found in clear water .... **S. (Nev) brachium**

6.9 KEY TO PUPAE OF THE GENUS SIMULIUM IN SOUTHERN AFRICA

[Pupae with long terminal hooks on the last abdominal segment belong to the genus *Prosimulium*, and are not included in this key (see Crosskey, 1969: 15). The Subgeneric status of each species is indicated within brackets (see Appendix A). Positive identification of *S. chutteri*, *S. bovis* and *S. wellmanni* requires adult male characters, which may be obtained by dissecting mature male pupae.]

1(0). Gill simple (formed of one type of filament: e.g., Figs. 6.17j & l, 6.18l, 6.19l) **2**

Gill complex (formed of two types of filaments: Figs. 6.20g & h, 6.21k & l, 6.22i & k, 6.29l, 6.33j) **27**

2(1). Gill with four or fewer terminal filaments (Figs. 6.10g, 6.12j, 6.14l, 6.15j-m, 6.23m & o, 6.24c & d, 6.25i, 6.27k, 6.31j, 6.35l) **3**

Gill with more than four terminal filaments (Figs. 6.11k, 6.13l, 6.16j & m, 6.17j & l, 6.18l, 6.19l, 6.20g & h, 6.21l, 6.22k, 6.28k, 6.29l, 6.30k, 6.32j, 6.33j, 6.34k) **16**

3(2). Cocoon slipper-shaped (Figs. 6.16j, 6.17j, 6.23m, 6.25i, 6.26i, 6.24a, 6.27k, 6.28i, 6.29l, 6.30j, 6.31j, 6.32j, 6.33j, 6.34k, 6.35k) **4**

Cocoon shoe-shaped (Figs. 6.10g, 6.11k, 6.12j, 6.13k, 6.14k, 6.15j, 6.18k, 6.20g, 6.21k, 6.22i) **12**

4(3). Gill with four terminal filaments (Figs. 6.14l, 6.15j-m, 6.23o, 6.24c & d, 6.25i, 6.26j, 6.27k) **5**

Gill with less than four terminal filaments (Figs. 6.10g, 6.12j, 6.31j, 6.35i & l) **10**

5(4). Gill filaments widely divergent; nodules on cephalothorax pale; cocoon with dorsal anteromedian projection (sometimes slight) (Figs. 6.25i, 6.27k) **6**

Gill filaments directed forwards; nodules on cephalothorax dark or pale; cocoon without dorsal anteromedian projection (Figs. 6.23m, 6.24a, 6.26i) **7**

6(5). Gill with two lateral filaments arising directly from basal trunk, and two median filaments arising from a secondary trunk (Fig. 6.27k); filaments roughly the same length as pupal body; filaments rounded apically; filament surface with minute nodules forming honey-comb pattern, seen at 40 × magnification (Fig. 6.27l); trichomes hair-like; cocoon with anterior margin poorly defined .... **S. (Nev) ruficorne** *

Gill with a very short common base from which two branches arise, one of which projects anteriorly, and one projects posteriorly: the anterior branch is slightly longer than the posterior branch (Fig. 6.25i); filaments longer than pupal body; filaments delicate and easily broken; filaments tapered and pointed apically; filament surface with minute nodules arranged in rows, seen at 40 × magnification (Fig. 6.25j); trichomes short and stout; cocoon with anterior margin well-defined .... **S. (Nev) katangae**

7(5). Gill filaments parallel (Figs. 6.24d, 6.26i); trichomes either hairlike or short and stout; cocoon coarsely or finely woven; male hind legs with banding pattern **8**

Gill filaments not parallel (Figs. 6.23o, 6.24c); trichomes hairlike; cocoon coarsely woven; male hind legs uniformly dark brown **9**

8(7). Gill filaments equal or subequal in length (Fig. 6.24d); ratio of gill length:breadth less than 3:1; all four filaments arise directly from base; length of longest filament shorter than length of pupal body; trichomes short and stout (Fig. 6.24e) .... **S. (Nev) narcaeum**

Gill with one long filament, two of equal length, and one short filament (Fig. 6.26i); ratio of gill length:breadth 3:1 or greater; filaments arise from two short unequal secondary stems; length of longest filament exceeding length of pupal body; trichomes hair-like; six compound pilous plate setae (Fig. 6.26k); cocoon finely woven .. **S. (Nev) nigritarse**

9(8). Length of longest filament shorter than pupal body (Fig. 6.23m); filaments arise from two short secondary stems; trichomes simple and bifid (Fig. 6.23k); anterior filament strongly bowed; cocoon coarsely woven, without perforations; eight simple pilous plate setae (Fig. 6.23n); cocoon with anterior margin well defined .... **S. (Nev) rutherfoordi**

Length of longest filament same length as pupal body (Fig. 6.24a); filaments arise directly from a very short common base; anterior filament partially bowed; cocoon coarsely woven, with small perforations; six simple pilous

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* *Simulium ruficorne* is a suspect species complex closely related to the *S. ornatipes* complex in Australia and New Guinea, with which it shares an an estimate 89% similarity in chromosome banding patterns (Bedo, 1989b). Gill structure is varied (Harrison, 1966; Crosskey & Büttiker, 1982), although specimens examined from southern Africa [Swakop River (SMI 4383), Johannesburg (RPS. 9a), Buffalo River (BRSO. 221a), Olifants River (RPS. 14), Richards Bay (RPS. 73), and Prieska (RPS. 71)] all had filaments of the type shown in Fig. 6.27k.

plate setae (Fig. 6.24b); cocoon with anterior margin poorly defined .... **S. (Nev) brachium**

10(4). Gill with two, thin-walled, tubular filaments (Fig. 6.35l); filament surface reticulated (Fig. 6.35m); anterior filament usually longer than posterior filament .. **S. (Pom) unicornutum**

Gill with single filament; without the above combination of characters **11**

11(10). Gill short, stout and barrel-shaped (Fig. 6.35i); filament surface reticulated (Fig. 6.35j) .... **S. (Pom) rotundum**

Gill long; filament surface crenulated; tubercles numerous (Fig. 6.31j) .... **S. (Pom) harrisoni**

12(3). Gill with four terminal filaments (Figs. 6.14l, 6.15j-m); cocoon with well-developed neck; trichomes simple; body 3 to 6 mm long; terminal abdominal tubercles not thorn-like; usually found in waterfalls in mountain streams **13**

Gill with three terminal filaments (Figs. 6.10g, 6.12j); cocoon with moderately developed neck; trichomes compound, large and conspicuos; body 2 to 3 mm long; terminal abdominal tubercles pointed, thorn-like and directed backwards; usually found in large rivers **15**

13(12). Gill with filaments of equal diameter; with knob-like basal projection (Figs. 6.15j & k); filaments not swollen basally . ... **S. (Fre) hessei**

Gill with tapered filaments; without the above combination of characters **14**

14(13). Gill with three filaments of equal length arising posteriorly, and one slightly longer bowed filament arising anteriorly (Fig. 6.14l); filaments slightly tapered and not swollen basally; cocoon white; male scutal setae golden; male hind legs uniformly dark .... **S. (Fre) debegene**

Gill with filaments arising in two pairs (Fig. 6.15l); filaments of even width and not swollen basally; anterior (lowermost) filament slightly separate from the others; male scutal setae black; male hind legs with banding pattern .... **S. (Fre) hirsutilateris**

Gill with three filaments arising posteriorly, and a slightly bowed filament arising anteriorly (Fig. 6.15m); filaments swollen basally; male scutal setae black; male hind legs with banding pattern .... **S. (Fre) empopomae** *

15(13). Gill composed of long, narrow, transparent, leaf-like filaments directed forwards (Fig. 6.12j); two filaments are united at the base; single dorsal filament with basal lobe; filament surface undifferentiated; cocoon with dorsal anteromedian projection; cocoonrigid witha definite shape .... **S. (Bys) griseicolle**

Gill composed of tubular filaments (Fig. 6.10g); filaments tapered and pointed apically; filament surface with nodules; cocoon without dorsal anteromedian projection; cocoon loosely woven and rather delicate .... **S. (Afr) gariepense**

16(2). Gill with 14 short, stout filaments with sharp-pointed blackened tips (Figs. 6.11k, n & o); filament surface with nodules; body 3.5 to 5.0 mm long; cocoon with well developed neck; usually found in waterfalls in mountain streams .... **S. (Ana) dentulosum** **

Gill filaments without sharp-pointed blackened tips; without the above combination of characters **17**

17(16). Gill filaments equal or subequal in length (Figs. 6.16j, 6.17j, 6.28i, 6.32j 6.34k) **18**

Gill filaments not equal in length (Figs. 6.13l, 6.18l, 6.19l, 6.24g, 6.30j) **22**

18(17). Gill with 18 thin, flexible filaments of equal length (Fig. 6.34k); all filaments arise directly from the base; filaments of equal width and deeply furrowed (Fig. 6.34m); head and thorax with compound, spine-like projections (Fig. 6.34l) .... **S. (Pom) merops**

Gill with 6 to 14 terminal filaments; filament surface with minute dots arranged in rows; without the above combination of characters **19**

19(18). Gill with 7 or 10 terminal filaments not arranged in a vertical plane; cocoon with dorsal anteromedian projection (Figs. 6.11i, 6.32j) **20**

Gill with 6 or 11 terminal filaments arranged in a vertical plane; cocoon without dorsal anteromedian projection (Figs. 6.16m, 6.17l) **21**

20(19). Gill with 6 to 8 (usually 7) terminal filaments (Fig. 6.28k); filaments often lying flat on the substrate (Fig. 6.28i); filaments not strongly divergent; filament branching 2, 3, 2 .... **S. (Pom) alcocki**

Gill with 10 terminal filaments (occasionally nine); filaments strongly divergent; filament branching 2, 5, 3 (Fig. 6.32j) .... **S. (Pom) impukane**

21(19). Gill with 11 terminal filaments branching 3, 5, 3

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* *Simulium empopomae* may be synonomous with *S. debegene* (Freeman & de Meillon, 1953: 156).

** Two gill forms were present in the Buffalo River, eastern Cape, of which form *emfulae* was the commoner of the two (Fig. 6.11k).

(Fig. 6.16m); length of longest filament shorter than pupal body; filament cuticle with minute dots arranged in rows (Fig. 6.16k); cocoon with open fenestrations; anterior margin poorly defined .... **S. (Meil) adersi**

Gill with 8 terminal filaments branching 3, 3, 2 (Fig. 6.17l); (gill may appear 6-filamented because of bifurcations towards apex); length of longest filament same length as pupal body; filament cuticle with minute dots forming reticulated pattern (Fig. 6.17m); cocoon without fenestrations; anterior margin well-defined .... **S. (Meil) hirsutum**

22(17). Gill with 8 or 9 short, stout, terminal filaments arranged in a single plane, resembling deer's antlers (Fig. 6.30j); dorsal abdominal segments with spine-combs; cocoon slipper-shaped .... **S. (Pom) cervicornutum**

Gill not antler-like; filaments not in a single plane; dorsal abdominal segments without spine-combs; cocoon shoe-shaped **23**

23(22). Gill with 11 short, stout and bananna-like terminal filaments, comprising two long dorsal and ventral basal filaments, three unbranched outer filaments, and three bifurcated internal filaments which are appressed to the surface of the thorax (Figs. 6.13k & l); filament surface smooth .... **S. (Edw) damnosum** s.l.

Gill without the above combination of characters **24**

24(23). Gill with 8 to 16 short, terminal filaments, comprising two long dorsal and ventral basal filaments, and smaller simple and bifurcated median filaments (Fig. 6.24g); filaments covered with minute hairs (seen at × 400 magnification) .. .. **S. (Met) natalense**

Gill with more than 20 terminal filaments, formed of one or more stout primary filaments branching into thin secondary filaments (Figs. 6.18l, 6.19l); filaments long and slender; without the above combination of characters **25**

25(24). Gill with long stem (Fig. 6.19l; coxite produced well beyond base of style (Fig. 6.19i); style with three to four large apical spines (Fig. 6.19i); ventral plate quadrate (Fig. 6.19j) .... **S. (Met) wellmanni**

Without the above combination of characters **26**

26(25). Coxite slightly produced beyond base of style (Fig. 6.19a); ventral plate without strong spines; shaped as in Figs. 6.19b & c; male scutum with three broad, dark, longitudinal bands (Fig. 6.19d) .... **S. (Met) chutteri**

Coxite not produced beyond base of style (Fig. 6.19e); ventral plate with strong spines, and shaped as in Figs. 6.19f & g; male scutum black with two white anterior triangles (Fig. 6.19h) .... **S. (Met) bovis**

27(1). Gill with single, fowardly-directed filament bearing

8 thread-like filaments (occasionally six to twelve); cocoon slipper-shaped (Figs. 6.29l, 6.33j) **28**

Gill formed of primary filaments bearing 16 to 20 thin secondary filaments; filaments not arising from long common stem; cocoon shoe-shaped (Figs. 6.20g & h, 6.21l, 6.22k) .. **29**

28(27). Gill formed of a single reticulated filament, with a slight rod-like thickening on the inner or dorsal margin; secondary filaments arise between the middle and the apex of the primary filament (Fig. 6.33j); ratio of gill length:breadth 2.5:1 ... . **S. (Pom) mcmahoni**

Gill formed of a single crenulated filament; secondary filaments arise from the apex (Fig. 6.29l); ratio of gill length:breadth 4.5:1 .... **S. (Pom) bequaerti**

29(27). Gill with large and semi-transparent basal filaments without secondaries (Fig. 6.22k); three dark and rigid filaments arise medianly, bearing secondary filaments; cocoon with well-developed neck; body 4 to 5 mm long ..... **S. (Met) vorax**

Cocoon with moderately developed neck; body 3 to 4 mm long; without the above combination of characters **30**

30(29). Gill with two large and semi-transparent basal filaments, each bearing a short secondary filament at the apex; median filaments arise basally and are equal or subequal in length (Fig. 6.21l); gill with 16 terminal filaments; pupal head flattened .... **S. (Met) letabum**

Gill without large and semi-transparent basal filaments; filaments not equal in length; gill with 18 to 22 terminal filaments **31**

31(30). Central primary filament simple (Fig. 6.20g) .... **S. (Met) medusaeforme**

Central primary filament forked (Fig. 6.20h) .... **S. (Met) hargreavesi**

8 thread-like filaments (occasionally six to twelve); cocoon slipper-shaped (Figs. 6.29l, 6.33j) **28**

Gill formed of primary filaments bearing 16 to 20 thin secondary filaments; filaments not arising from long common stem; cocoon shoe-shaped (Figs. 6.20g & h, 6.21l, 6.22k) .. **29**

28(27). Gill formed of a single reticulated filament, with a slight rod-like thickening on the inner or dorsal margin; secondary filaments arise between the middle and the apex of the primary filament (Fig. 6.33j); ratio of gill length:breadth 2.5:1 ... . **S. (Pom) mcmahoni**

Gill formed of a single crenulated filament; secondary filaments arise from the apex (Fig. 6.29l); ratio of gill length:breadth 4.5:1 .... **S. (Pom) bequaerti**

29(27). Gill with large and semi-transparent basal filaments without secondaries (Fig. 6.22k); three dark and rigid filaments arise medianly, bearing secondary filaments; cocoon with well-developed neck; body 4 to 5 mm long ..... **S. (Met) vorax**

Cocoon with moderately developed neck; body 3 to 4 mm long; without the above combination of characters **30**

30(29). Gill with two large and semi-transparent basal filaments, each bearing a short secondary filament at the apex; median filaments arise basally and are equal or subequal in length (Fig. 6.21l); gill with 16 terminal filaments; pupal head flattened .... **S. (Met) letabum**

Gill without large and semi-transparent basal filaments; filaments not equal in length; gill with 18 to 22 terminal filaments **31**

31(30). Central primary filament simple (Fig. 6.20g) .... **S. (Met) medusaeforme**

Central primary filament forked (Fig. 6.20h) .... **S. (Met) hargreavesi**

6.10 ILLUSTRATIONS

[Most drawings are based on material housed in the Albany Museum, Grahamstown. A few published drawings, with sources acknowledged, are included for sake of completion. Species are arranged as in Appendix A.]

S. gariepense
Car (1983a)

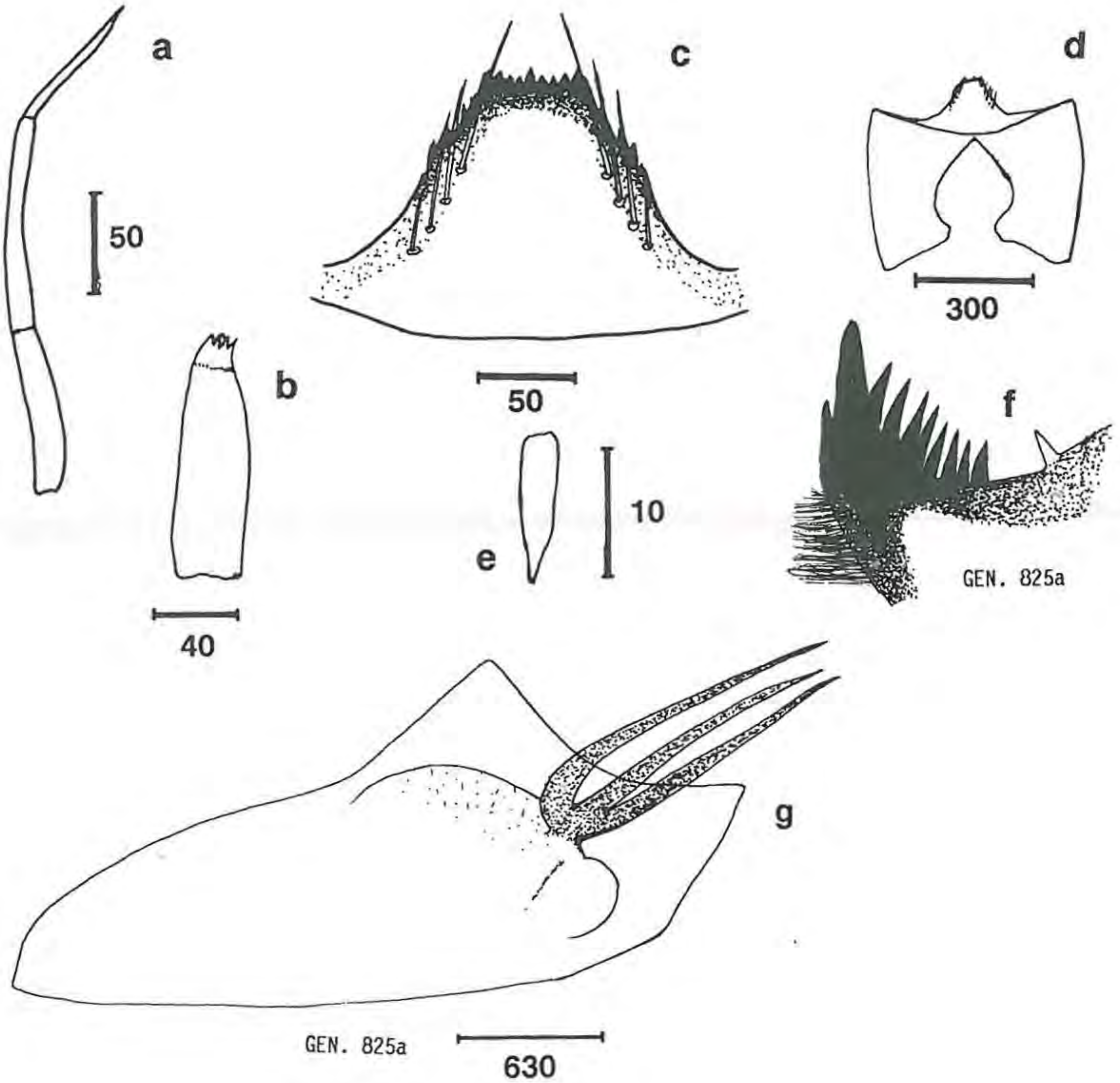


Fig. 6.10 S. (Afrosimulium) gariepense: Larva - **a**, antenna. **b**, maxillary palp. **c**, hypostomium. **d**, head ventral. **e**, abdominal seta. **f**, apex of mandible. Pupa - **g**, pupa. [Scale in μm].

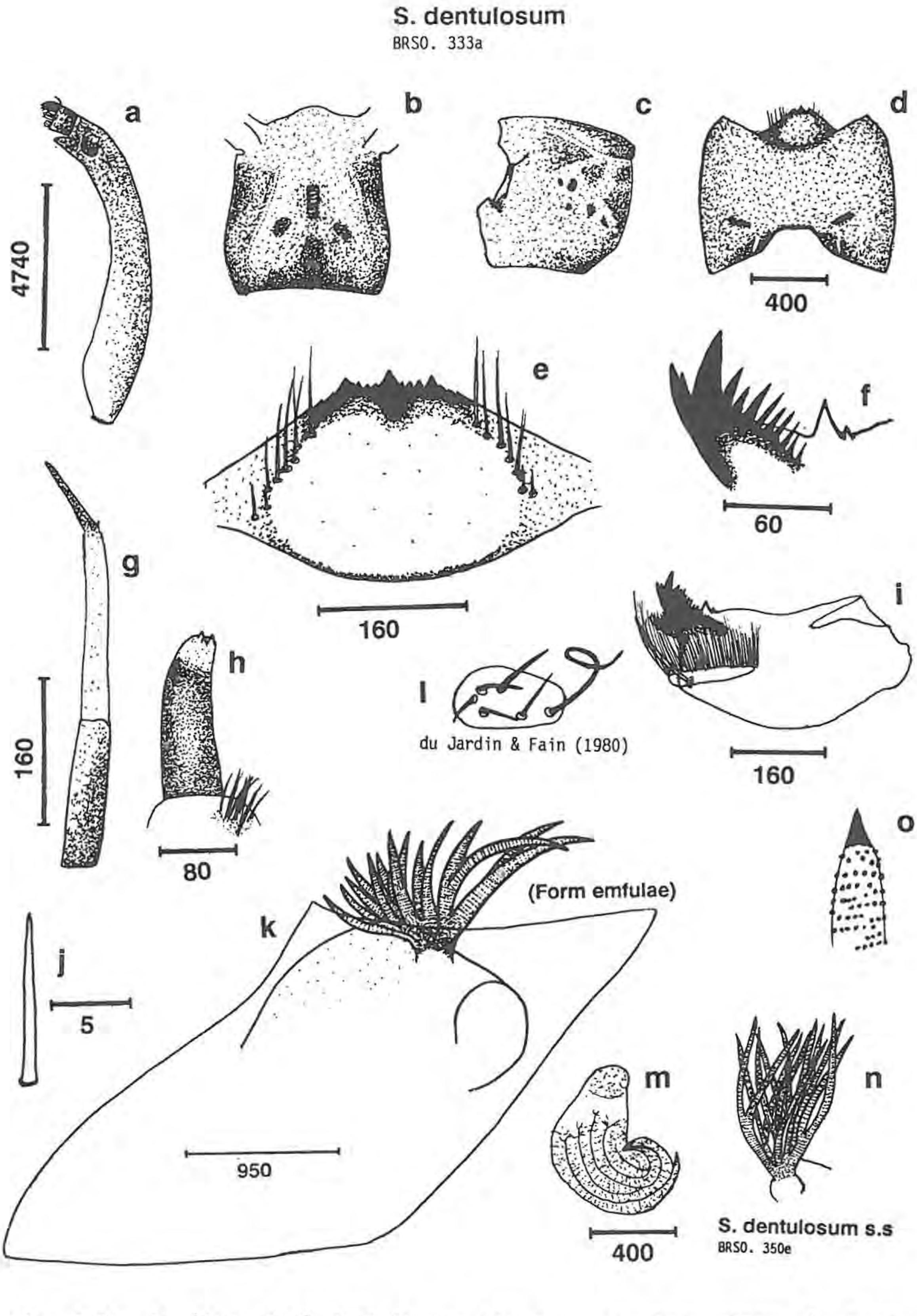


Fig. 6.11 S. (**Anasolen**) **dentulosum**: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillary palp. **i**, mandible. **j**, abdominal seta. Pupa - **k**, pupa of **S. dentulosum** form **emfulae**. **l**, pilous plate. **m**, gill-spot. **n**, pupal gill of **S. dentulosum** s.s.. **o**, apex of gill filament. [Scale in μm].

S. griseicolle
RPS. 21

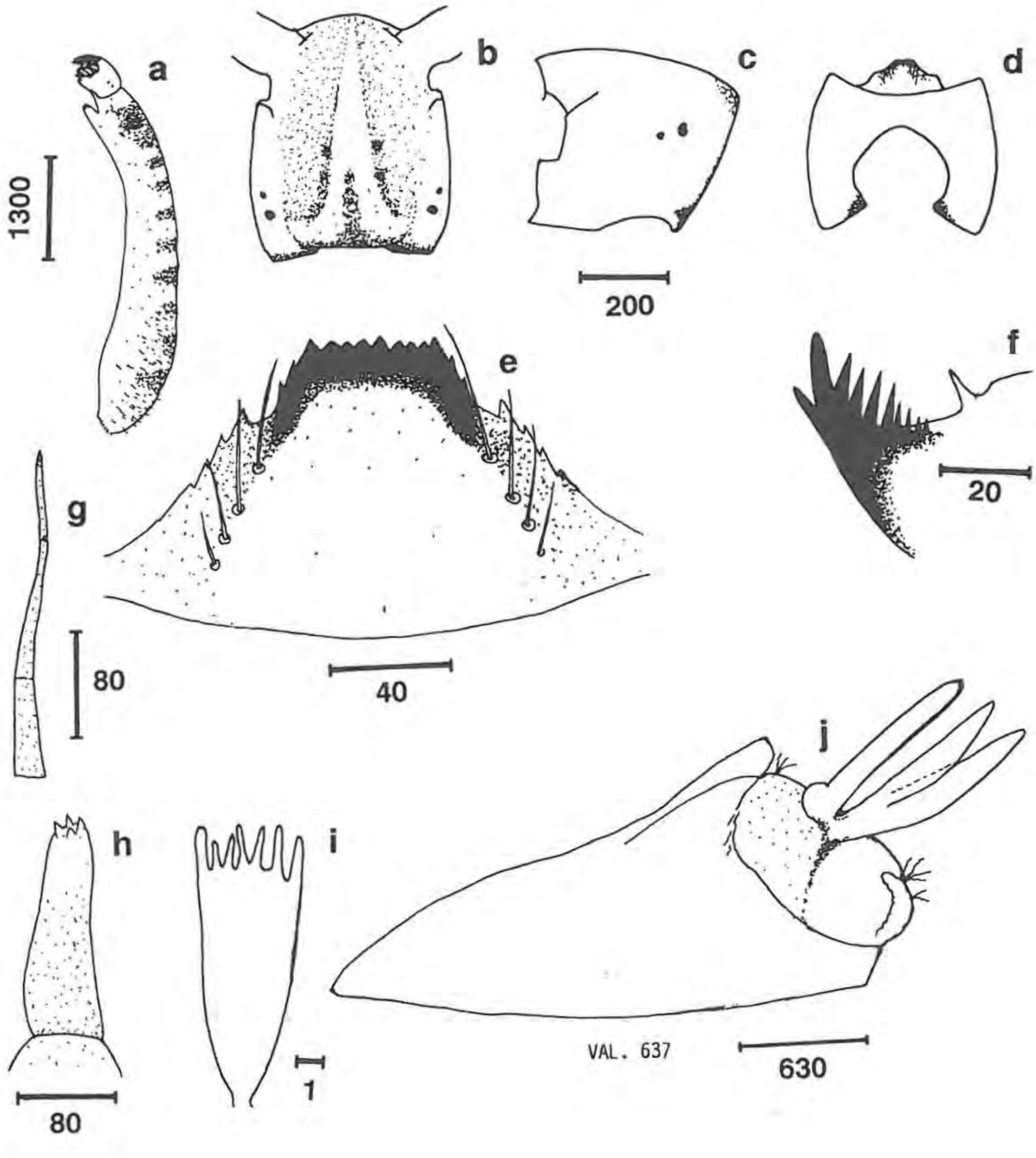


Fig. 6.12 S. (Byssodon) griseicolle: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillary palp. **i**, abdominal seta. Pupa - **j**, pupa. [Scale in μm].

S. damnosum s.l.
BRSO. 348d

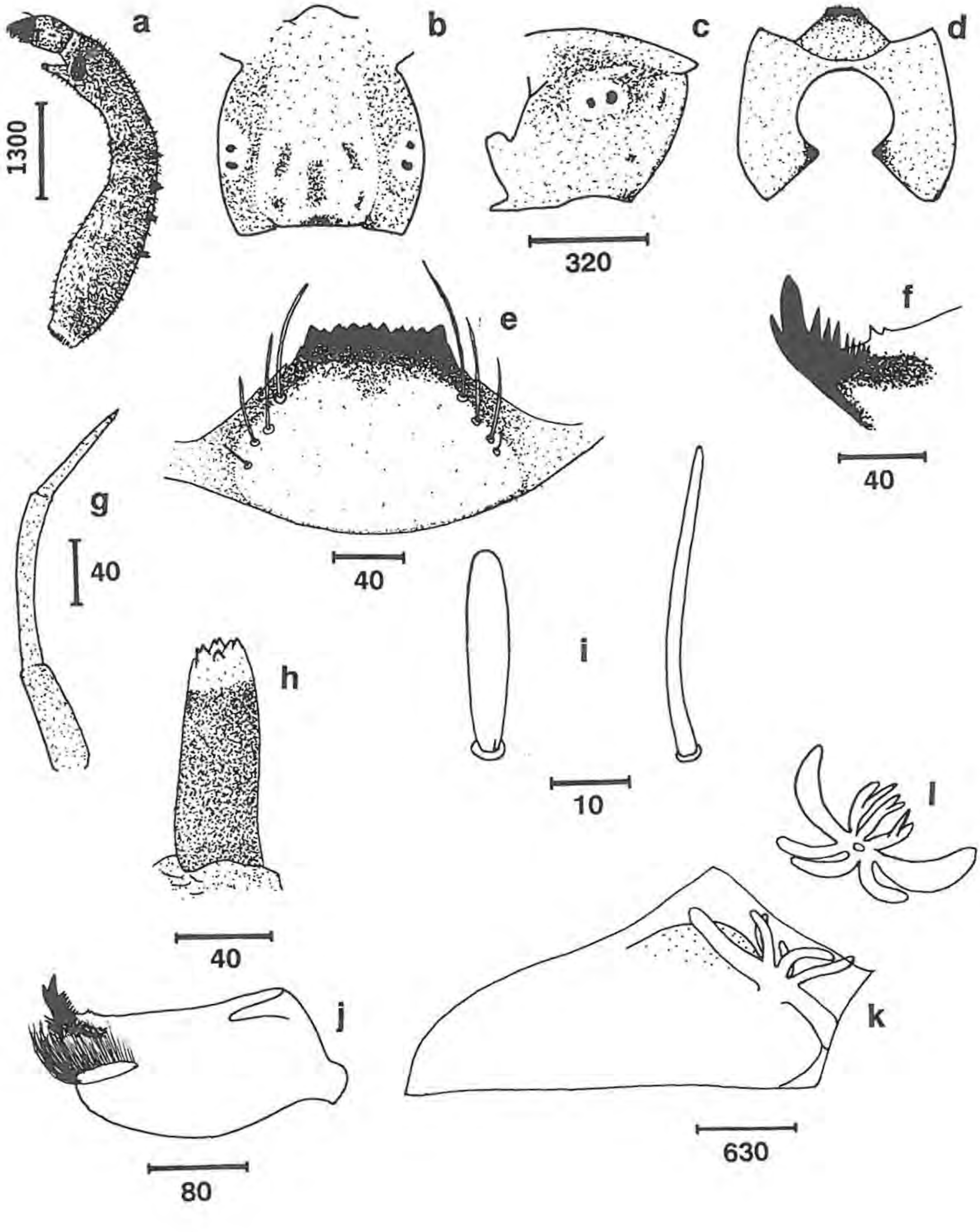


Fig. 6.13 S. (Edwardsellum) damnosum: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillary palp. **i**, abdominal setae. **j**, mandible. Pupa - **k**, pupa. **l**, pupal gill. [Scale in μm].

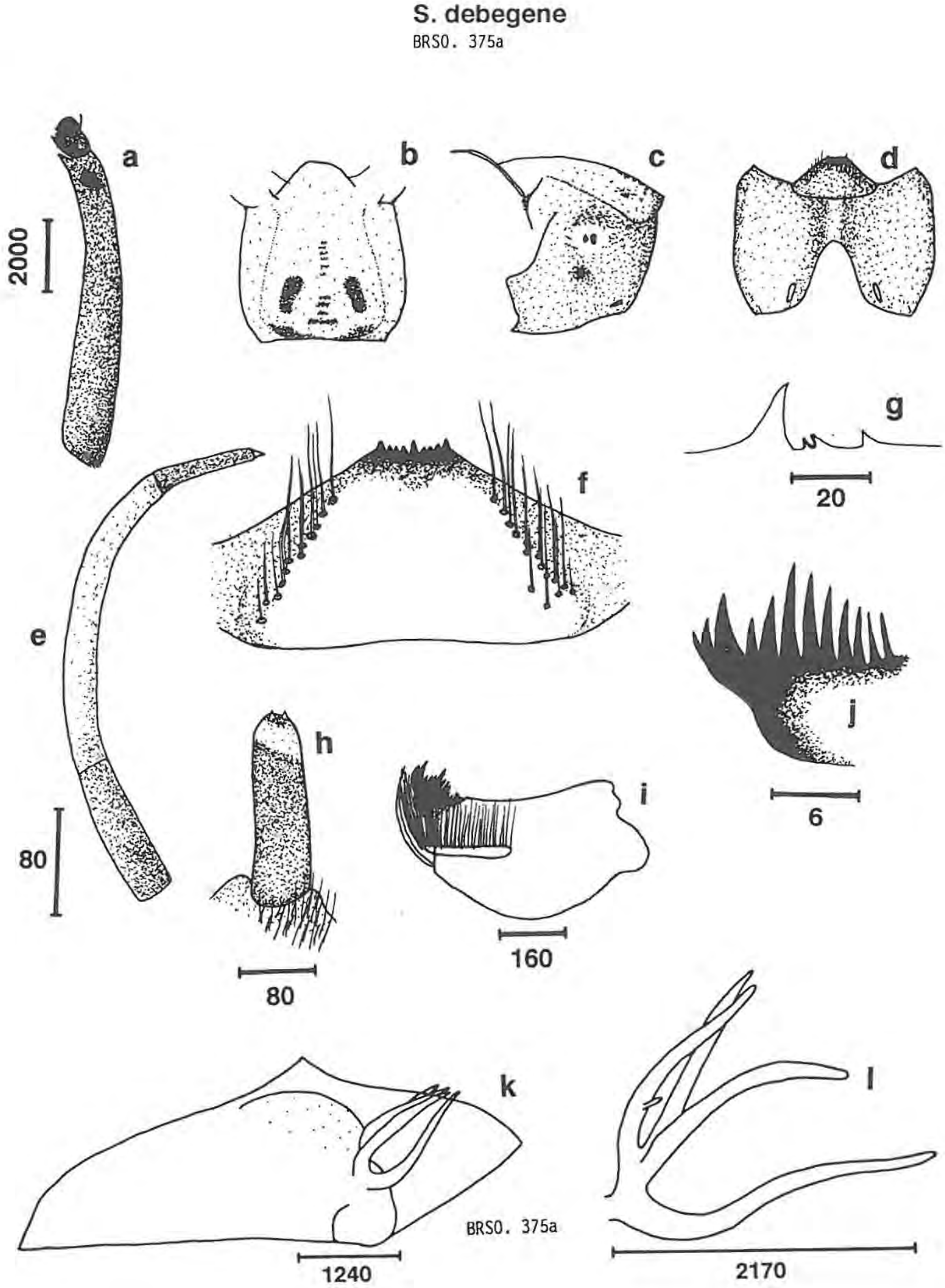


Fig. 6.14 S. (Freemanellum) debegene: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, hypostomium. **g**, posterior serrations. **h**, maxillary palp. **i**, mandible. **j**, apex of mandible. Pupa - **k**, pupa. **l**, pupal gill. [Scale in μm].

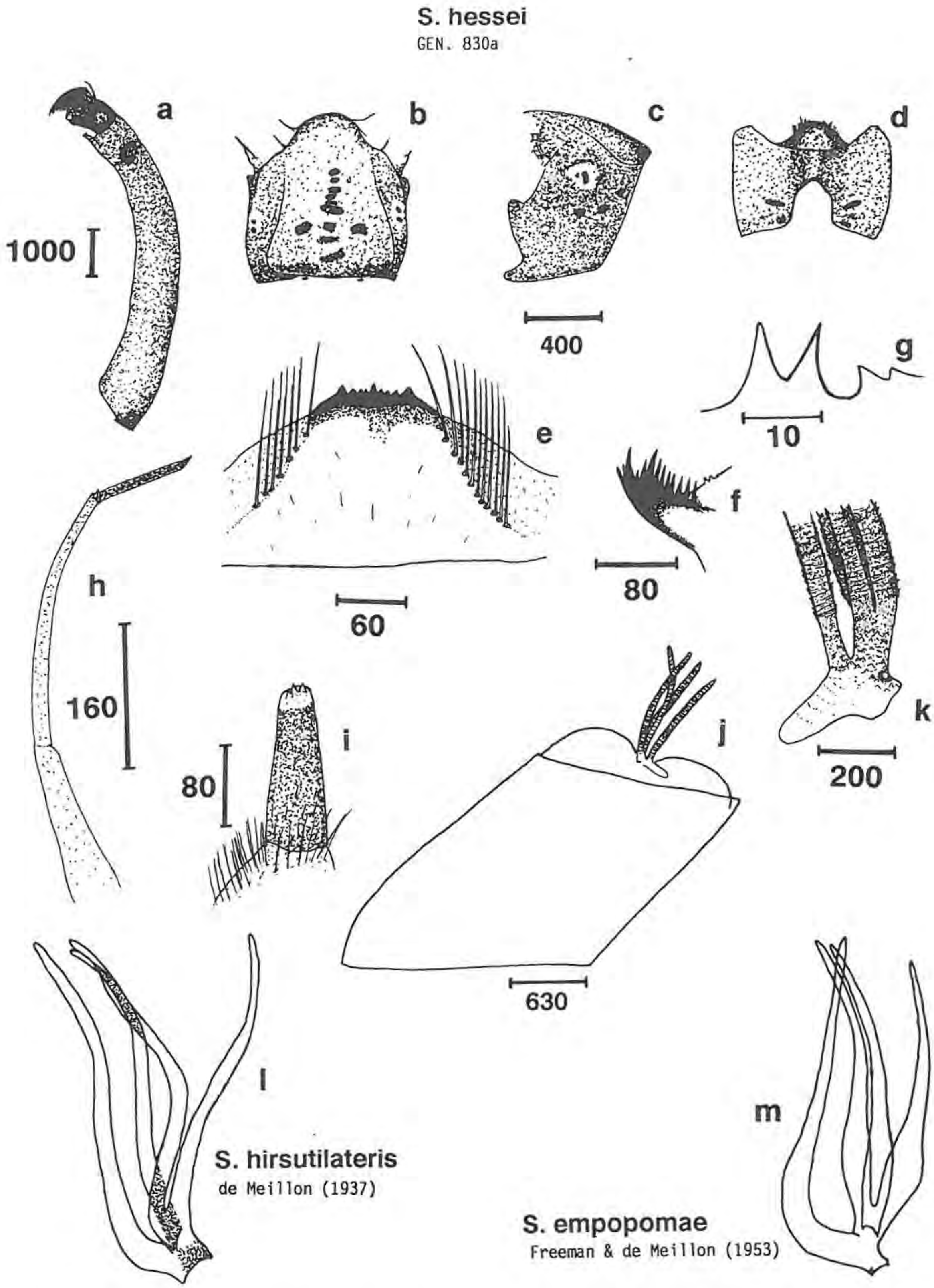


Fig. 6.15 S. (Freemanellum) hessei: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, posterior serrations. **h**, antenna. **i**, maxillary palp. Pupa - **j**, pupa. **k**, base of pupal gill. **S. (Freemanellum) hirsutilateris** **l**, pupal gill. **S. (Freemanellum) empopomae** **m**, pupal gill. [Scale in μm].

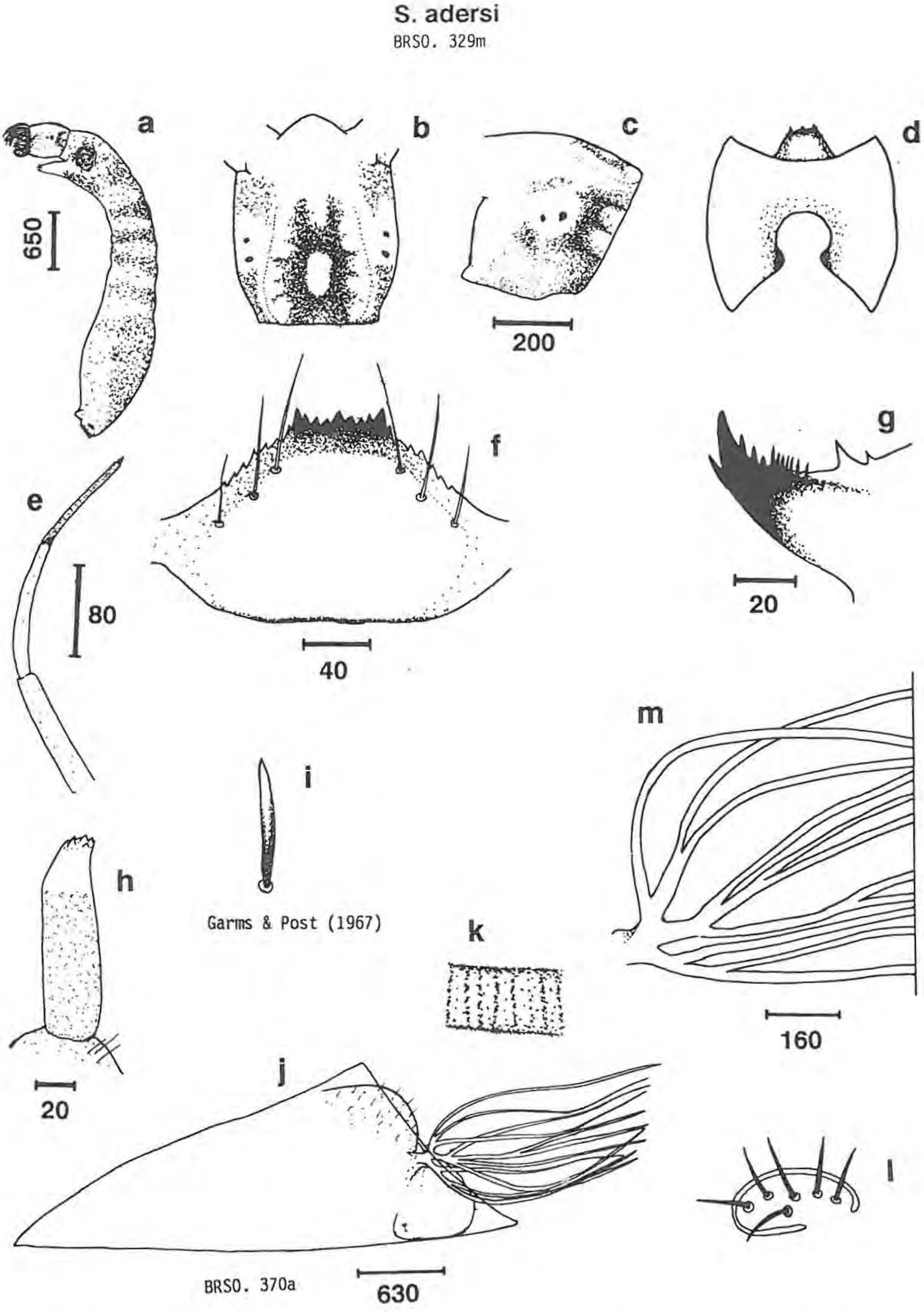
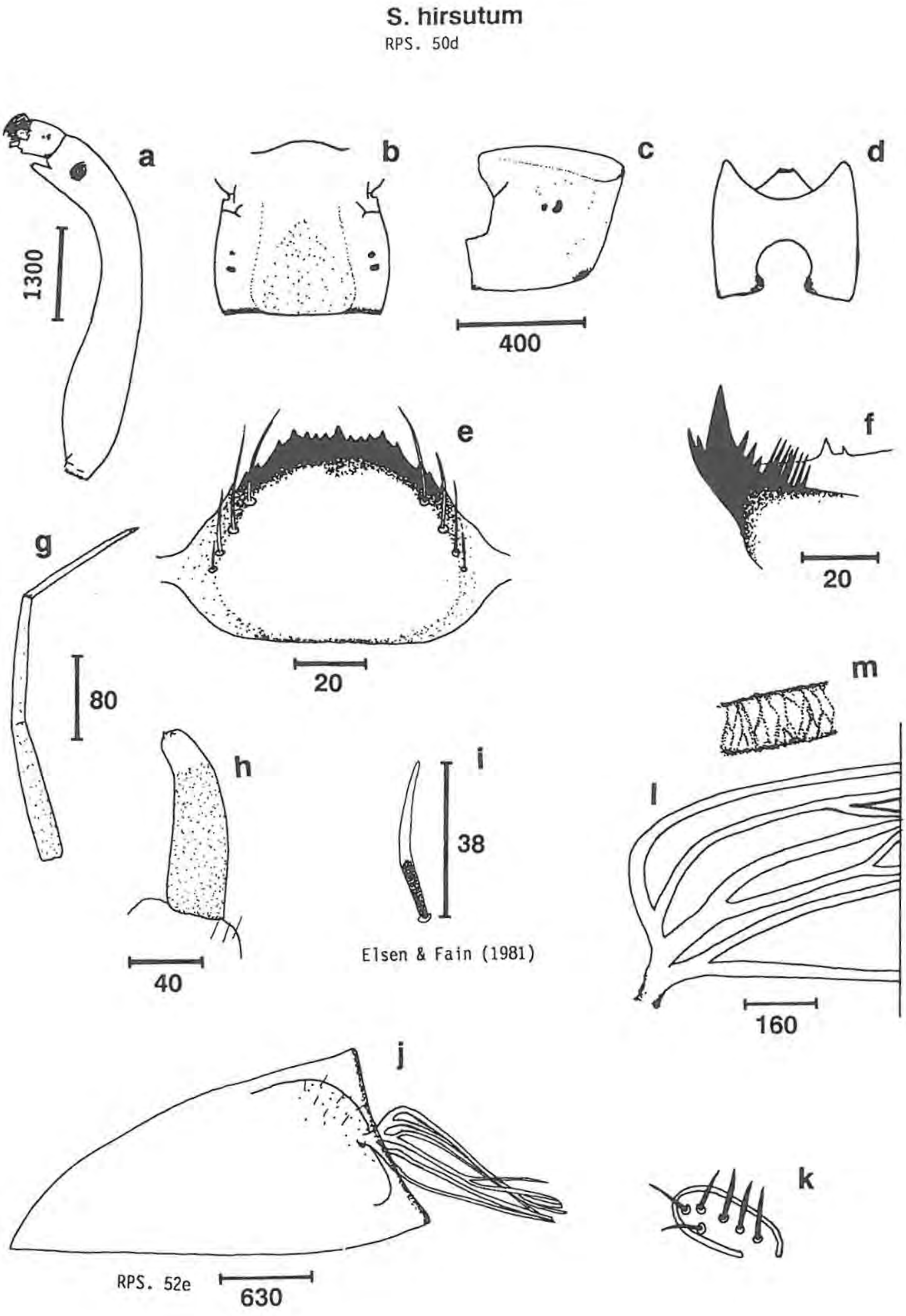


Fig. 6.16 S. (Meilloniellum) adersi: Larva - **a**, body shape. **b**, head dorsal, showing negative pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, hypostomium. **g**, apex of mandible. **h**, maxillary palp. **i**, abdominal setae. Pupa - **j**, pupa. **k**, gill filament. **l**, pilous plate. **m**, base of pupal gill. [Scale in µm].



Elsen & Fain (1981)

Fig. 6.17 S. (Meilloniellum) hirsutum: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillary palp. **i**, abdominal seta. Pupa - **j**, pupa. **k**, pilous plate. **l**, base of pupal gill. **m**, fill filament. [Scale in μm].

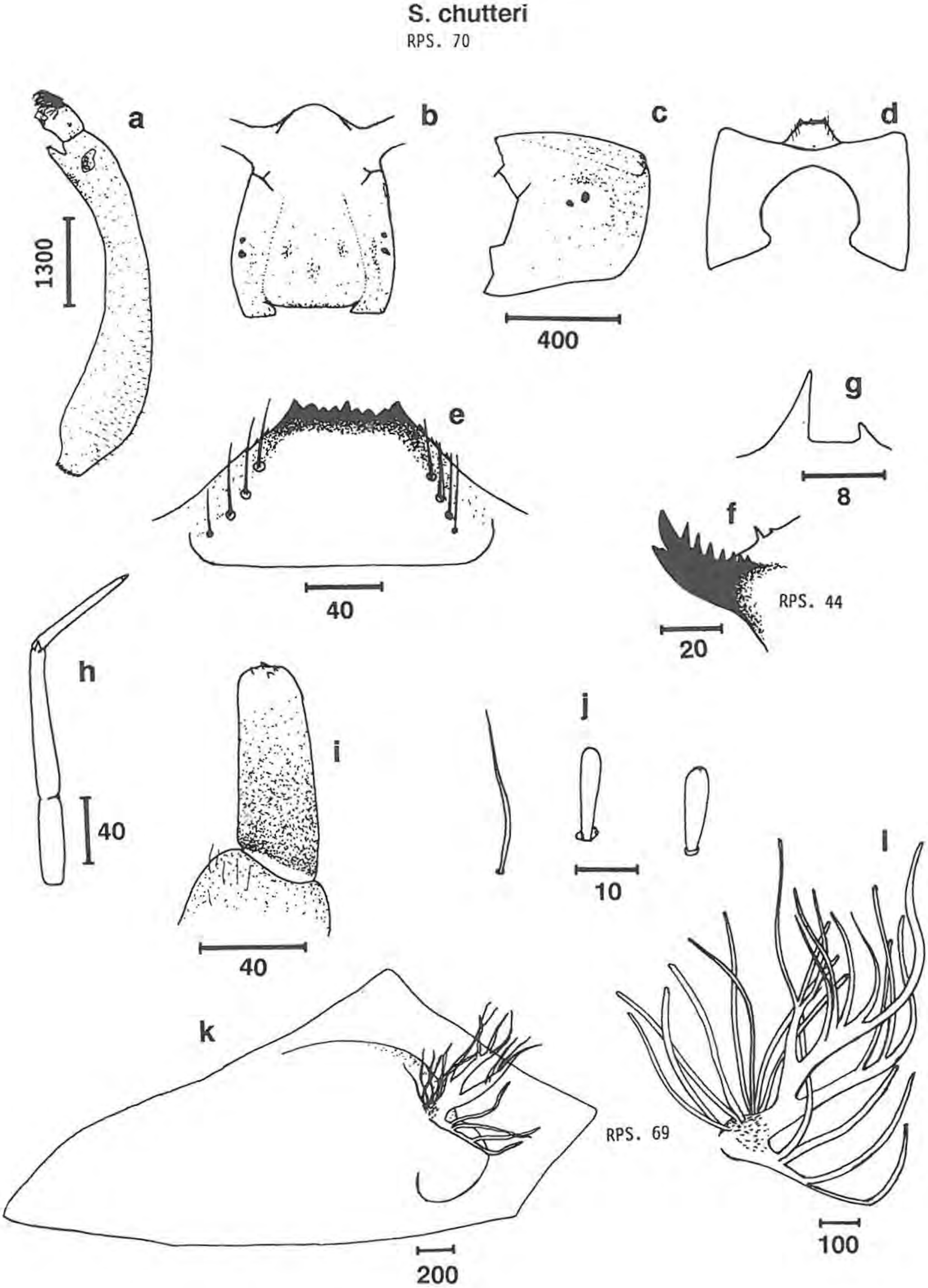


Fig. 6.18 S. (Metomphalus) chutteri: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, posterior serrations. **h**, antenna. **i**, maxillary palp. **j**, abdominal setae. Pupa - **k**, pupa. **l**, pupal gill. [Scale in μm].

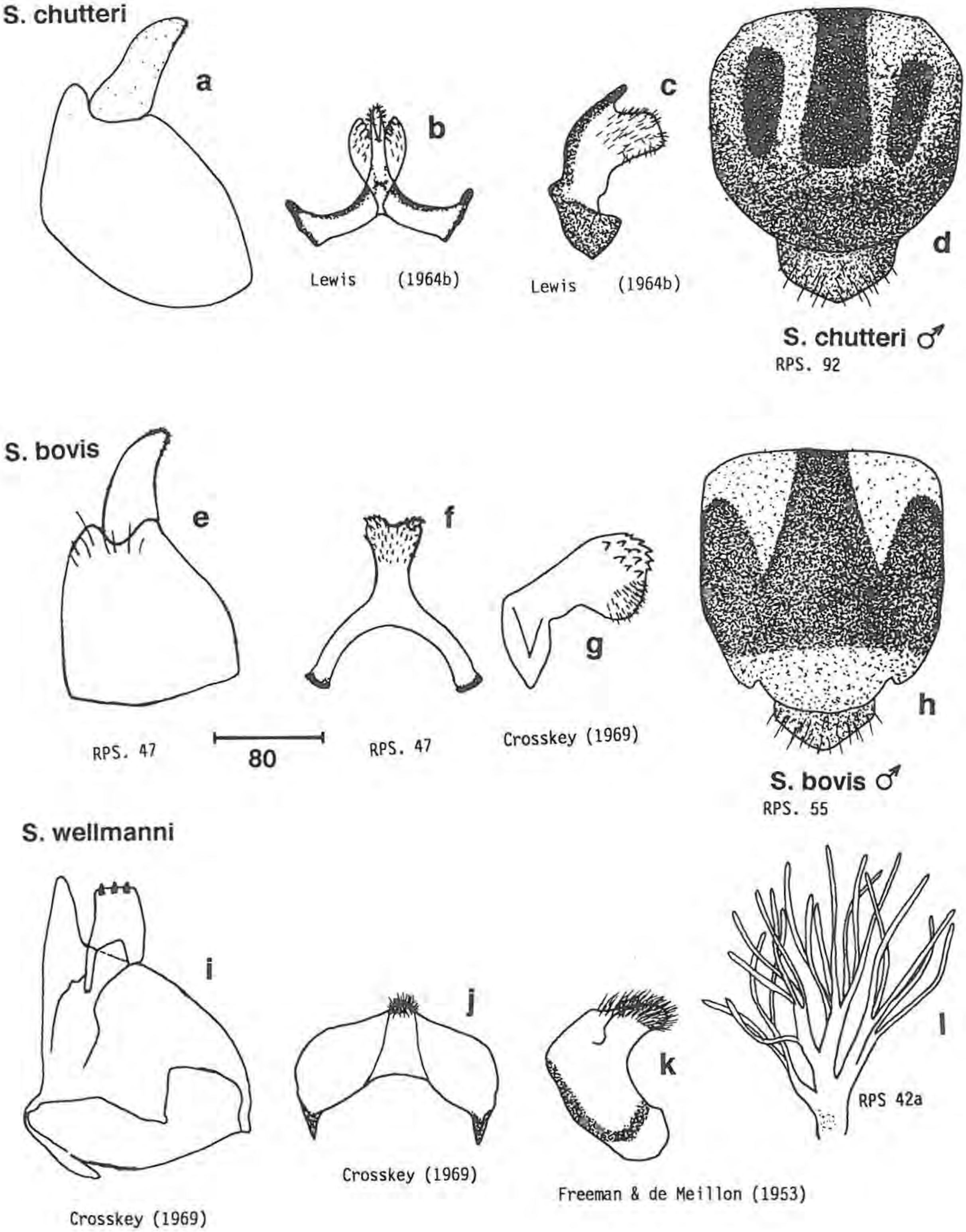


Fig. 6.19 **S. (Metomphalus) chutteri**: male - **a**, coxite and style. **b**, ventral plate. **c**, ventral plate in profile. **d**, scutal pattern. **S. (Metomphalus) bovis** **e**, coxite and style. **f**, ventral plate. **g**, ventral plate in profile. **h**, scutal pattern. **S. (Metomphalus) wellmanni** **i**, coxite and style. **j**, ventral plate. **k**, ventral plate in profile. Pupa - **l**, pupal gill. [Scale in μm].

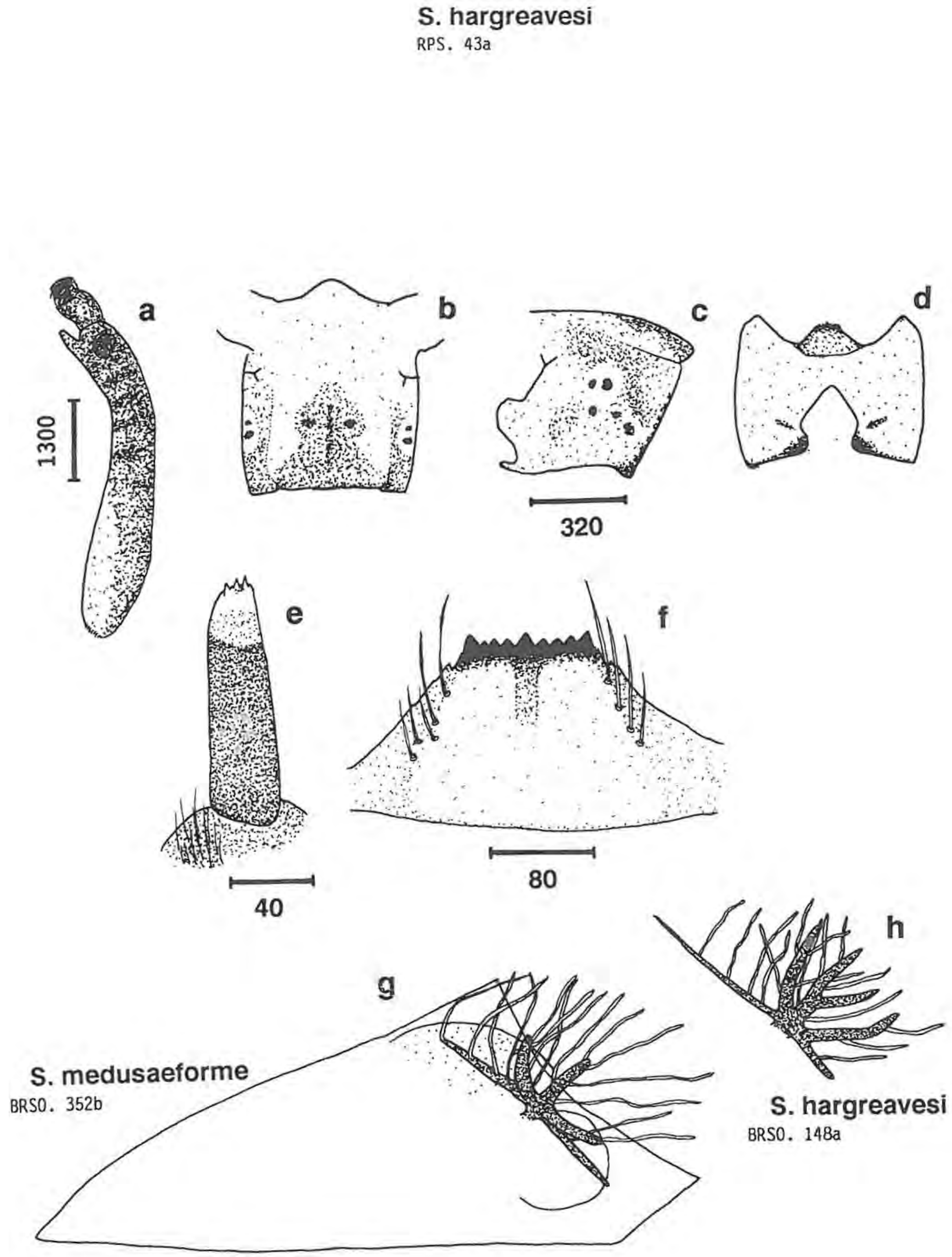


Fig. 6.20 **S. (Metomphalus) hargreavesi**: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, maxillary palp. **f**, hypostomium. Pupa - **g**, **S. (Metomphalus) medusaeforme**: Pupa. **h**, **S. (Metomphalus) hargreavesi**: pupal gill. [Scale in μm].

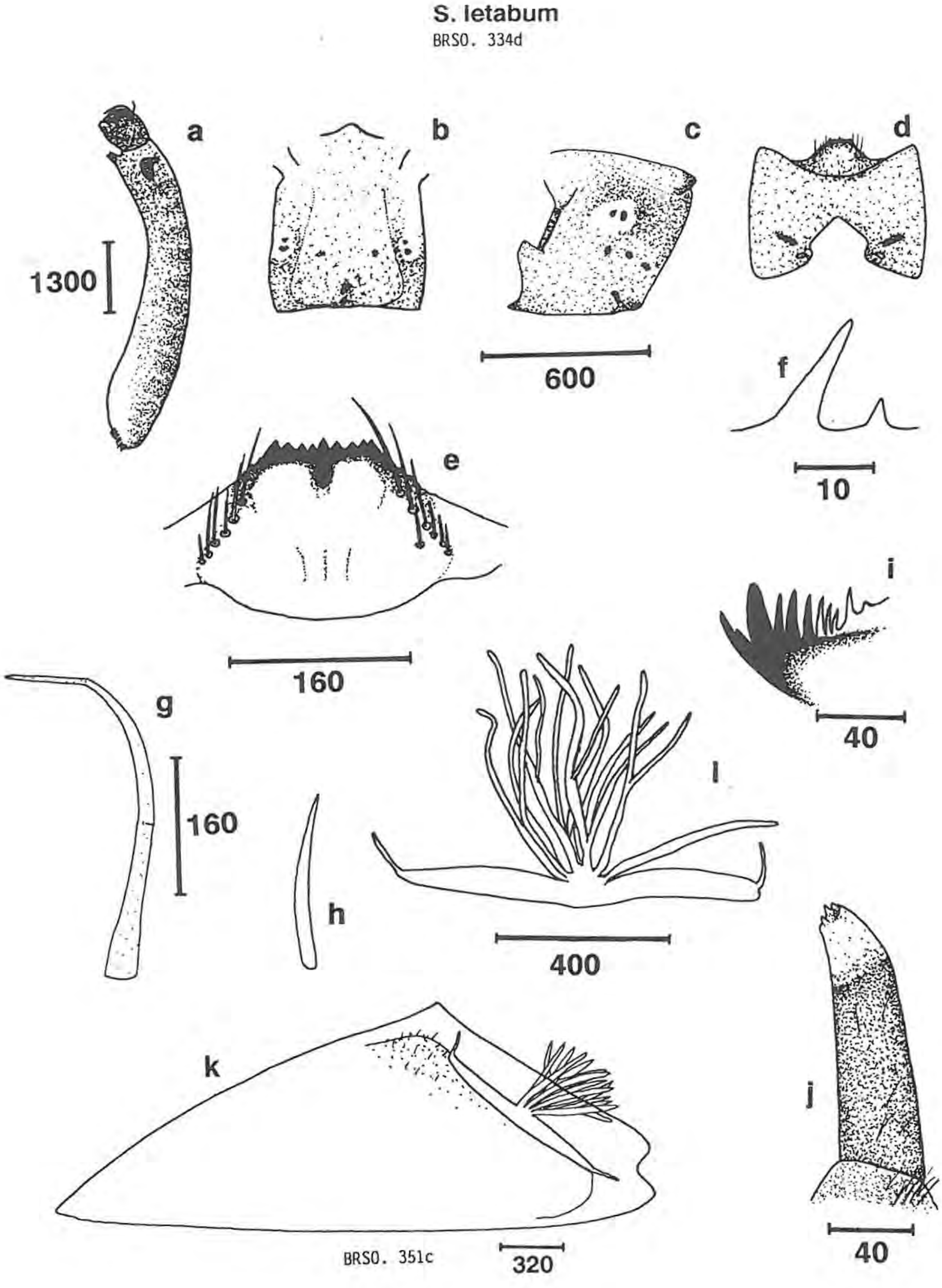


Fig. 6.21 **S. (Metomphalus) letabum**: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, posterior serrations. **g**, antenna. **h**, abdominal seta. **i**, apex of mandible. **j**, maxillary palp. Pupa - **k**, pupa. **l**, pupal gill. [Scale in μm].

S. vorax

BRSO. 325g

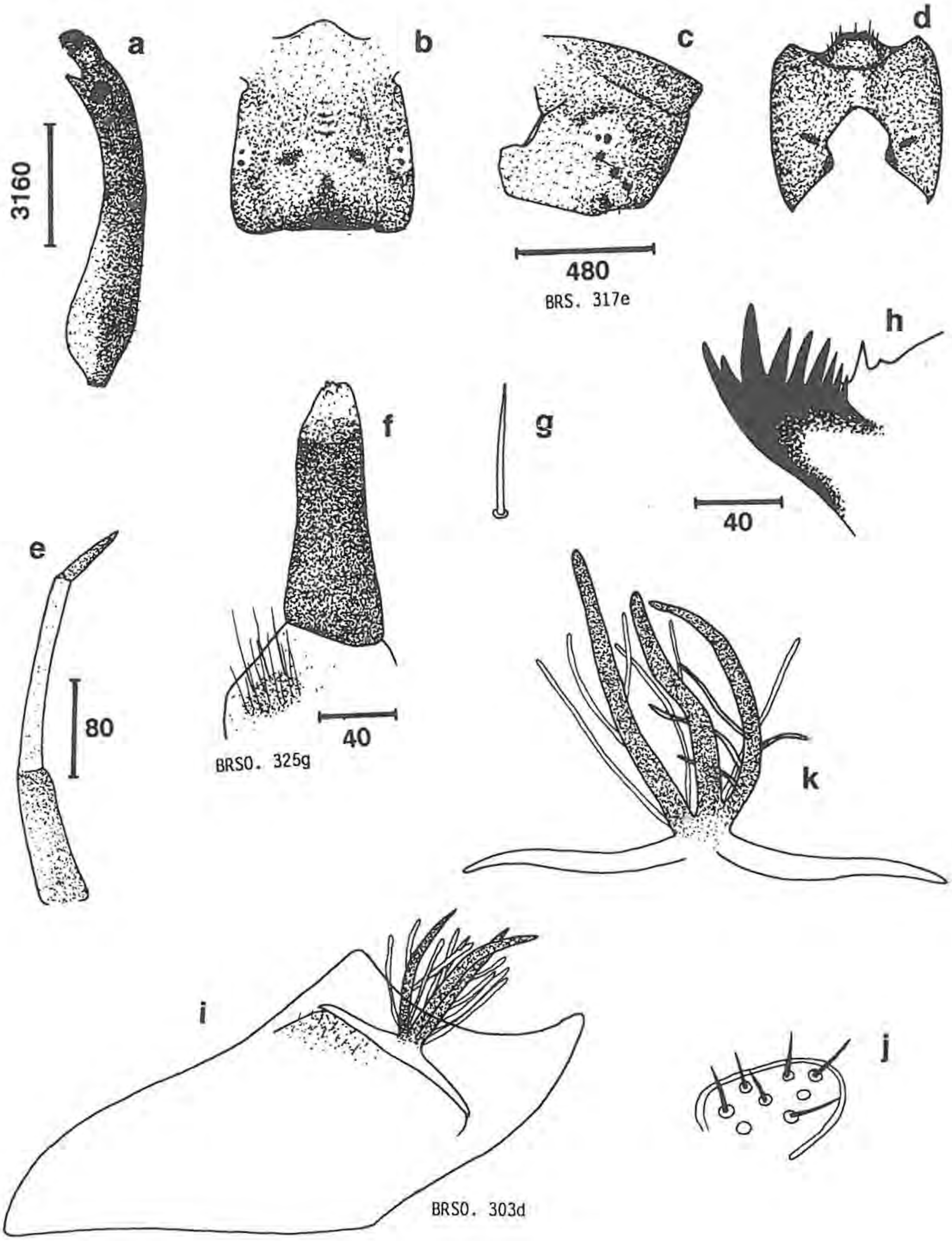


Fig. 6.22 S. (Metomphalus) vorax: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, maxillary palp. **g**, abdominal seta. **h**, apex of mandible. Pupa - **i**, pupa. **j**, pilous plate. **k**, pupal gill. [Scale in μm].

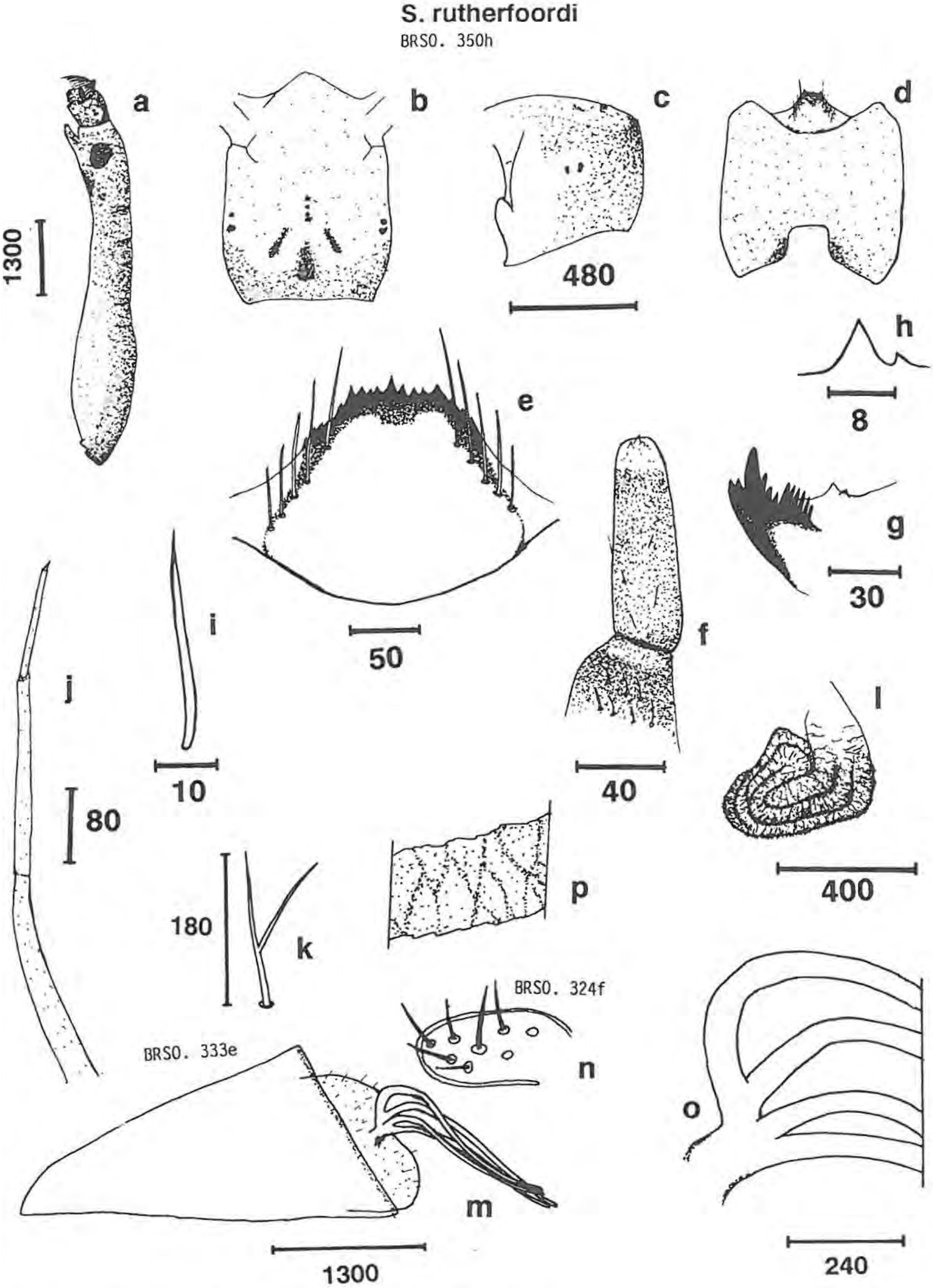


Fig. 6.23 S. (Nevermannia) rutherfoordi: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, maxillary palp. **g**, apex of mandible. **h**, posterior serrations. **i**, abdominal seta. **j**, antenna. Pupa - **k**, pupal trichomes. **l**, gill-spot. **m**, pupa **n**, pilous splate. **o**, base of pupal gill. **p**, gill filament. [Scale in μm].

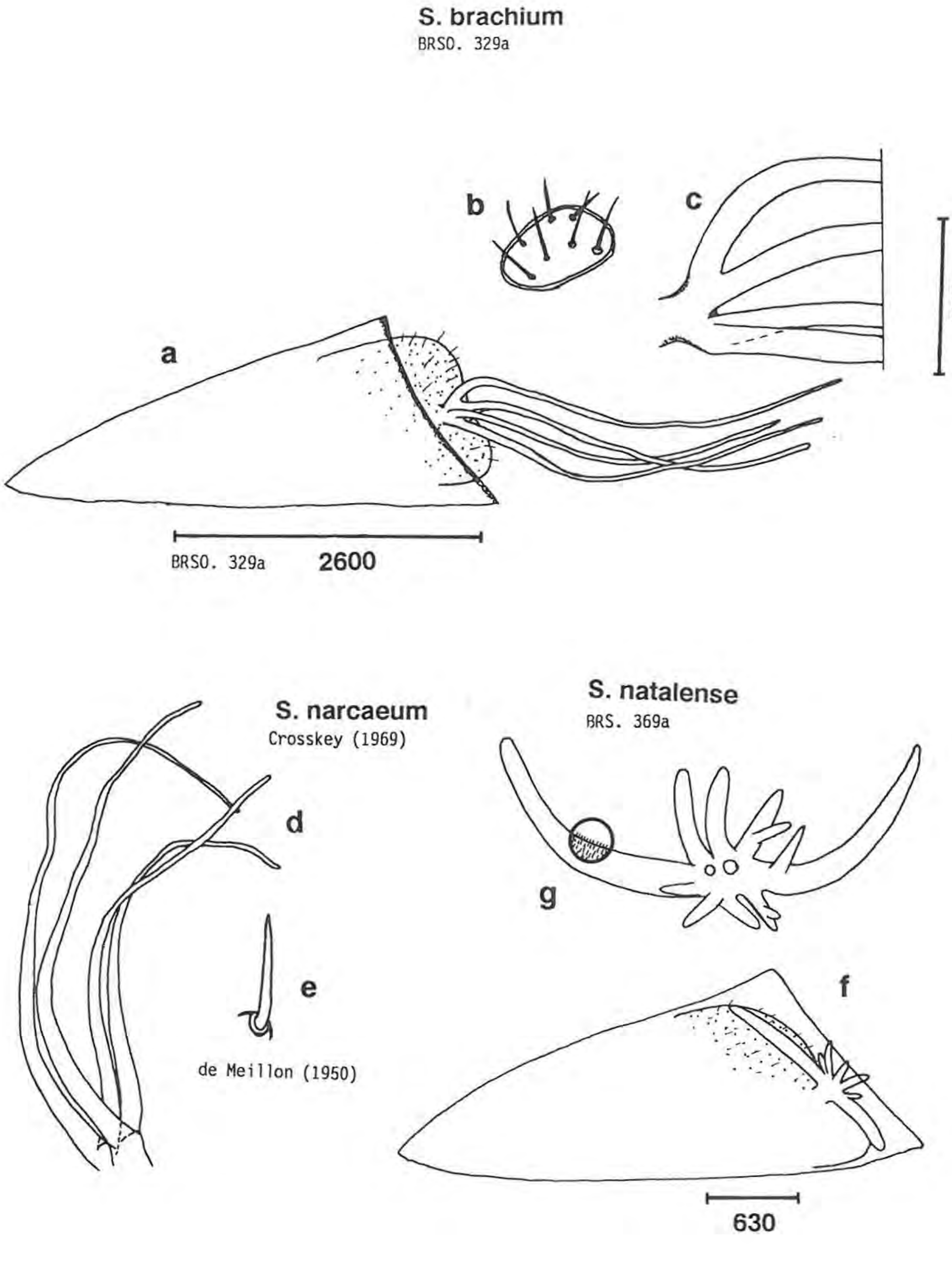


Fig. 6.24 **S. (Nevermannia) brachium**: Pupa - **a**, pupa. **b**, pilous plate. **c**, base of pupal gill. **S. (Nevermannia) narcaeum** **d**, pupal gill. **e**, pupal trichome. **S. (Metomphalus) natalense** **f**, pupa. **g**, gill filament showing setae. [Scale in µm].

S. katangae
RPS. 46f

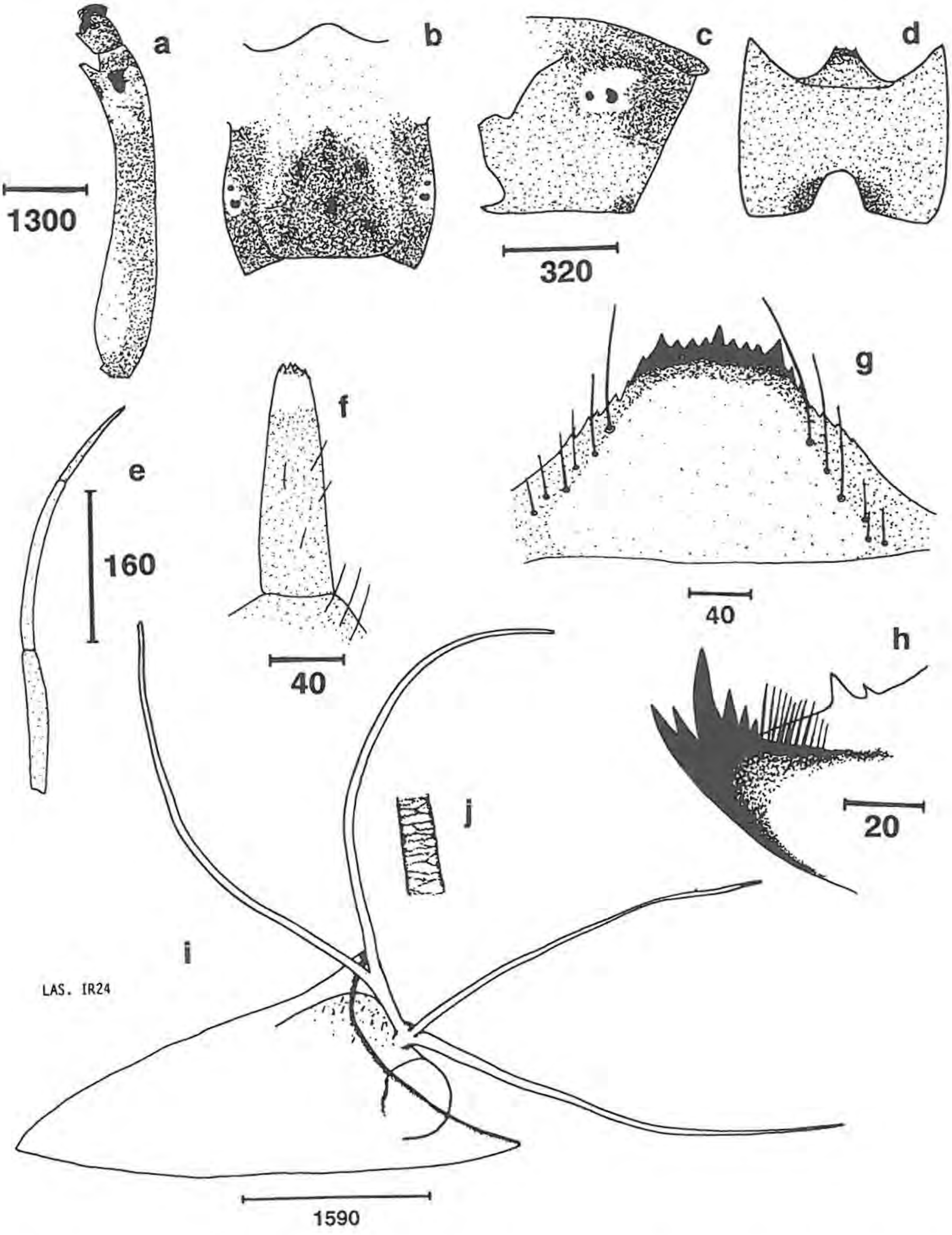
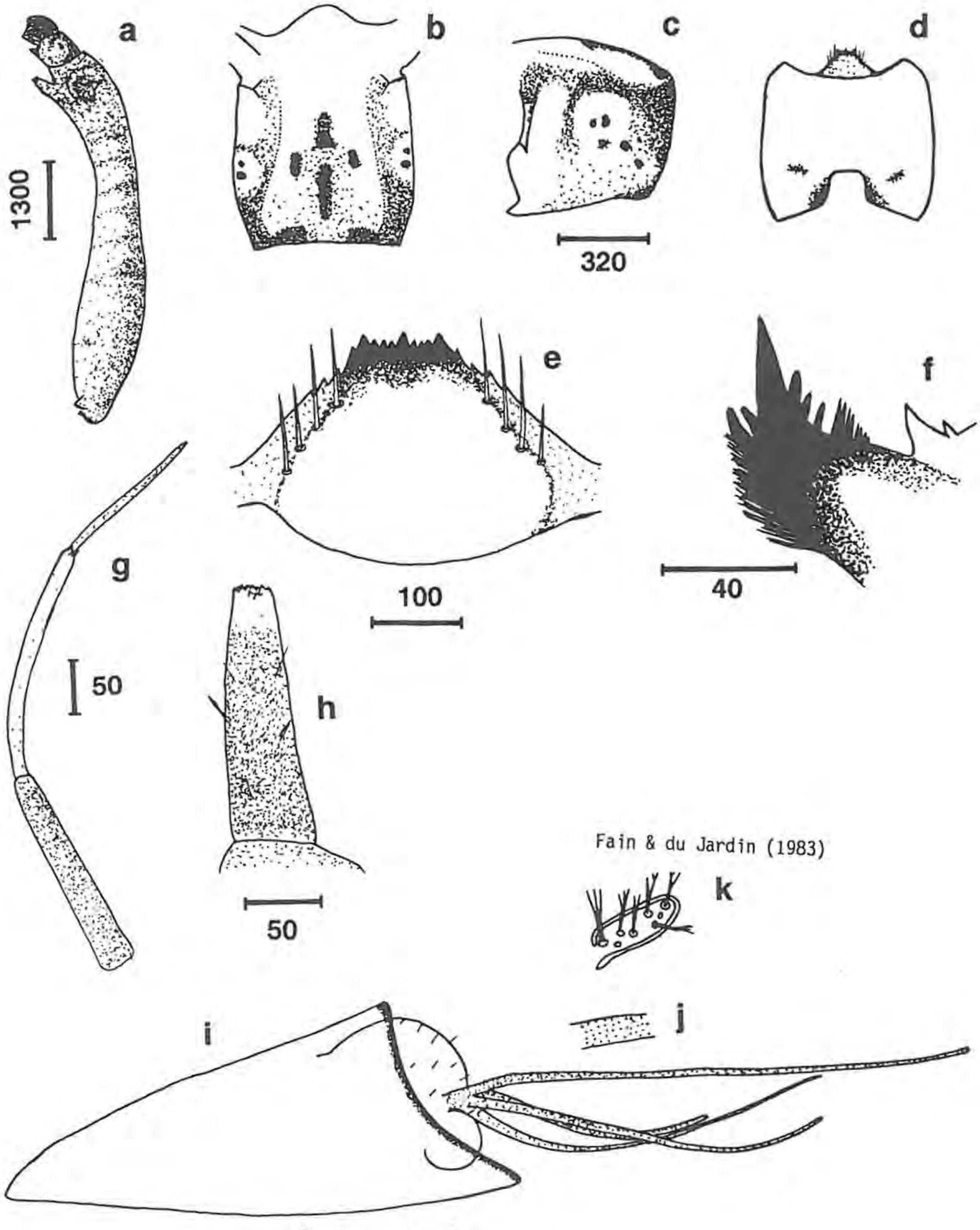


Fig. 6.25 **S. (Nevermannia) katangae**: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, maxillary palp. **g**, hypostomium. **h**, apex of mandible. Pupa - **i**, pupa. **j**, gill filament. [Scale in μm].

S. nigritarse s.l.
GEN. 810



Fain & du Jardin (1983)

Fig. 6.26 S. (Nevermannia) nigritarse s.l.: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillary palp. Pupa - **i**, pupa. **j**, gill filament. **k**, pilous plate. [Scale in μm].

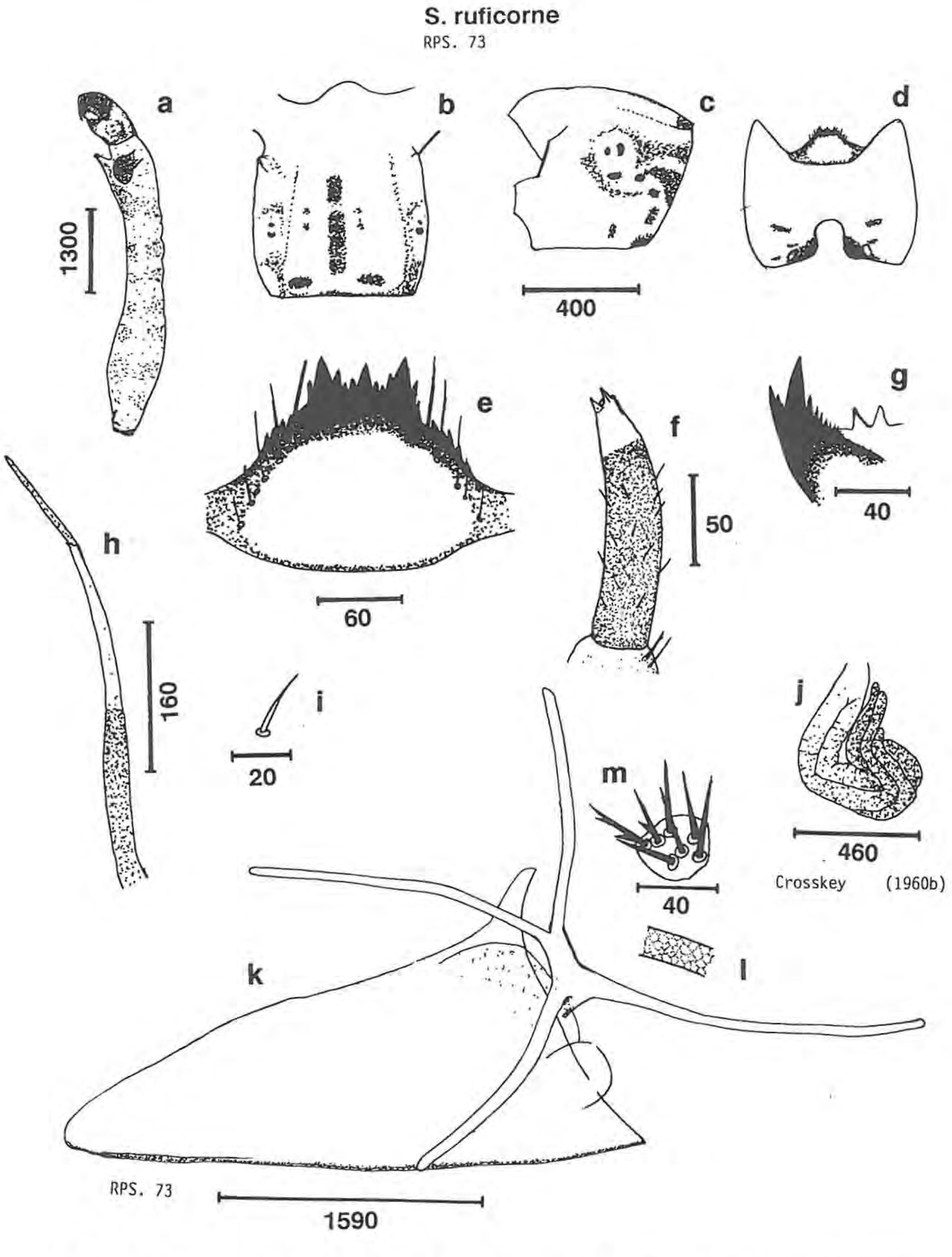
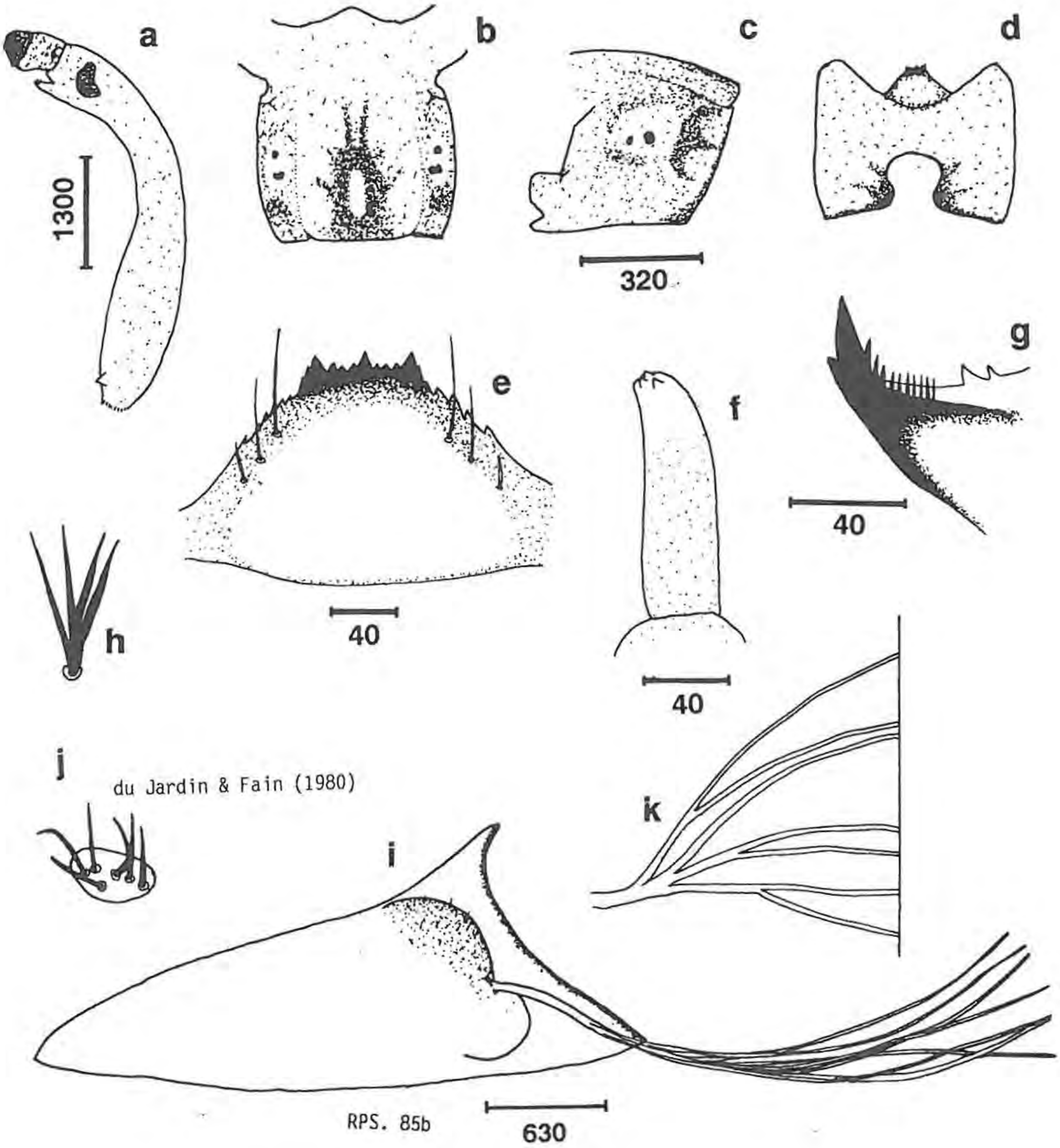


Fig. 6.27 S. (Nevermannia) ruficorne: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, maxillary palp. **g**, apex of mandible, showing two large and characteristic posterior serrations. **h**, antenna. **i**, abdominal seta. Pupa - **j**, gill-spot. **k**, pupa. **l**, gill filament. **m**, pilous plate. [Scale in μm].

S. alcocki
RPS. 81b



du Jardin & Fain (1980)

RPS. 85b

Fig. 6.28 **S. (Pomeroyellum) alcocki**: Larva - **a**, body shape. **b**, head dorsal, showing negative pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, maxillary palp. **g**, apex of mandible. **h**, abdominal seta. Pupa - **i**, pupa. **j**, pilous plate. **k**, base of pupal gill. [Scale in µm].

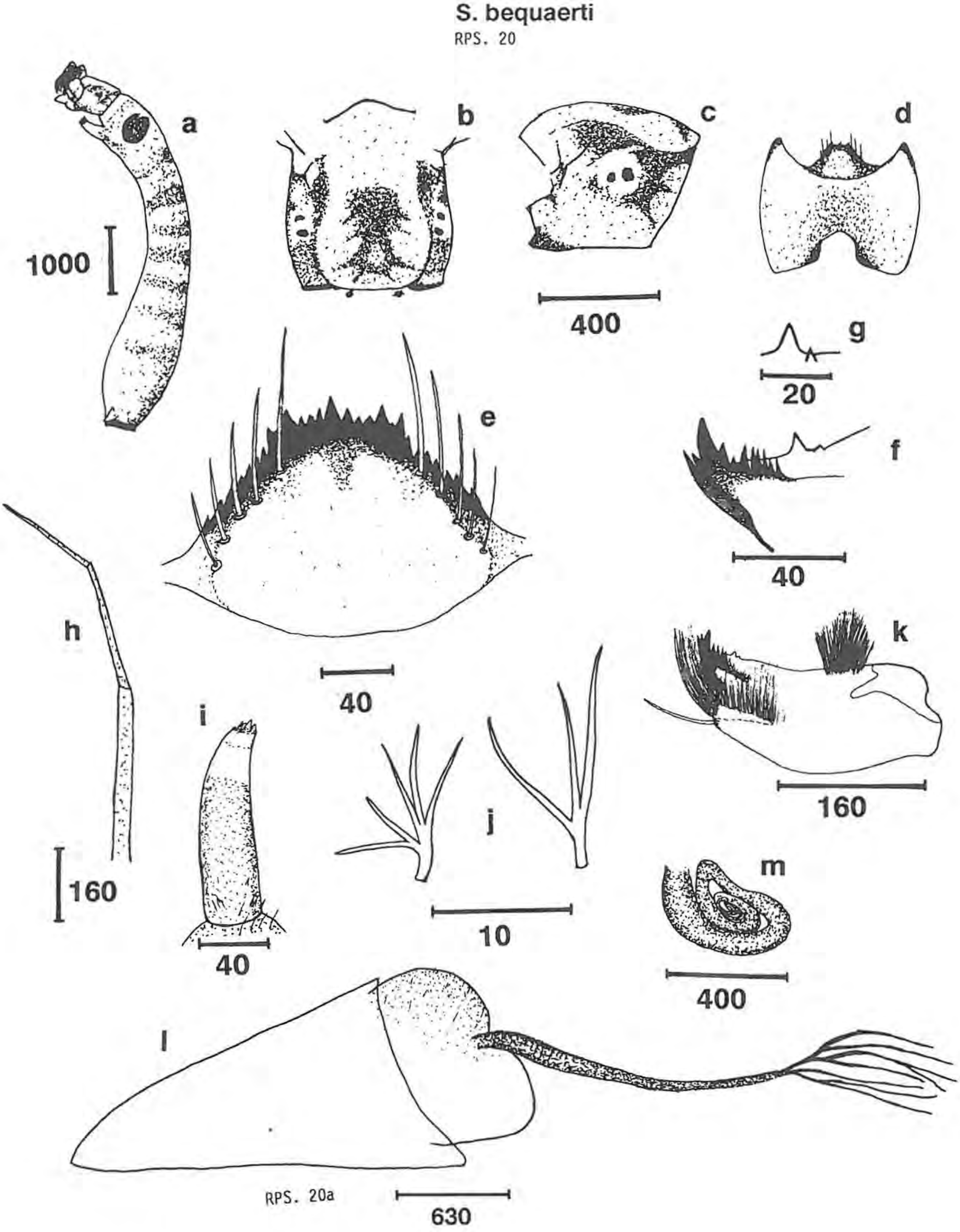

S. bequaerti
RPS. 20

Fig. 6.29 S. (Pomeroyellum) bequaerti: Larva - **a**, body shape. **b**, head dorsal, showing negative pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, posterior serrations. **h**, antenna. **i**, maxillary palp. **j**, abdominal setae. **k**, mandible. Pupa - **l**, pupa. **m**, gill-spot. [Scale in μm].

S. cervicornutum
RPS. 36a

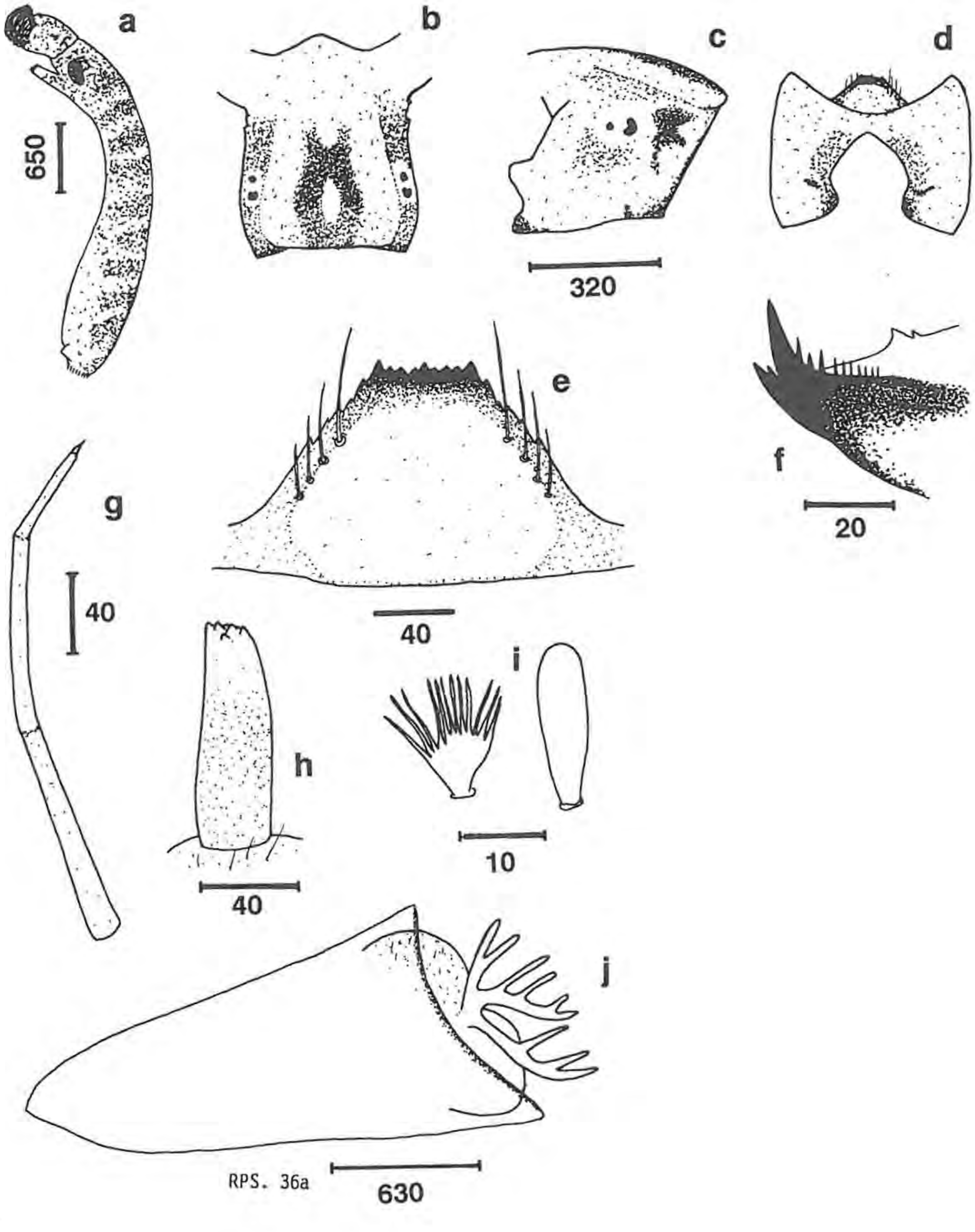
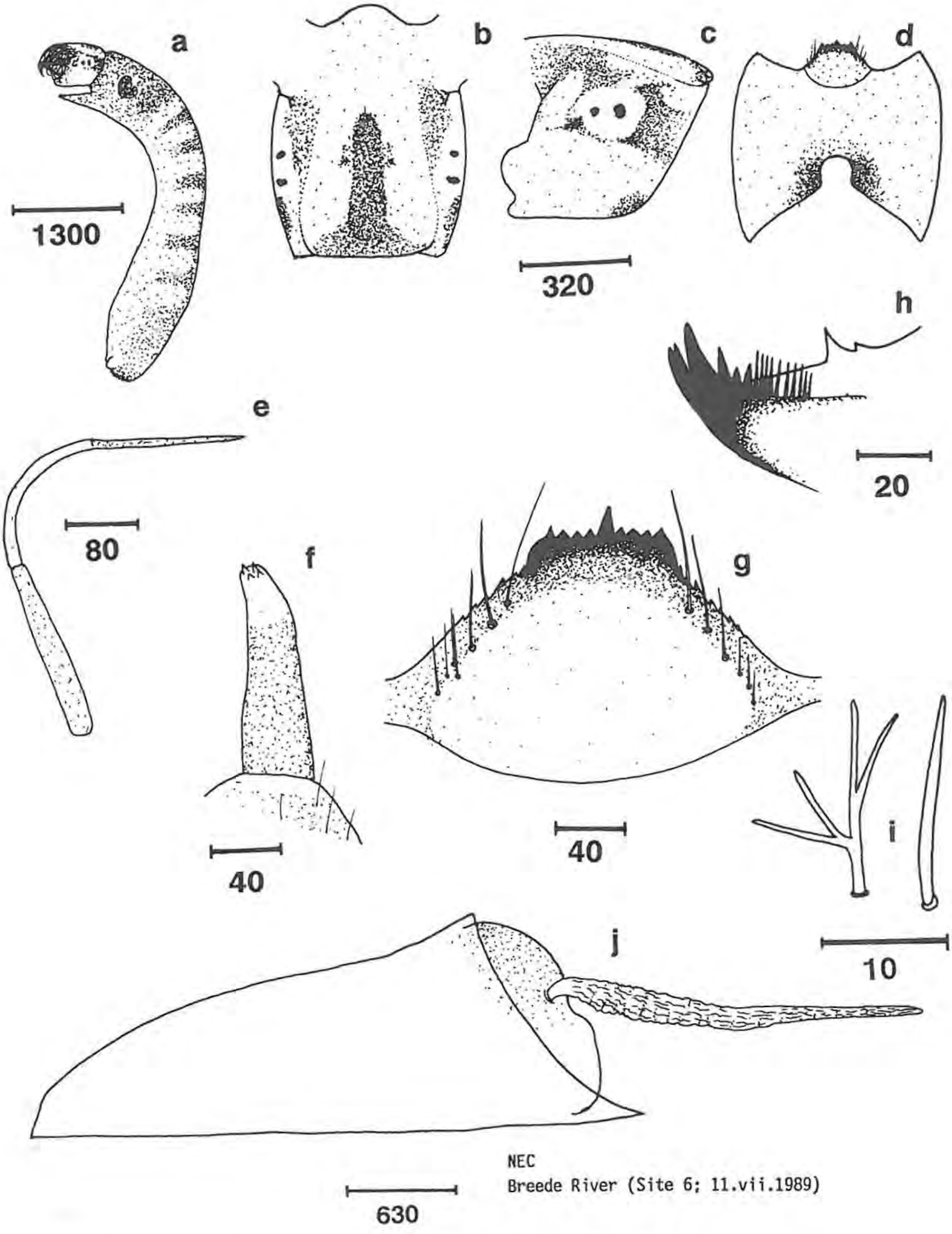


Fig. 6.30 S. (Pomeroyellum) cervicornutum: Larva - **a**, body shape. **b**, head dorsal, showing negative pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillary palp. **i**, abdominal setae. Pupa - **j**, pupa. [Scale in μm].

S. harrisoni
NEC, Stellenbosch
Breede River (Site 25; 17.vii.1989)



NEC
Breede River (Site 6; 11.vii.1989)

Fig. 6.31 S. (Pomeroyellum) harrisoni: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, maxillary palp. **g**, hypostomium. **h**, apex of mandible. **i**, abdominal seta. Pupa - **j**, pupa. [Scale in μm].

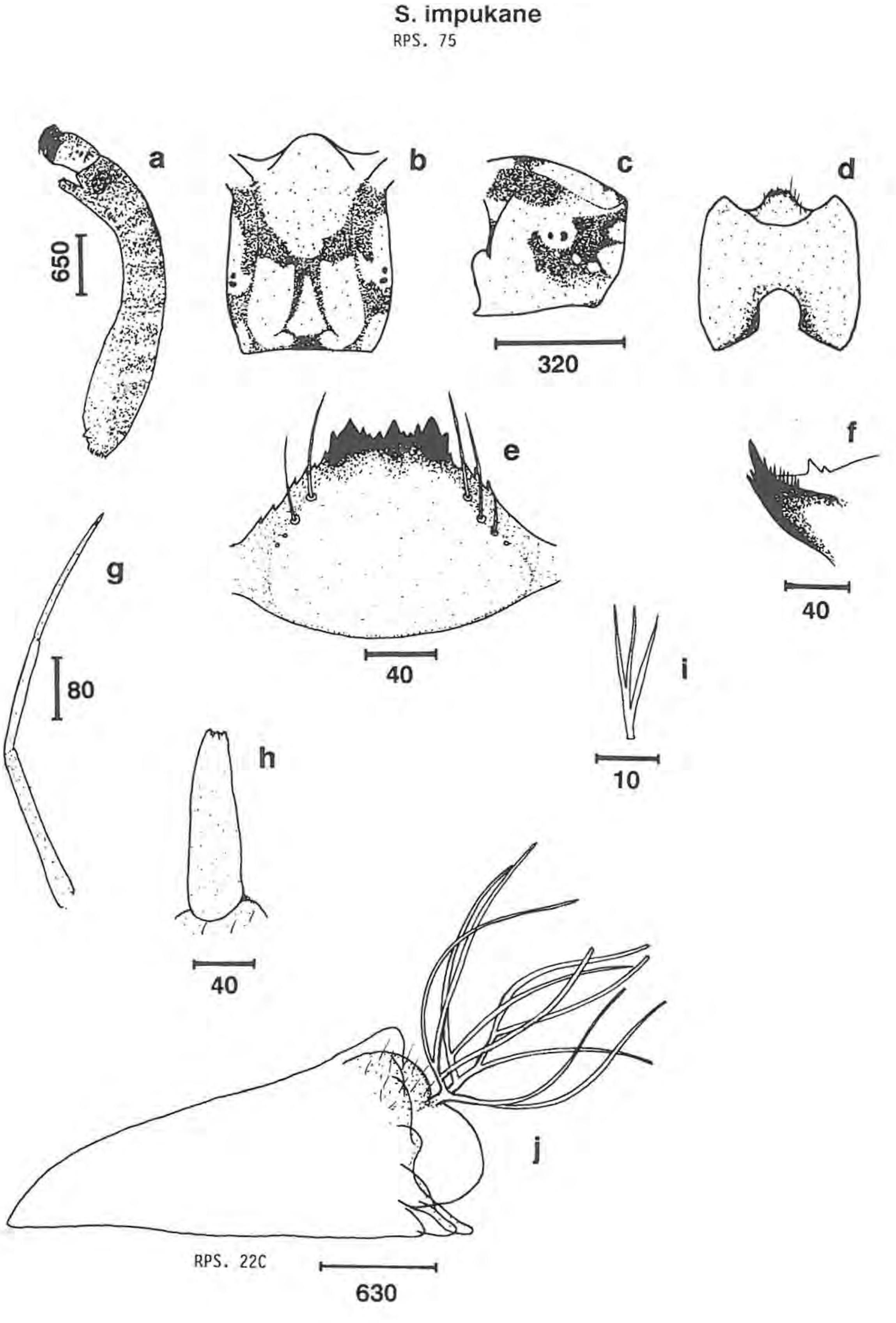


Fig. 6.32 S. (Pomeroyellum) impukane: Larva - **a**, body shape. **b**, head dorsal, showing negative pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, hypostomium. **f**, apex of mandible. **g**, antenna. **h**, maxillry palp. **i**, abdominal seta. Pupa - **j**, pupa. [Scale in μm].

S. mcmahoni

RPS. 70b

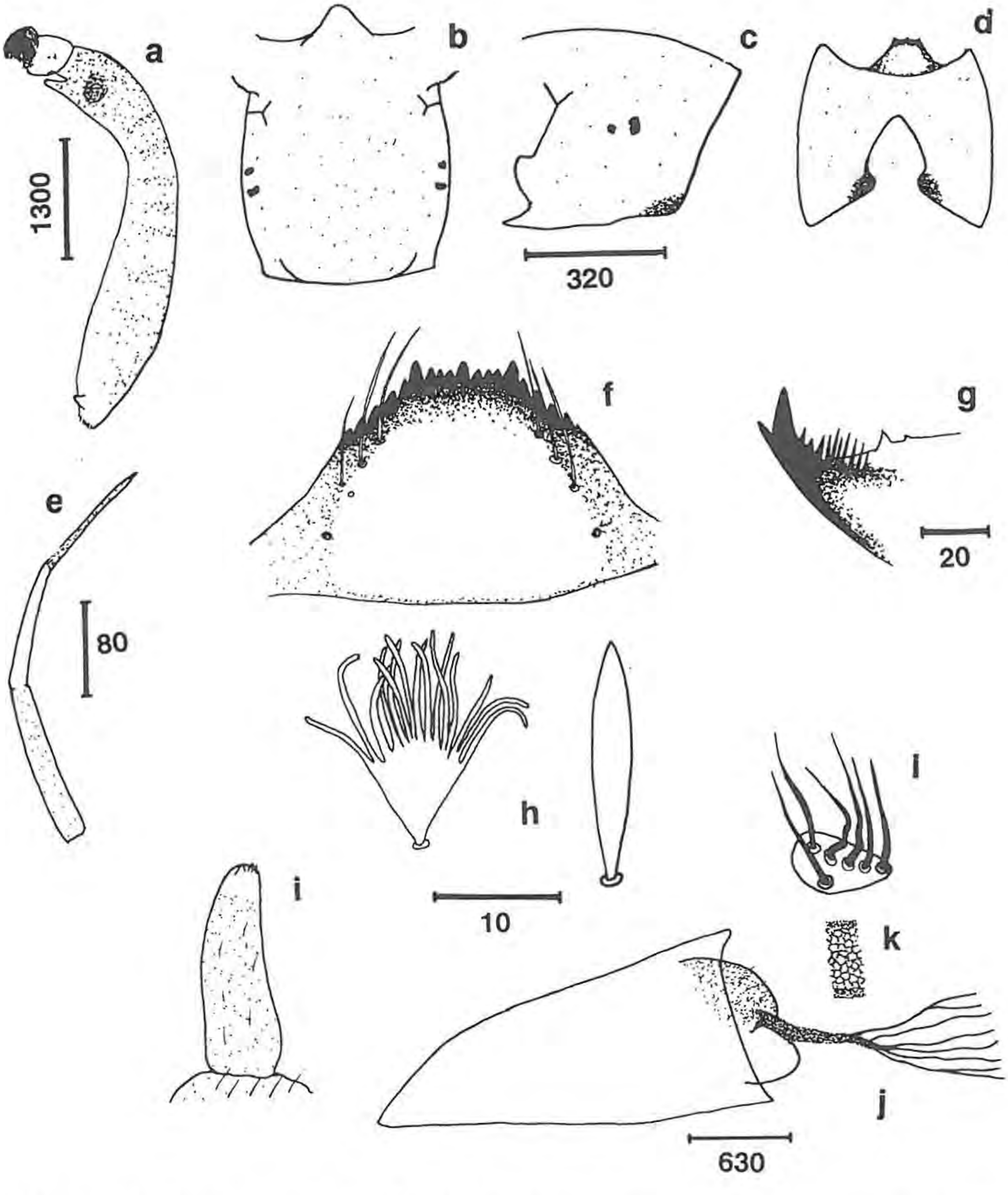


Fig. 6.33 S. (Pomeroyellum) mcmahoni: Larva - **a**, body shape. **b**, head dorsal. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, hypostomium. **g**, apex of mandible. **h**, abdominal setae. **i**, maxillary palp. Pupa - **j**, pupa. **k**, gill filament. **l**, pilous plate. [Scale in μm].

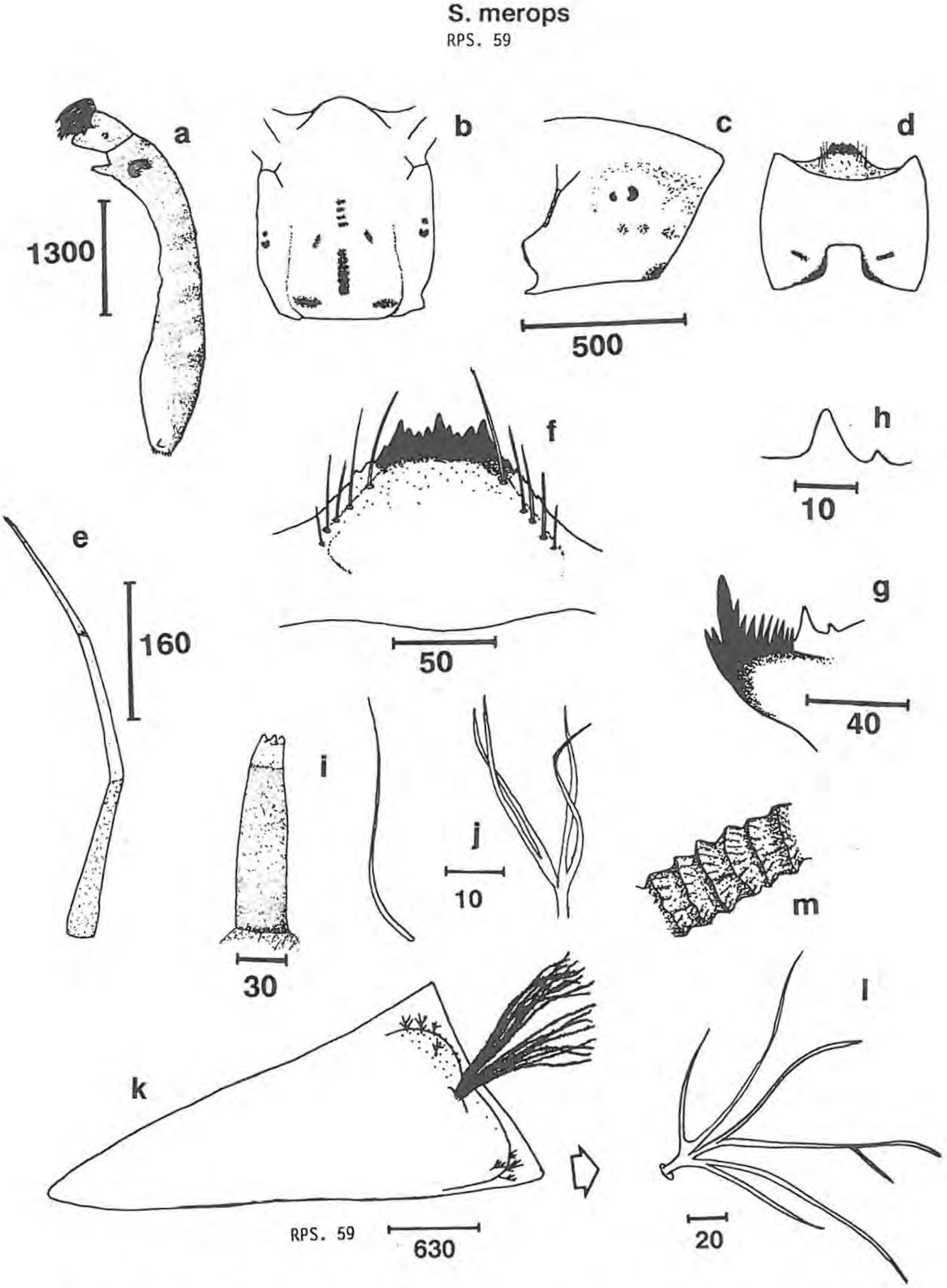


Fig. 6.34 S. (Pomeroyellum) merops: Larva - **a**, body shape. **b**, head dorsal, showing positive pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, hypostomium. **g**, apex of mandible. **h**, posterior serrations. **i**, maxillary palp. **j**, simple and compound abdominal setae. Pupa - **k**, pupa. **l**, pupal trichomes. **m**, gill filament. [Scale in μm].

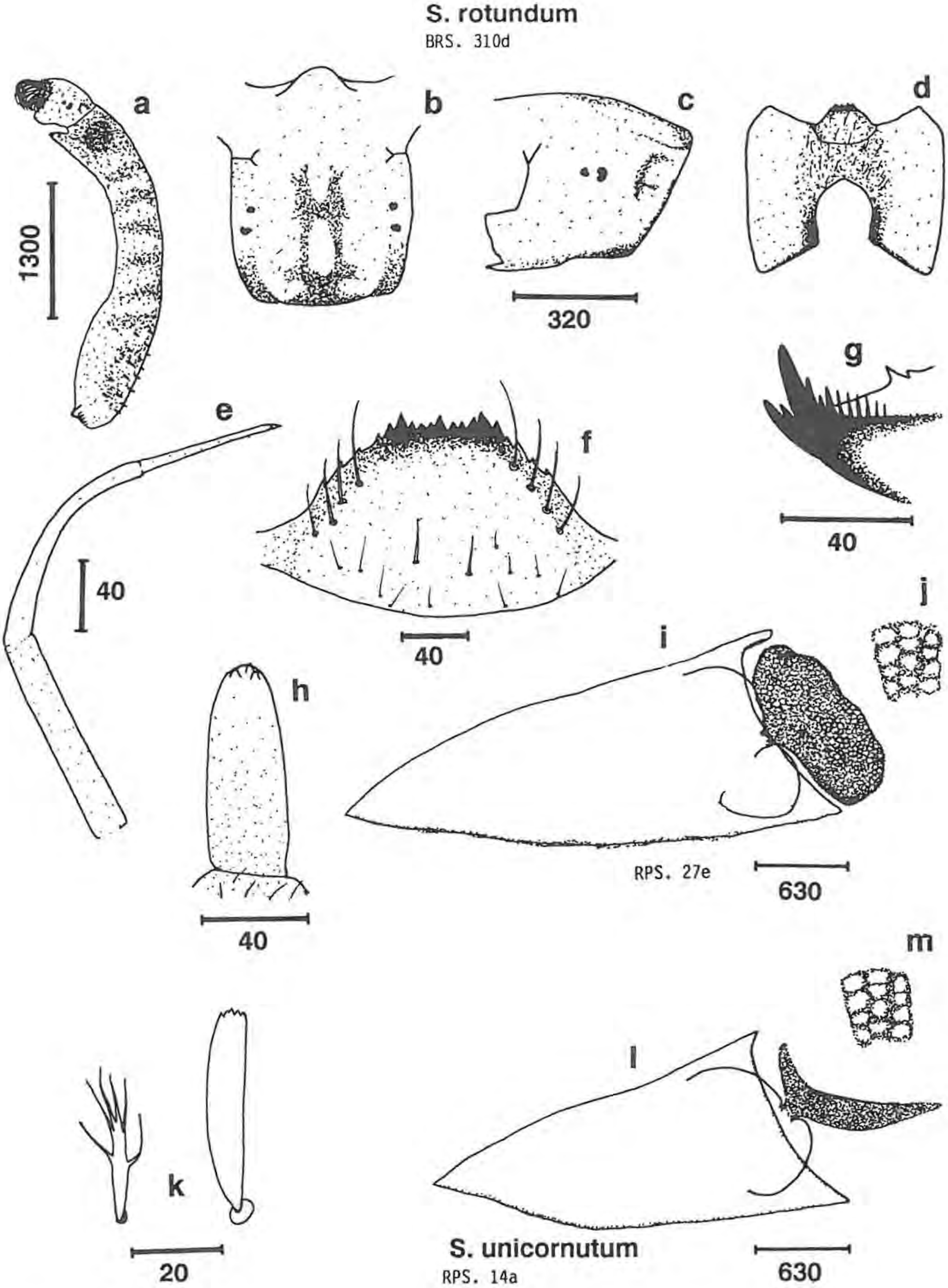


Fig. 6.35 S. (Pomeroyellum) rotundum: Larva - **a**, body shape. **b**, head dorsal, showing negative pigmentation pattern. **c**, head lateral. **d**, head ventral. **e**, antenna. **f**, hypostomium. **g**, apex of mandible. **h**, maxillary palp. Pupa - **i**, pupa. **j**, pupal gill surface. **k**, abdominal setae. **S. (Pomeroyellum) unicornutum l**, pupa. **m**, pupal gill surface. [Scale in μm].

7 DISTRIBUTION AND ABUNDANCE OF BLACKFLIES IN THE BUFFALO RIVER

7.1 INTRODUCTION

This chapter describes the effects of impoundment on the distribution and abundance of blackflies in the Buffalo River. In addition, the functional importance of blackfly larvae to material processing in the Buffalo River is investigated.

Most blackfly larvae are filter-feeders, and are considered an important interface which link processes that occur in the water column with those that occur on the stream bed (McCullough et al., 1979; Wallace & Merritt, 1980). High population densities of blackfly larvae are theoretically capable of removing all suspended material within 600-900 m of stream bed (Maciolek & Tunzi, 1968; Ladle et al., 1972; McCullough et al., 1979; de Moor, 1982a). The importance of blackfly larvae to material transport in streams depends on the relationship between discharge, stream width, population density and seston concentration. At times of high discharge, streams function as physical systems, with little biological contribution (Hynes, 1970a, 1975). At low discharge, biological processes become more important, to the extent that food may become limiting for blackfly larvae (Morin & Peters, 1988).

7.2 METHODS

Benthic invertebrates were collected from 'stones-in-current' biotope at 16 sites in the Buffalo River, using a 25 × 25 cm Box sampler (Fig. 7.1a; Merritt & Cummins, 1978), with a mesh size of 80 μm. Rocks and stones within the area of the sampler were scrubbed clean in the catching net and then removed. The substrate was then stirred vigorously, and suspended material was swept into the catching net. Three randomly selected replicate samples were taken at each site at roughly bimonthly intervals between April and December 1986, after which sampling was monthly until April 1988. Samples were fixed separately in 8% formaldehyde for at least 24 hrs, after which they were transfered to 80% ethanol before sorting and counting.

Fig. 7.1 **a**, Box sampler used in regular sampling of benthic invertebrates in the Buffalo River. Typical blackfly larval biotopes - **b**, riffle at Site 1, **c**, riffle at Site 11, and **d**, the spillway of Bridle Drift (B4).

Most samples contained large numbers of invertebrates (exceeding 500, and up to 23,000), and these were subsampled in the following way: A random subsample not exceeding 100 individuals of each major taxonomic group (Simuliidae, Ephemeroptera, Trichoptera, Chironomidae and 'Others') was removed and identified. The remaining sample was then divided by sieving into macro- (> 1 mm) and micro- (< 1 mm) components (Allanson & Kerrich, 1961). Each component was spread evenly onto a tray with 100 ruled subdivisions (Marchant et al., 1985). Major taxonomic groups in 32% of the subdivisions were counted with a scanning binocular microscope. (See Table 7.1 for a worked example.) Samples which contained few invertebrates (less than about 500) where identified and counted without subsampling. Results are expressed as individuals per m^2. Sites were classified using two-way indicator species analysis (TWINSPAN; Hill, 1979), based on the frequency of occurrence (as a percentage) of blackfly taxa in three Box samples. Pseudospecies cut levels used were 0, 1, 5, 20 and 50.

Table 7.1 A hypothetical example to illustrate the method used to calculate benthic invertebrate relative population densities. See text for full explanation.

Taxa	Random subsample	Macro	Micro	Total (per box)	Total m^{-2}
Simuliidae	100	370	150	1,725	27,600
S. adersi	50				13,800
S. vorax	25				6,900
S. letabum	25				6,900

Current speed preferences of mature larvae were determined by removing and identifying individual larvae from substrates situated in a wide range of current speeds. The current speed at each locality were a mature larva was found was measured at 60% depth with an Ott^R current meter, as recommended by Statzner et al. (1988).

The proportion of suspended material ingested by blackfly larvae was estimated from an average individual ingestion rate of 0.2 mg hr^{-1} (McCullough et al., 1979; Morin et al, 1988b; Scott, 1990), larval population densities per m^{2}, water discharge per metre width of stream, and the concentration of suspended material.

7.3 RESULTS

Blackfly larvae constituted between 7 and 35% (range of median values at all sites) of the invertebrate fauna in riffles in the Buffalo River (Fig. 7.2). Other invertebrate groups which were common in stones-in-current biotope included Chironomidae (8 to 39%) and Ephemeroptera (6 to 37%). Trichoptera were numerically important downstream of Rooikrans (B2) (8 to 17%), but were rare in riffles upstream of Rooikrans (B2) (<2%).

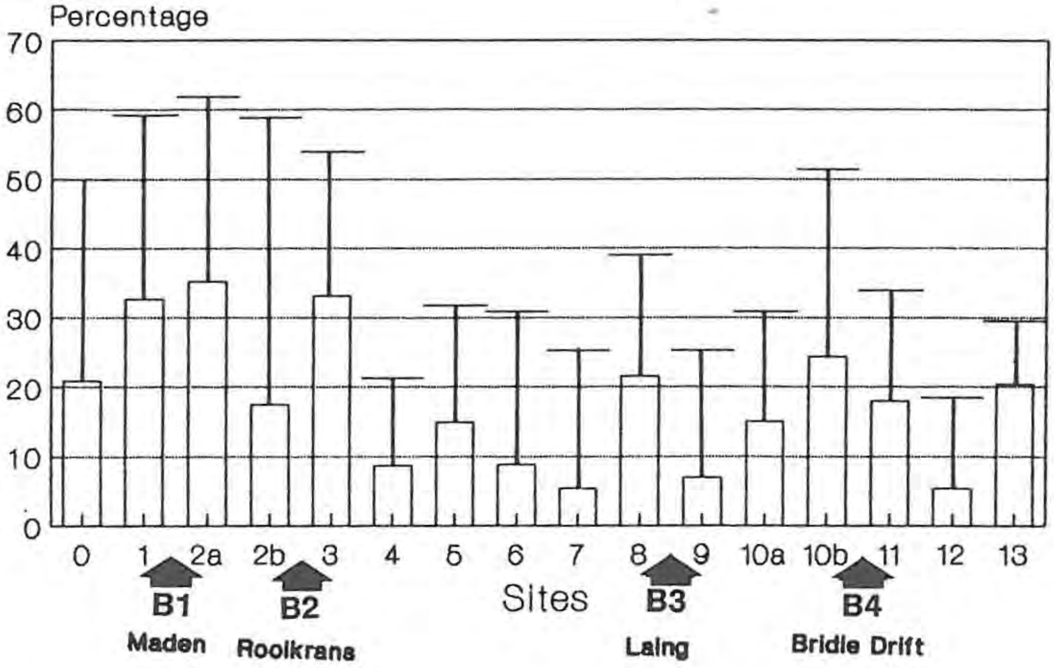


Fig. 7.2 Median abundance of blackflies relative to other riffle-dwelling invertebrates in the Buffalo River, expressed as a percentage. Data are based on the numbers of blackflies and total numbers of invertebrates in each of three Box samples collected monthly between 1986 and 1988. Positions of impoundments (**B1** to **B4**) are indicated. Bars indicate 75th percentiles.

Twenty species of blackflies were found in the Buffalo River, of which 18 were distinguishable as larvae (Table 7.2). Apart from 5 widespread taxa, blackflies in the Buffalo River were divided into those restricted to waterfalls and mountain torrents (*S. dentulosum* and *S. debegene*), those found in the upper foothill stony run zone (*S. rutherfoordi* and *S. letabum*), those found in the upper part of the lower foothill stony run zone (*S. impukane*, *S. rotundum*, *S. bequaerti* and *S. alcocki*) and rare species (*S. ruficorne*, *S. mcmhoni*, *S. hirsutum*, *S. chutteri* and *S. natalense*). A

TWINSPAN classification of the occurrence of blackfly larvae suggested 3 groups (Fig. 7.3). The headwater site (Site 0) separated clearly from the rest of the river, and was characterised by the absence of *S. damnosum* s.l. (Fig. 7.3). The headwater site was consistently dominated (numerically) by *S. dentulosum* (Fig. 7.4), although *S. rutherfoordi* were often present on rocks and trailing vegetation in slow-flowing water. Another species found in mountain torrents, *S. debegene*, was uncommon in regular Box sampling at Site 0, but appeared in high numbers at a waterfall between Sites 0 and 1 in August and September 1989. Pupae of the rare *S. natalense* were also collected between Sites 0 and 1, but not during regular monthly box-sampling.

The second level TWINSPAN split separated the upper/middle reaches of the river (Sites 1-5 & 7) from the lower reaches (Sites 6 & 8-13; Fig. 7.3). The upper/middle reaches were dominated by *S. medusaeforme/hargreavesi*, and to a lesser extent *S. nigritarse/brachium* (Fig. 7.4), and was characterised by high numbers of taxa (8-15) compared to further downstream (6-7; $P<0,001$, Student's *t*-test). Three Box samples usually contained between 3 and 4 blackfly taxa, but up to 8 were collected at times (Table 7.2).

Table 7.2 Frequency of occurrence (expressed as a percentage) of all blackfly taxa, and the median, maximum and total number of blackfly taxa at 16 sites in the Buffalo River. Data are based on the presence of larvae (or pupae) collected monthly in three Box samples between 1986 and 1988. The values indicate the probability of finding a taxon in three Box samples at any time of the year. Stars (*) indicate the presence of rare taxa collected by hand, but not found in Box samples. Plus signs (+) indicate taxa which were common in impoundment outlets. Minus signs (-) indicate the opposite. The positions of impoundments (**B1** to **B4**) are indicated by colons. Larvae which could not be identified to species level are indicated by combined names (e.g., *S. med/harg.*).

	Sites		:			:							:				:			
Taxa	0	1	:	2b	2c	:	3	4	5	6	7	8	:	9	10a	10b	:	11	12	13
Widespread taxa			:			:							:				:			
+ S. med/harg.	11	61	:	57	57	:	100	79	75	55	31	63	:	26	30	37	:	60	38	75
+ S. nig/brach.	22	61	:	52	50	:	75	84	70	75	62	68	:	47	70	62	:	50	38	40
+ S. adersi	11	28	:	61	35	:	80	42	45	65	75	84	:	68	85	93	:	90	72	90
+ S. damnosum s.l.	-	5	:	19	21	:	15	5	20	30	43	21	:	15	15	43	:	70	44	35
S. vorax	-	28	:	19	7	:	15	21	10	5	18	-	:	5	10	12	:	5	17	25
Mountain torrent taxa			:			:							:				:			
S. dentulosum	55	14	:	5	-	:	5	-	-	-	12	-	:	-	-	-	:	-	-	-
S. debegene	11	-	:	-	-	:	-	-	-	-	-	-	:	-	-	-	:	-	-	-
Upper foothill stony run taxa			:			:							:				:			
- S. rutherfoordi	55	38	:	4	-	:	5	-	-	-	-	-	:	-	-	-	:	-	-	-
- S. letabum	11	10	:	5	7	:	5	5	-	-	6	-	:	5	-	-	:	-	-	-
Lower foothill stony run taxa			:			:							:				:			
- S. impukane	-	71	:	4	21	:	20	52	35	-	6	-	:	-	-	-	:	-	-	5
S. rotundum	-	5	:	5	7	:	10	63	50	10	18	-	:	-	-	6	:	-	-	-
S. bequaerti	-	5	:	5	7	:	25	47	35	-	12	-	:	-	-	6	:	-	-	-
S. alcocki	-	5	:	5	-	:	-	15	10	-	-	-	:	-	-	-	:	5	5	-
Rare taxa (in the Buffalo River)			:			:							:				:			
S. ruficorne	*	5	:	-	-	:	-	-	-	5	-	*	:	-	-	-	:	-	-	-
S. mcmahoni	-	5	:	-	-	:	5	-	-	6	-	-	:	-	-	-	:	-	-	-
S. hirsutum	-	-	:	-	-	:	-	-	-	-	-	-	:	-	5	-	:	-	-	-
S. chutteri	-	-	:	-	7	:	5	-	-	-	6	-	:	-	5	-	:	-	-	-
S. natalense	-	*-	:	-	-	:	-	-	-	-	-	-	:	-	-	-	:	-	-	-
Median number of taxa per visit	2	4	:	3	4	:	3	4	4	3	3	3	:	2	2	2	:	3	3	3
Max. number of taxa per vist	4	7	:	6	8	:	6	8	7	5	7	6	:	5	4	5	:	5	5	5
Total number of taxa	8	15	:	12	10	:	13	10	9	8	11	5	:	6	7	7	:	6	6	6
Number of visits	9	21	:	21	14	:	20	19	20	20	16	19	:	19	20	16	:	20	18	20
			B1 Maden			B2 Rooikrans							B3 Laing				B4 Bridle Drift			

The distribution of *S. nigritarse*/*brachium* showed a disjunction between Site 1 and Sites 3 to 10a (Fig. 7.4). The lower reaches of the river were dominated by *S. adersi*. *Simulium damnosum* s.l. were present throughout most of the river, but were particularly common downstream of Bridle Drift (B4) (Fig. 7.4; Table 7.2).

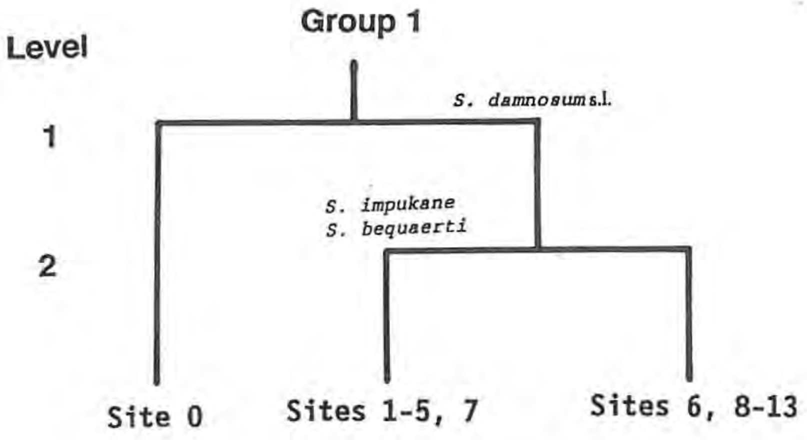


Fig. 7.3 TWINSPAN classification of sites in the Buffalo River to level 2, based on frequency of occurrence of blackfly larvae in three Box samples collected between 1986 and 1988. Taxa which best characterise the differences between subsequent clusters are shown at the bifurcation of each dichotomy where applicable.

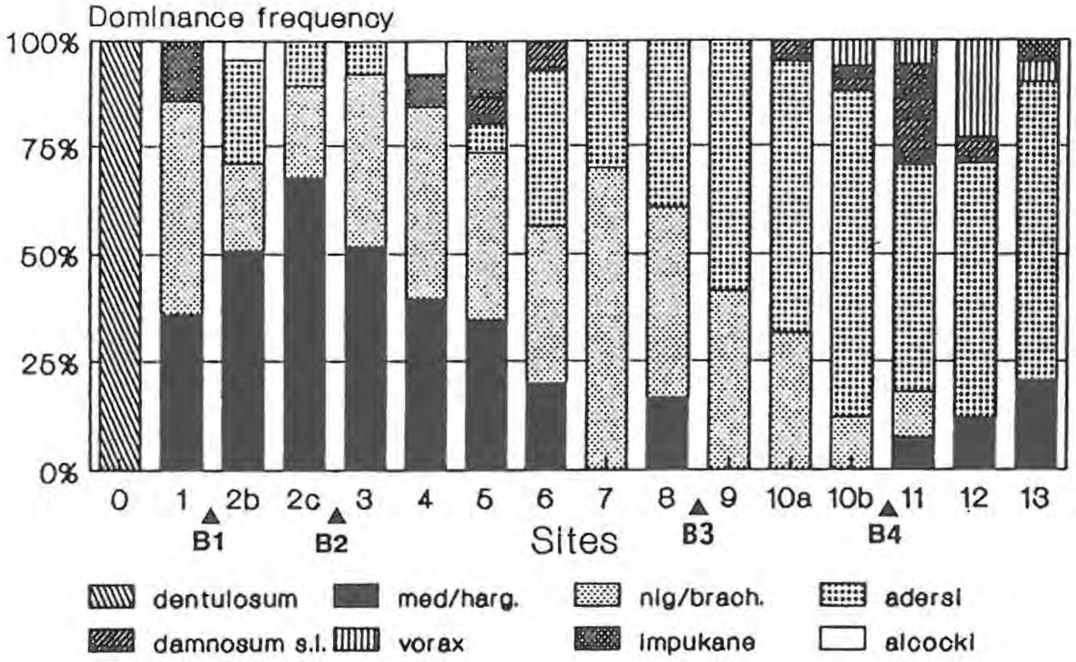


Fig. 7.4 Dominance frequency (expressed as a percentage) of blackfly taxa at 16 sites in the Buffalo River. Data are based on the numerical dominance of larvae in three Box samples. The positions of impoundments (**B1** to **B4**) are indicated.

Three-way analysis of variance of log(n+1) transformed blackfly population densities showed that there were significant seasonal and spatial differences (Table 7.3). Highest population densities were found at Site 10b (median=6 780 m^{-2}; max=146 300 m^{-2}), Site 13 (median=5 600 m^{-2}; max=46 800 m^{-2}) and Site 8 (median=5 328 m^{-2}; max=79 700 m^{-2}; Fig. 7.5). Lowest population densities were found at Site 0 (median=110 m^{-2}; max= 22 150m^{-2}), Site 9 (median=162 m^{-2}; max=33 150 m^{-2}) and Site 2c (median=209 m^{-2}; max=49 400 m^{-2}; Fig. 7.5). Highest population densities occurred in spring and summer (September to February). The spring fauna was generally dominated by *S. nigritarse*/*brachium*, whereas the summer fauna was generally dominated by *S. adersi* (Fig. 7.6). *Simulium medusaeforme*/*hargreavesi* and *S. damnosum* s.l. were present throughout the year (Fig. 7.6).

Table 7.3 Analysis of variance on log(n+1) transformed blackfly larval population densities (per m^2) versus time (Visit), distance (Site) and replicate (Box). NS=Not significant. *** = P<0.001.

	d.f.	Sum of Squares	Mean Square	F Ratio	Significance
Visit	18	254.4	14.1	11.4	***
Site	15	235.6	15.7	12.6	***
Box	2	1.1	0.6	0.5	NS
Total	746	1372.2			

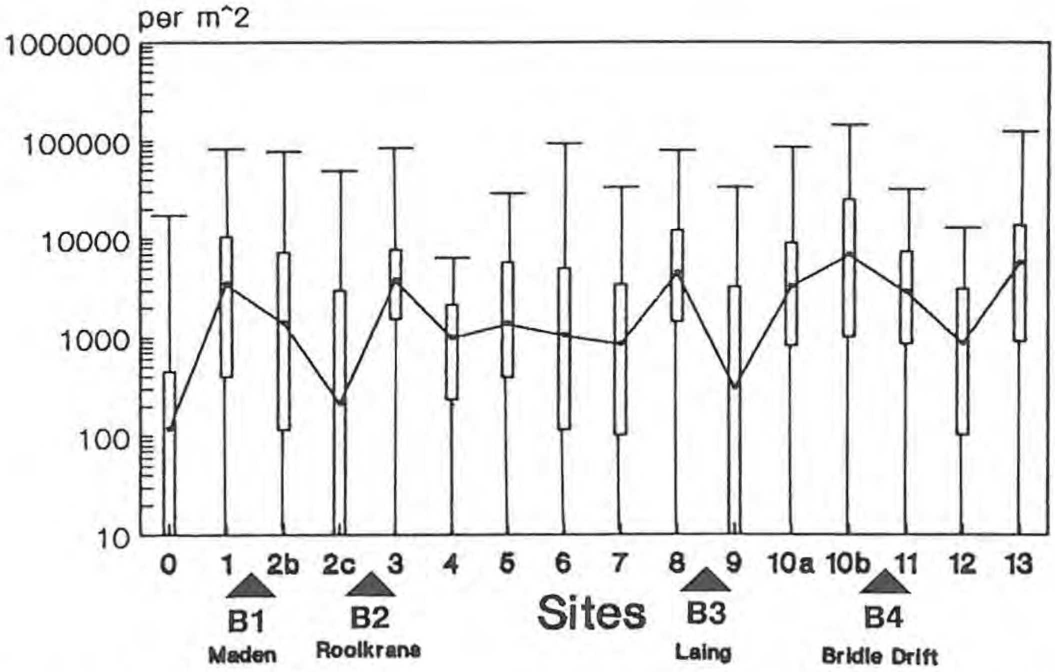


Fig. 7.5 Median population densities (per m^2) of larval blackflies in riffles at 16 Sites in the Buffalo River. Top and bottom of each box indicate the 75th and 25th percentiles, and the vertical lines indicate maxima. Positions of the impoundments (**B1** to **B4**) are indicated.

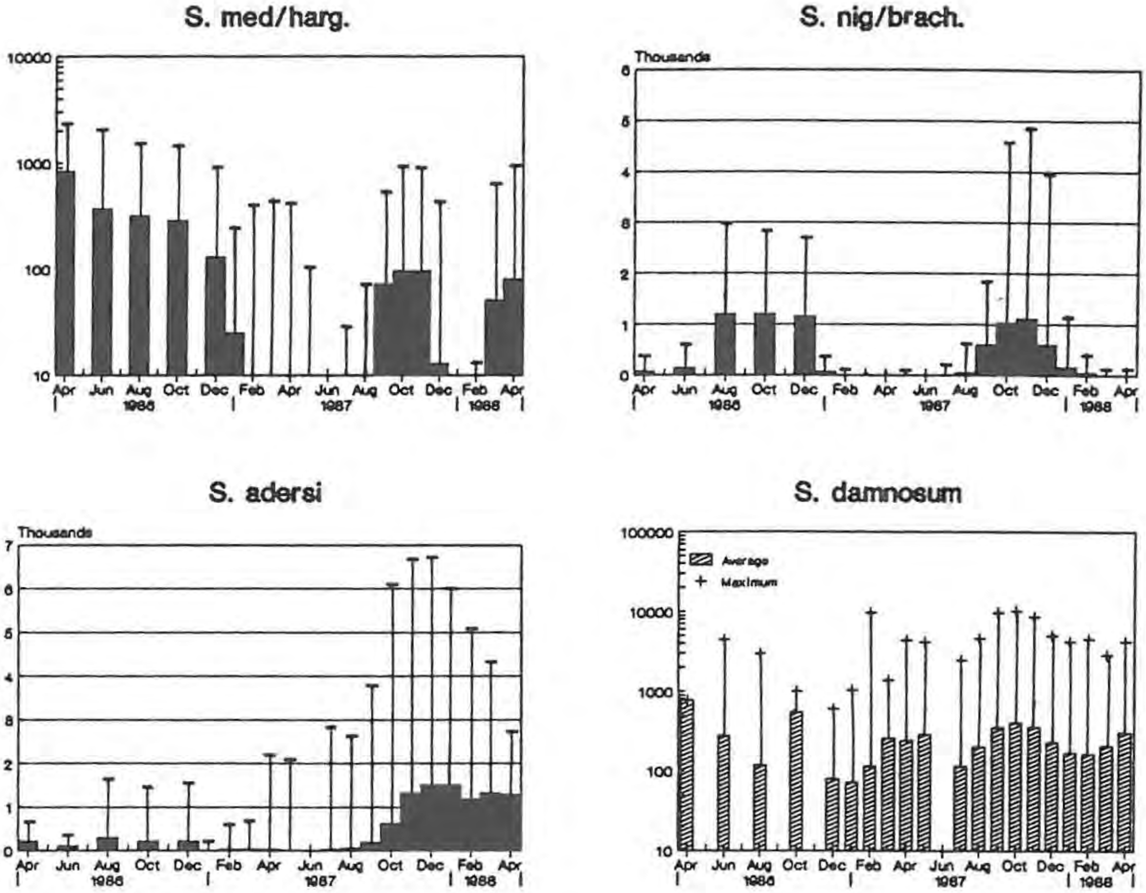


Fig. 7.6 Seasonality of four common blackfly taxa in the Buffalo River. Data are based on a 3-point running mean of the median frequency of occurrence at all sites per month, except for the results of *S. damnosum* s.l., which are presented as 3-point running means and maxima because of the few numbers involved.

Four blackfly taxa were common in impoundment tailwaters in the Buffalo River, and 3 taxa were negatively effected by impoundment (Table 7.2). Site 1 (upstream of Maden (B1)) was characterised by high numbers of blackfly taxa (with a total of 15; Table 7.2), most often dominated by *S. nigritarse/brachium*, and to a lesser extent, *S. medusaeforme/hargreavesi* (Fig. 7.7). *Simulium impukane* were present at Site 1 for a large proportion of the time (71% of the samples; Table 7.2), although numbers were seldom high (Fig. 7.7). In March 1987, *S. letabum* were found at high population densities at Site 1 for the first time, and were not found again until the following April (Fig. 7.7). The blackfly fauna downstream of Maden (B1) was usually dominated by *S. medusaeforme/hargreavesi* (Fig. 7.4), although *S. adersi* and *S. nigritarse/brachium* were numerous at times (Fig. 7.7). There were no blackflies downstream of Maden (B1) during low-flow (Fig. 7.7).

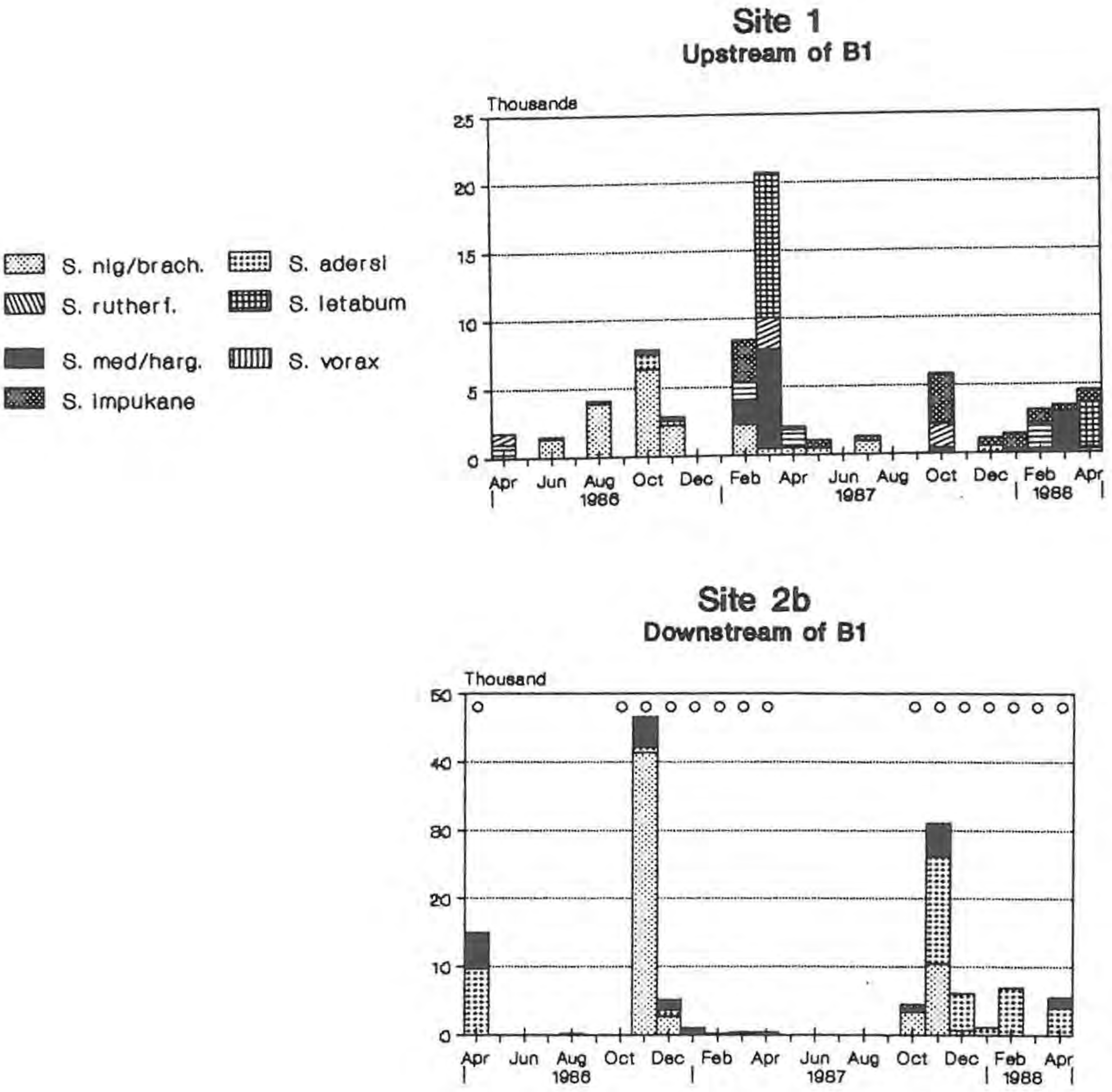


Fig. 7.7 Population densities (per m^2) of blackfly taxa upstream and downstream of Maden (B1) in the Buffalo River between April 1986 and April 1988. Circles indicate times when Maden (B1) was overflowing. Each histogram represents the mean number (per m^2) in three Box samples. Note that the y-axis scales are different.

Site 2c was most often dominated by *S. medusaeforme/hargreavesi* (Fig. 7.4). These flies were also very common downstream of Rooikrans (B2) (Fig. 7.8), and were common in the canals leading to and from the trout hatchery near Rooikrans (B2). The blackfly fauna at Sites 4 and 5 differed from the rest of the river by having a high proportion of species that were rare in the rest of the river (particularly *S. bequaerti* and *S. rotundum* and *S. impukane*) (Table 7.2).

The blackfly fauna downstream of Laing (B3) (Site 9) usually consisted of a single taxon (either *S. adersi*, *S. nigritarse/brachium* or *S. medusaeforme/hargreavesi*), but there were no consistent seasonal trends (Fig. 7.9).

The blackfly fauna at Site 10a (upstream of Bridle Drift (B4)) was almost always dominated by *S. adersi*, and shows a similar abundance pattern to Site 8 (Figs. 7.9 & 7.10). *Simulium damnosum* s.l. were the most common blackflies downstream of Bridle Drift (B4), particularly during low-level releases, although other species (particularly *S. adersi*) were also present (Fig. 7.10).

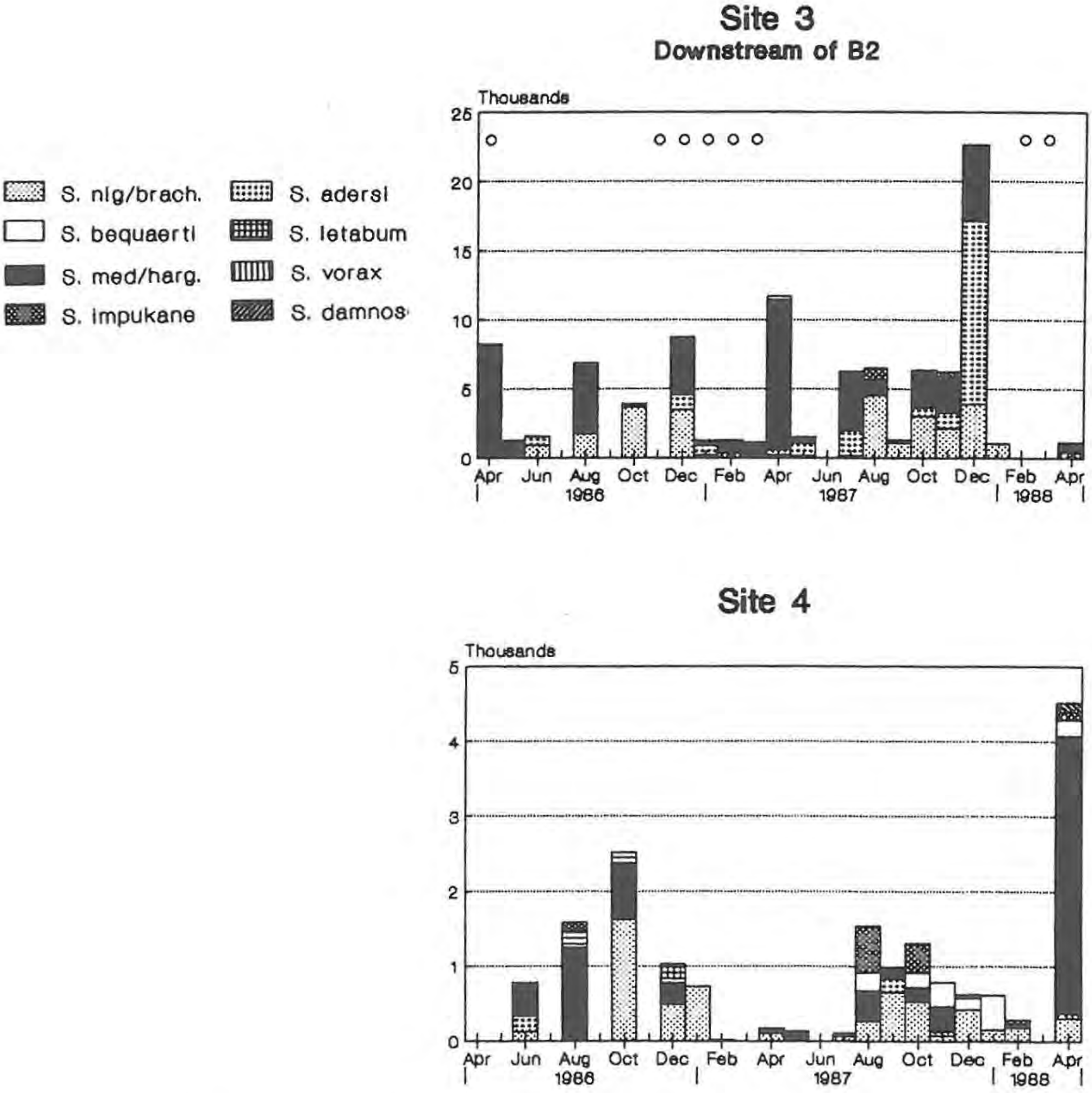
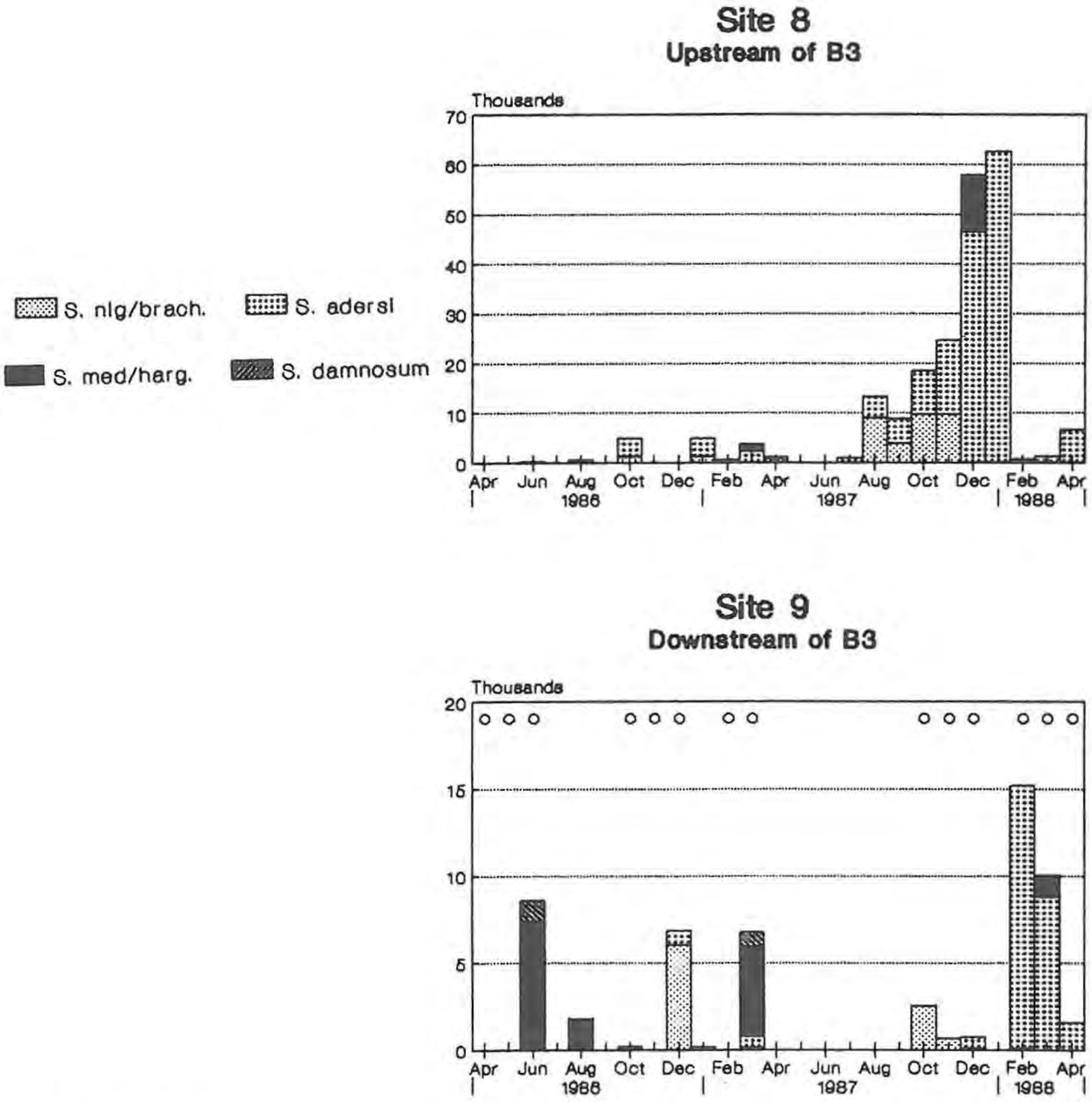


Fig. 7.8 Population densities (per m^2) of blackfly taxa downstream of Rooikrans (B2) in the Buffalo River between April 1986 and April 1988. Circles indicate times when Rooikrans (B2) was overflowing. Each histogram represents the mean number (per m^2) in three Box samples. Note that the y-axis scales are different.


Site 8
Upstream of B3

Site 9
Downstream of B3

Fig. 7.9 Population densities (per m^2) of blackfly taxa upstream and downstream of Laing (B3) in the Buffalo River between April 1986 and April 1988. Circles indicate times when Laing (B3) was overflowing. Each histogram represents the mean number (per m^2) in three Box samples. Note that the y-axis scales are different.

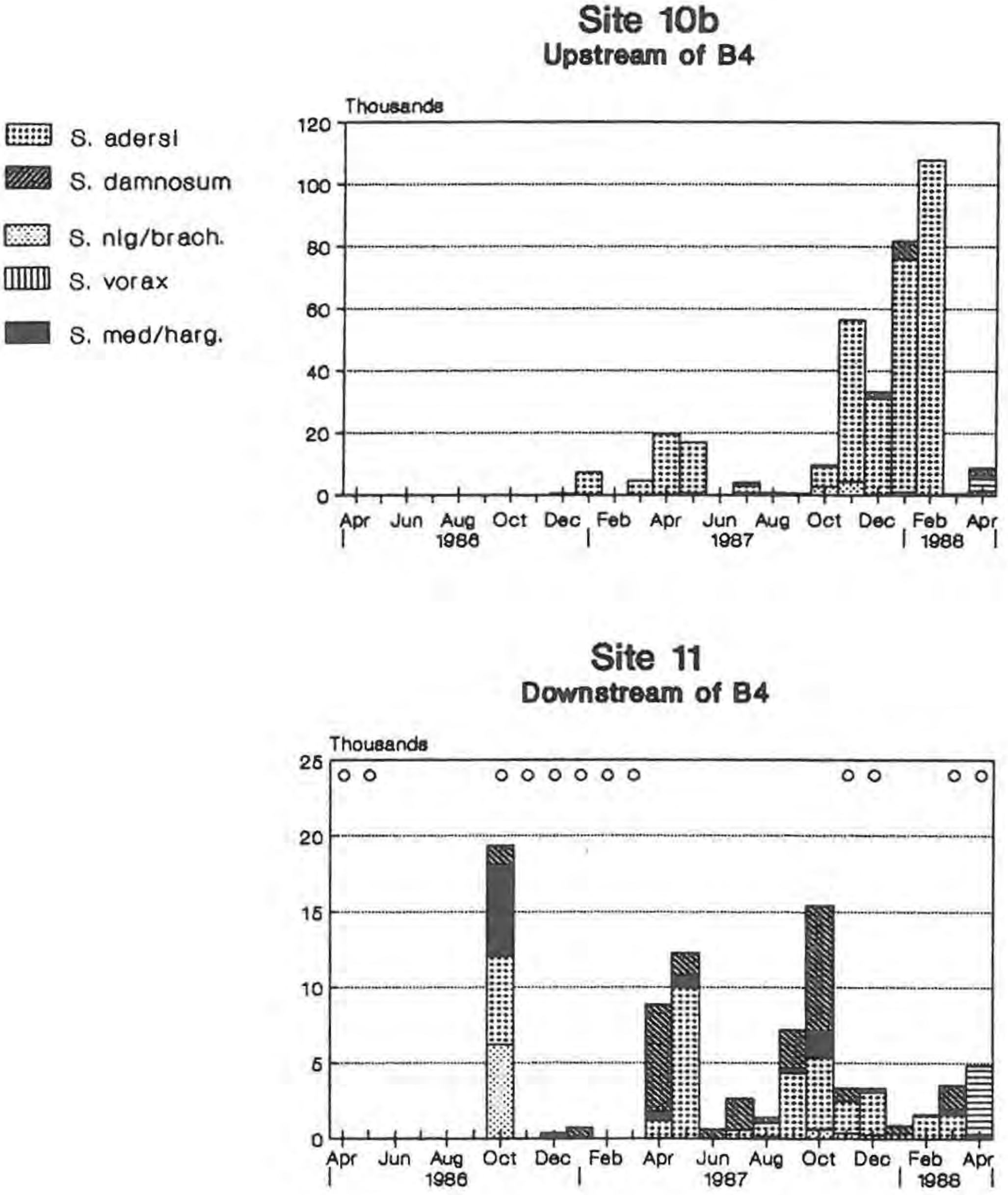


Fig. 7.10 Population densities (per m^2) of blackfly taxa upstream and downstream of Bridle Drift (B4) in the Buffalo River between April 1986 and April 1988. Sampling at Site 10b began in December 1986. Circles indicate times when Bridle Drift (B4) was overflowing. Each histogram represents the mean number (per m^2) in three Box samples. Note that the y-axis scales are different.

There were no significant differences in the total population densities of blackfly larvae upstream and downstream of impoundments Maden (B1), Laing (B3) and Bridle Drift (B4) when they were overflowing (Mann-Whitney *U*-test, $P>0.05$; Fig. 7.11). Population densities downstream of Rooikrans (B2) during overflow were significantly higher compared to upstream (Mann-Whitney *U*-test, $P<0.001$; Fig. 7.11), but this was attributable to low gradient and unsuitable flow conditions for blackfly larvae at the upstream site (Site 2c), rather than high population at the downstream site. At times, for example, the impounded waters of Rooikrans (B2) backed up and flooded most of Site 2c. During low-flow, blackfly population densities were significantly lower downstream of all impoundments except Rooikrans (B2), where numbers were significantly higher ($P<0.001$) because of compensatory releases through the trout hatchery and the absence of compensatory releases from Maden (B1). Surface-released water from Bridle Drift (B4) had lower blackfly population densities compared to bottom-released water (Fig. 7.11).

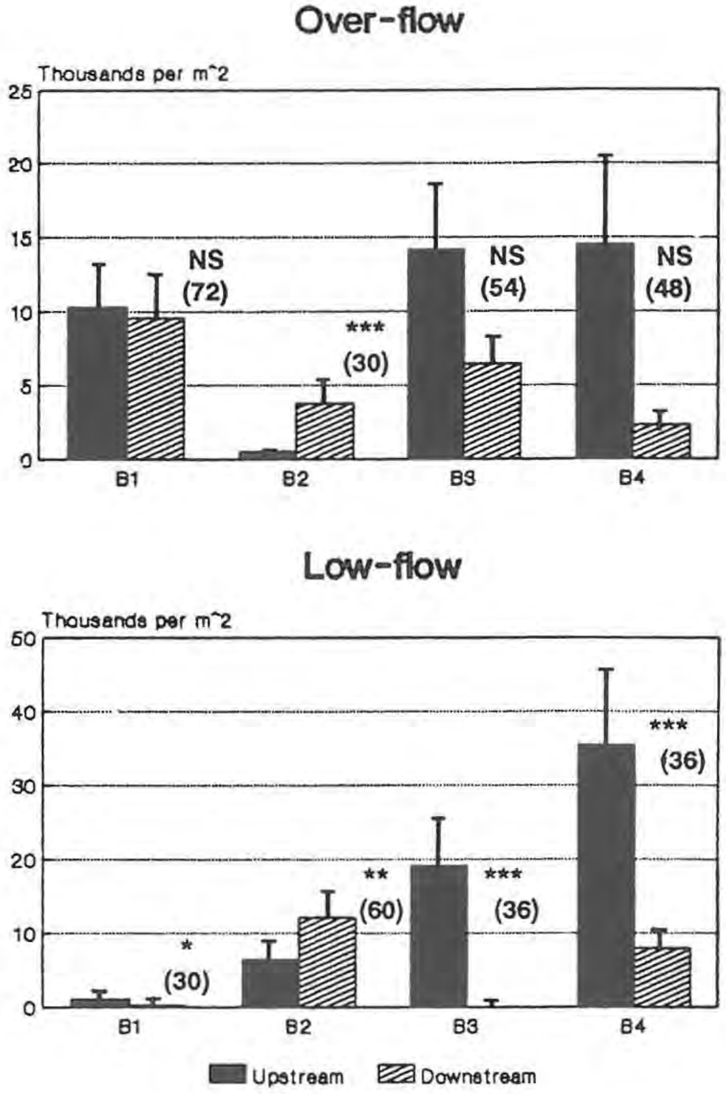


Fig. 7.11 Mean population densities of blackfly larvae upstream and downstream of the four mainstream impoundments (**B1** to **B4**) in the Buffalo River when impoundments where overflowing, and during 'low flow', when they were not overflowing. Vertical lines indicate one standard error. Mann-Whitney *U*-test. NS=Not Significant, $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$. Number of samples are indicated in brackets.

There was a very clear spatial zonation of blackfly taxa along a current speed gradient. *Simulium adersi* were usually found in waters where the current speed was less than 0.5 ms^{-1} (maximum 0.9 ms^{-1}: Fig. 7.12). *Simulium damnosum* s.l. were found in faster-flowing water, where current speeds were up to 1.3 ms^{-1}, whereas *S. chutteri* (data from the Great Fish River) were found in current speeds of up to 2.3 ms^{-1} (Fig. 7.12).

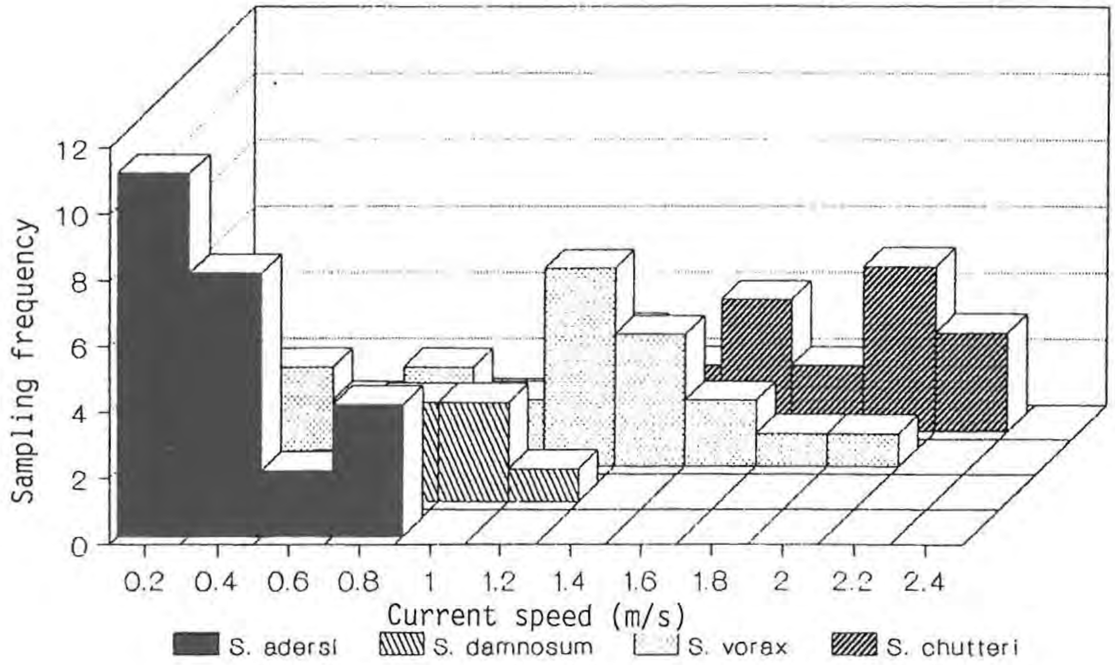


Fig. 7.12 Current speed preferences of four blackfly taxa. Sampling frequency represents the number of times a particular taxa was found at a particular current speed.

The polluted Sites 8 & 13 did not show a characteristic blackfly fauna, although they often had high population densities of *S. adersi* (Figs. 7.4 & 7.9). Most blackflies in the Buffalo River were found under a wide range of pH's (6 to 8), with the exceptions of *S. rutherfoordi*, which were found in acidic to neutral water (pH 5.5 to 7.5; Fig. 7.13a), and *S. damnosum* s.l., which were consistently found in neutral to alkaline water (pH 6.5 to 8.9; Fig. 7.13b).

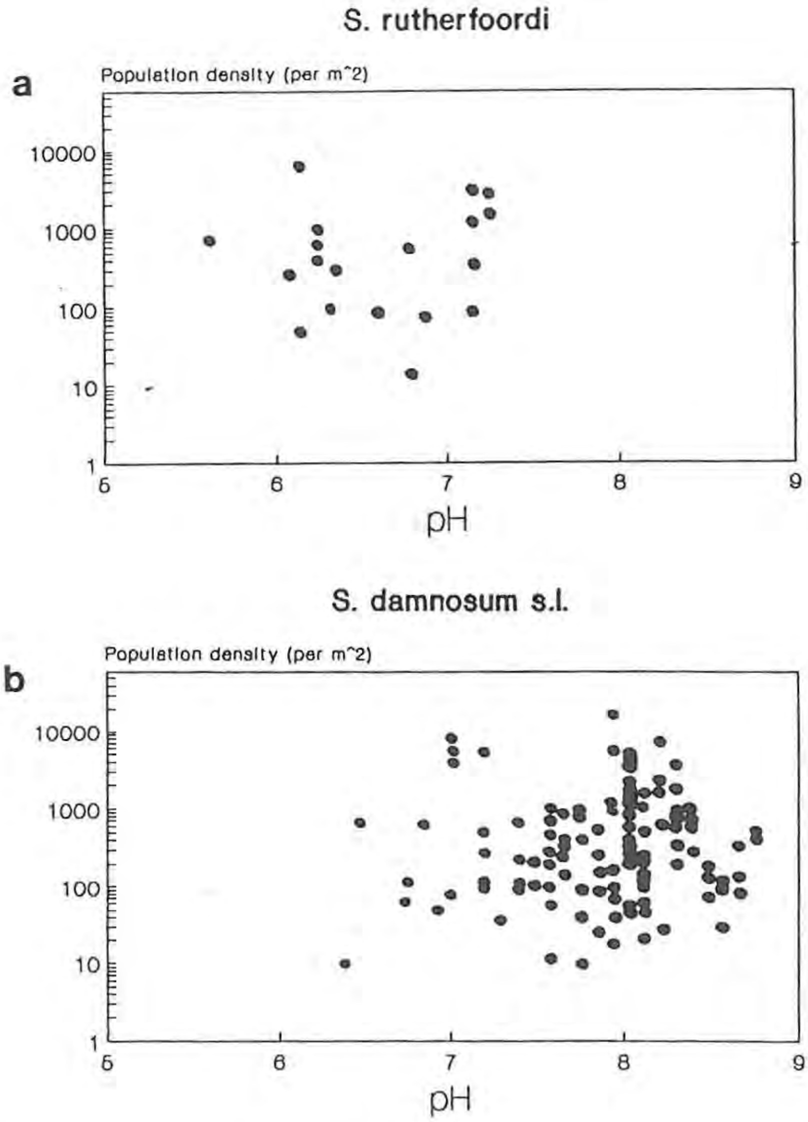


Fig. 7.13 Population densities of (**a**) *S. rutherfoordi* and (**b**) *S. damnosum* s.l. per box sample colleced in the Buffalo River, expressed as a function of pH.

The majority of blackfly taxa in the Buffalo River where found in water with a low concentration of suspended material (<50 mg/l; Fig. 7.14a). When the concentration of suspended material exceeded 50 mg/l, no more than four blackfly taxa were present (Fig. 7.14b).

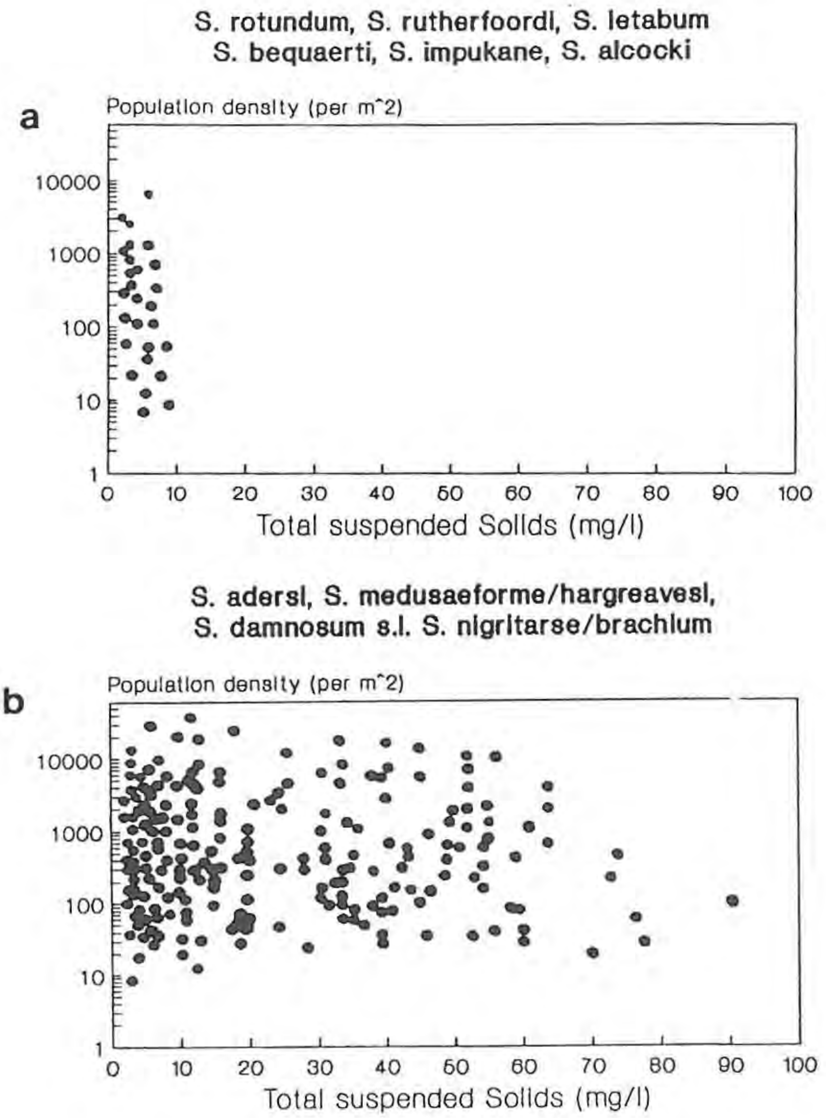


Fig. 7.14 Population densities of blackfly taxa per box sample collected in the Buffalo River, expressed as a function of Total Suspended Solids: (**a**) *S. impukane*, *S. rutherfoordi*, *S. vorax*, *S. letabum*, *S. dentulosum*, *S. alcocki*, *S. rotundum* and *S. bequaerti*, (**b**) *S. adersi*, *S. damnosum*, *S. medusaeforme/hargreavesi* and *S. nigritarse/brachium*.

Blackflies were one of the first invertebrates to colonise impoundment tailwaters when impoundments started overflowing. With time, the ratio of Simuliidae:Trichoptera decreased: it took between 60 to 150 days for Trichoptera to colonise impoundment outlets (Fig. 7.15). Trichoptera were poorly represented downstream of Bridle Drift (B4) during bottom-release, whereas during surface-release, they were well represented (Fig. 7.15).

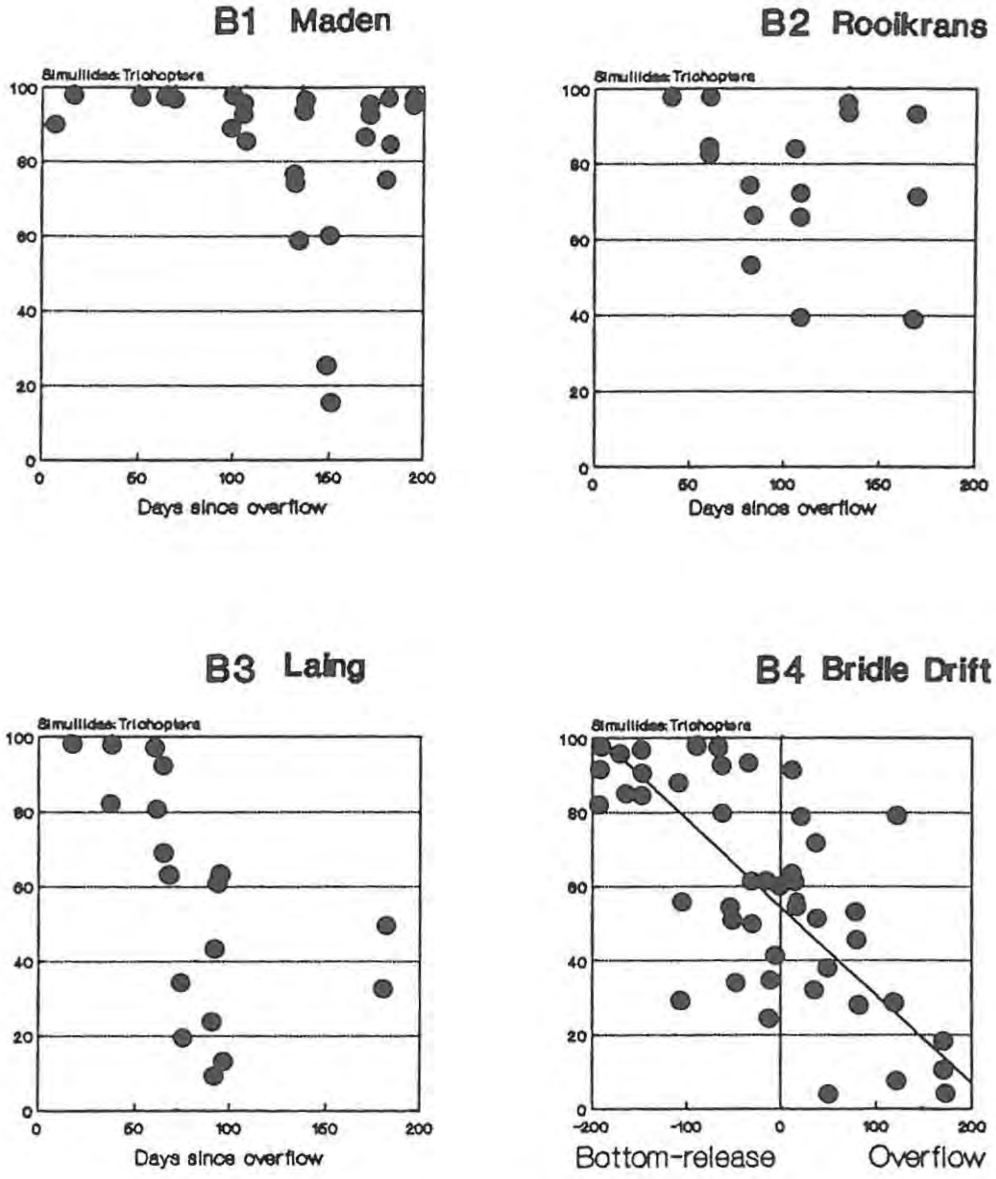


Fig. 7.15 The ratio of population densities of Simuliidae:Trichoptera per box sample, as a function of days since overflow of the four impoundments in the Buffalo River (B1 to B4).

The arrows in Fig. 7.16 demarcate the conditions under which blackfly larvae may have a significant effect on material transport in the Buffalo River. This occurred when the ratio of discharge (ls^{-1}) to stream width (m) was less than 30:1, when the population density exceeded 1000 m^{-2}, and when the concentration of suspended material was less than 100 mg^{l-1} (Fig. 7.16). All three of these conditions were met in 23% of the Box samples (n=835). The concentration of suspended material in the Buffalo River was less than 100 mgl^{-1} on 88% of the sampling occasions, whereas the ratio of discharge:stream was below the threshold value of 30:1 for 70% of the time, and population densities exceeded 100 m^{-2} in 56% of the samples.

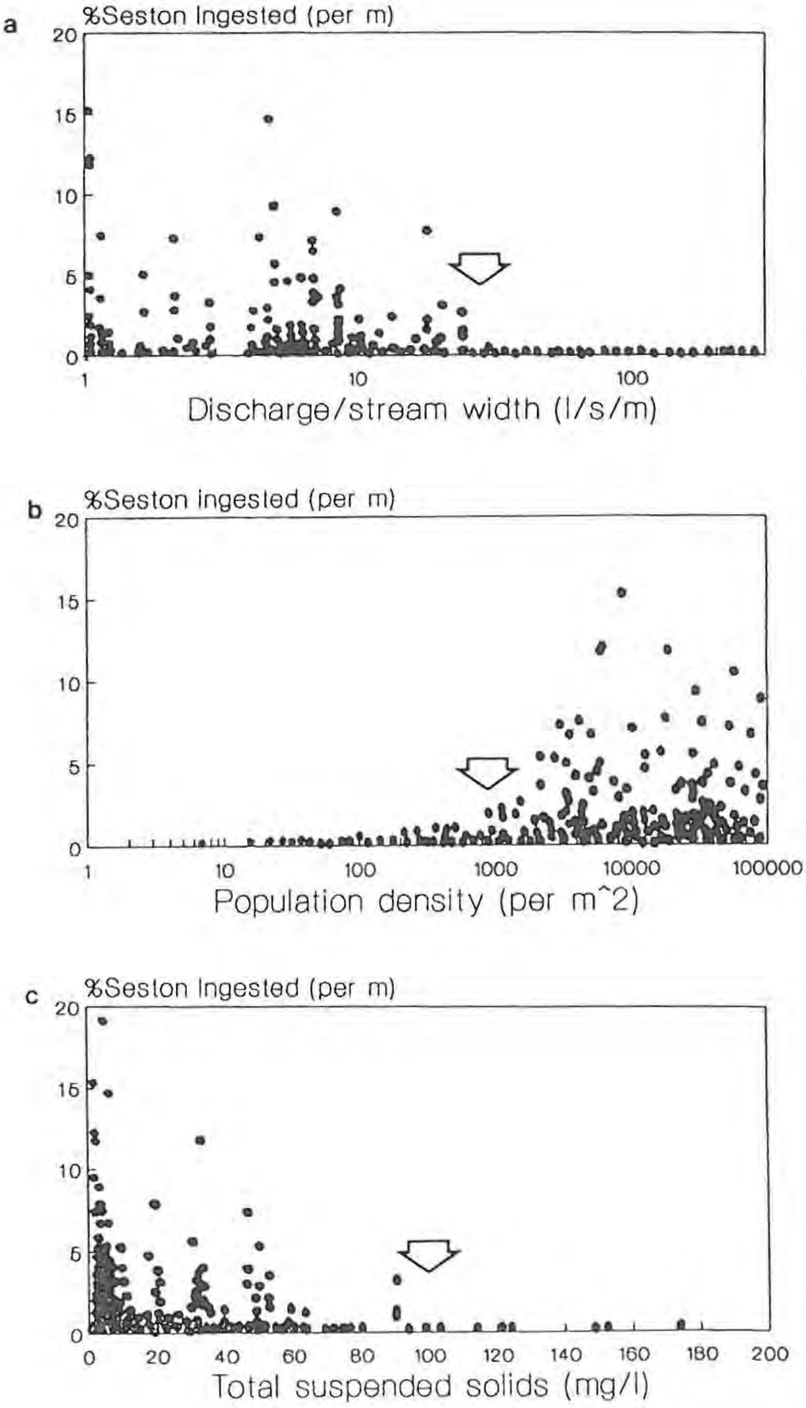


Fig. 7.16 Estimated percentage seston ingested by blackfly larvae at 16 sites in the Buffalo River as a function of (**a**) stream discharge/stream width, (**b**) log(x+1) population density (per m^2), and (**c**) Total Suspended Solids (mg/l). Arrows indicate thresholds above or below which blackfly larvae are likely to be important in material processing.

7.4 DISCUSSION

Most ecological studies on river invertebrates in southern Africa have concluded that silt, turbidity, water temperature and flow play an important part in the seasonal variation and distribution of riverine invertebrates (Harrison & Elsworth, 1958; Harrison, 1965a; Oliff & King, 1964; Chutter, 1969; de Moor, 1982a). However, causative relationships between faunal distribution and environmental variables are likely to be complex, and not fully explained within a single framework. For example, a temperature of 20°C in autumn is not comparable to the same temperature in spring because of differences in life-history stages. Furthermore, given the same set of environmental conditions, a number of responses may occur because of chance events (Steward-Oaten et al., 1986). For example, floods may transport larvae to places in the river where they do not usually occur, or strong winds may transport gravid females to areas they are not usually found. In addition, different environmental variables come into play at different spatial and temporal scales (Reiners, 1986; Minshall, 1988). For example, hydrodynamics may be important in influencing larval distribution on a micro-scale, but may be unimportant when applied to their distribution within a catchment, or region. Similarly, predation by hydropscychid Trichoptera may only become important once a river has been flowing for some time (Hemphill & Cooper, 1983). A further problem inherent in relating environmental variables to faunal distributions and/or abundances is the *response time* of faunal populations to changes in environmental conditions: populations may take weeks or even months to respond to, or recover from, rapid environmental changes.

The Buffalo River is only 140 km long, yet supports no fewer than

20 blackfly species, five of which were common throughout most of the river. Blackflies in the Buffalo River constituted between 5 and 35% (median values) of the total number of riffle-dwelling invertebrates (Fig. 7.2). By comparison, the Orange/Vaal River system, which is the longest in southern Africa (2 300 km), also supports an estimated 20 blackfly species, only one of which (*S. chutteri*) is common. Blackflies in the Orange and Vaal Rivers constitute over 80% of the riffle-dwelling fauna (Chutter, 1968; de Moor, 1982a; pers. obs.).

Although population densities of blackfly larvae downstream of impoundments were high at times, there was no evidence to suggest that densities in impoundment outlets were higher than in other parts of the river (Fig. 7.11). Likewise, the abundance of blackflies relative to other riffle-dwelling macroinvertebrates was not altered by impoundments (Fig. 7.2). The absence of a filter-feeding guild below impoundments in the Buffalo River is puzzling, and could not be attributed to high levels of suspended organic material throughout the river, because impoundments in the Buffalo River were generating nodes of organic material (Chap. 5). A more likely explanation for the general absence of a filter-feeding guild below impoundments in the Buffalo River centres on the management of impoundments: Like many impoundments in arid regions, impoundments in the Buffalo River are used for water storage, and compensatory releases were minimal (see Table 2.1 & Fig. 2.6).

Ironically, highest blackfly population densities were at sites least affected by impoundment management (Sites 8, 10b & 13). However, impoundments in the Buffalo River did alter blackfly species composition, favouring five taxa (*S. meduseaforme*, *S. hargreavesi*, *S. nigritarse*/*brachium*, *S. adersi* and *S. damnosum* s.l.) at the expense of others (*S. rutherfoordi*, *S. letabum* and *S. impukane*). These five taxa were common throughout the regulated section of the Buffalo River (downstream of Maden (B1)), and were found under a wide range of water conditions (e.g., Fig. 7.14b). Taxa which were uncommon, (including several members of the Subgenus *Pomeroyellum*), were restricted to clear water conditions in the upper reaches of the river (Fig. 7.14a). Although 'riverine' species (particularly members of the Subgenus *Pomeroyellum*) appeared at Sites 4 and 5 (2.6 and 6.4 km downstream of Rooikrans (B2) respectively), there was no obvious replacement of outlet species by riverine species downstream of other impoundments.

Most species of blackflies in the Buffalo River were found where current speeds were less than 1 ms^{-1}, and a few specialized taxa were found in faster-flowing water. The zonation of blackfly taxa along a current speed gradient has important implications for sampling blackfly larvae, particularly in large and inaccessable rivers, where samples taken from the edge may give biased estimates of species occurrence and abundance. This was not the case in the Buffalo River, where all the riffles were accessible.

The importance of temperature to blackfly abundance is illustrated by the occurrence of a spring/summer peak in abundance (Fig. 7.6), although this was dependent on their being sufficient flow in the river (Figs. 7.7-7.10). One of the conclusions of Chapter 3 was that seasonal temperature changes in the Buffalo River were greater than longitidinal temperature changes down the river (Fig. 3.2). However, the distribution of upper-reach [cold-water] species did not extend further downstream during winter months, which suggests that winter temperature is not important to the *distribution* of blackflies, possibly because adults are not active at this time of the year. Summer temperatures, on the other hand, correspond well with the distribution of upper-reach species, and may be an important factor limiting blackfly distribution.

Water chemistry did not have an immediately obvious effect on blackflies in the Buffalo River: Polluted sites (Sites 8 & 13) did not exhibit a characteristic blackfly fauna, although densities of blackfly larvae at polluted sites were often high. This indicates that blackfly larvae are not good water quality indicators, and are able to tolerate moderately eutrophic conditions.

The threshold concentration of suspended material below which blackfly larvae may become important in material processing in the Buffalo River (100 mg l^{-1}) is comparable to other studies which have shown that ingestion rate does not increase at seston concentrations exceeding 100 mg l^{-1} (Hart & Latta, 1986) and 50 mg l^{-1} (Gaugler & Molly, 1980).

A limitation of this study was that impoundment-induced changes in species composition are likely to have been underestimated because of the inability to distinguish the larvae of some of the most common and widespread blackfly taxa to species level. For example, the disjunction in distribution of *S. nigritarse/brachium* between Site 1 and Sites 3 to 10a (Fig. 7.4), may indicate ecological preferences of the two species. Examination of pupae indicated that *S. brachium* were more common upstream of Maden (B1)(Site 1), whereas *S. nigritarse* were more common further downstream (Sites 3 to 10a). The inability to distinguish these species as larvae, and the occurence of species complexes (*S. damnosum* and almost certainly *S. adersi*) may have masked some important changes which were overlooked in the present study.

A further limitation of this study was that species may have been overlooked by not sampling between Sites 0 and 1. This is where the river is its steepest and most pristine, but was inaccessible for regular sampling. Furthermore, this study was conducted over three years of 'average' flow conditions: there were no droughts and no floods. Three years does not adequately cover the 20 year rainfall oscillations for southern Africa described by Tyson (1978). Seasonal changes in blackfly occurrence were not consistent between years (Fig. 7.6), emphasising that long-term series are required for adequate monitoring of the factors influencing blackfly distribution.

8 DISTRIBUTION AND ECOLOGY OF BLACKFLIES IN SOUTHERN AFRICA

8.1 INTRODUCTION

The previous chapter (Chap. 7) investigated the effects of impoundments on the distribution and abundance of blackflies in the Buffalo River, and concluded that impoundments did not alter overall population densities of blackfly larvae, but did alter blackfly species composition, favouring five taxa (*S. meduseaforme*, *S. hargreavesi*, *S. nigritarse*, *S. adersi* and *S. damnosum* s.l.) at the expense of others (*S. rutherfoordi*, *S. letabum* and *S. impukane*). Comparative studies of stream invertebrates have shown that regional differences, such as water quality, catchment land-use and latitude, may be more important to invertebrate distribution than longitudinal changes within a single catchment (Minshall et al., 1983; Wright et al., 1984; Marchant et al., 1985; Corkum & Currie, 1987; Ormerod & Edwards, 1987). This raises the question as to whether the observations within a single catchment (in this case the Buffalo River) are consistent with regional trends. Factors which are likely to be important in the distribution of blackfly larvae include physical features of the river (e.g., gradient, flow, turbidity and temperature), chemical characteristics of the river (whether pristine or polluted), and biological interactions (such as predation, competition and parasitism). The relative importance of these factors is poorly understood (Ross & Merritt, 1987). Some studies have shown that blackfly larval distribution is closely related to longitudinal changes, such as distance from source and stream size (Brönmark et al., 1984; Corkum & Currie, 1987; Adler, 1987) whereas other studies have found blackfly distribution patterns to be associated with chemical (Grunewald, 1981) and substrate characteristics (Ormerod & Edwards, 1987). Changes in the quality and availability of freshwater in Africa as a result of the growing human population have changed blackfly species composition; For example, industrial and urban pollution on the outskirts of Kinshasa, Zaire, have prevented the colonisation of *Simulium damnosum* s.l. in streams that were previously active foci of onchocerciasis (or 'river blindness'), a disease transmitted mainly by members of the *S. damnosum* complex (Henry et al., 1984). Similarly, deforestation has led to changes in the distribution of members of the *S. damnosum* complex in West Africa (Garms, 1973; Garms & Vajime, 1975), and that of *S. neavei* in Kenya (Buckley, 1951). Crosskey and Ashford (1981) suggest that blackflies are likely to disappear from Libya as the rivers there are drained due to increased urbanisation. Similarly, there is a likelihood of extinction of *Prosimulium* species in the south-western Cape as a result of habitat destruction (de Moor, pers. comm.).

This chapter examines whether the effects of impoundments on blackflies in the Buffalo River are typical of impoundments elsewhere in southern Africa, and identifies life-history characteristics and environmental requirements of impoundment-outlet taxa. Distribution records for each species are presented, and the ecology of each species is summarised.

8.2 METHODS

Distribution records were based on (1) material collected by the author throughout southern Africa during 1987-1990, (2) material collected by Ms B. A. Curtis and S. Bethune in Namibia, (**3**) collections housed in Albany Museum, Grahamstown and (**4**) the South African Institute for Medical Research, Johannesburg, (**5**) records from the Veterinary Research Institute, Pretoria, and (**6**) published records.

Presumed female host preferences were based on the shape of tarsal claws: females feeding on birds have claws with a large basal tooth, whereas those feeding on mammals have simple claws (Crosskey, 1973: 126; Sasaki, 1988). Exceptions include *S. evillense* and *S. gariepense*, both of which have claws with a large basal tooth, indicating ornithophily, although they are recorded as feeding on mammals.

8.3 DESCRIPTIONS OF REGIONAL STREAM-TYPES AND SPECIES ECOLOGY

The majority of blackflies in southern Africa are found in the southern and western region, where rainfall exceeds 500 mm per annum (Fig. 8.2). Within this region, 9 taxa are widespread (and do not show specific biogeographical affinities), 21 taxa have restricted distributions (detailed below), and a further 5 taxa are rare. With the exception of *S. ruficorne*, blackflies are largely absent from the dry central Karroo, Kalahari and Namib deserts. Based on habitat preferences of blackfly immatures, as well as other biogeographical studies of stream invertebrates (Harrison & Agnew 1962; Harrison, 1965b; Harrison & Hynes, 1988), southern Africa may be divided into five blackfly 'stream-types'.

1. Cool, acid streams of the south-western and southern Cape. These drain Table Mountain Sandstone, stretching between Cape Town in the west and Port Elizabeth in the east. Two species (*S. merops*

& *S. hessei*) are endemic to these streams. A third species (*S. harrisoni*) has a more restricted distribution, and is only found in the south-western Cape [apart from a single record in Zambia (Freeman & de Meillon, 1953: 86)].

2. Mountain streams, usually draining Afro-montane forest regions (Drakensburg Mountains). Six species are restricted to these fast-flowing torrents (*S. dentulosum*, *S. natalense*, *S. letabum* and members of the Subgenus *Freemanellum*: *S. debegene*, *S. empopomae* & *S. hirsutilateris*).

3. Warm, alkaline (and often turbid) streams and rivers (Swaziland, Natal lowlands, Transvaal lowveld and eastern Cape). Typified by 5 taxa, (*S. bequaerti*, *S. cervicornutum*, *S. damnosum* s.l., *S. hargraevesi*, *S. rotundum*), all of which are widespread in tropical Africa.

4. Large rivers, often carrying high concentrations of suspended sediments (e.g., the Orange, Great Fish, Vaal and Limpopo Rivers). Five taxa are restricted to such rivers (*S. bovis*, *S. chutteri*, *S. gariepense*, *S. griseicolle* and *S. mcmahoni*).

5. Temporary streams, trickles and springs, covering most of the central and eastern part of southern Africa (Karroo, Kalahari desert and the Namib desert). Often highly mineralised, and temperature ranges are extreme. A single taxon, *S. ruficorne* is commonly found in these conditions.

Widespread taxa

S. (Meilloniellum) adersi Pomeroy, 1922

Fig. 8.8

One of the most common blackflies in southern Africa, although larvae are easily confused with those of S. hirsutum, and their occurrence may be overestimated. Absent from the Orange River, and scarce in the south-western Cape. Common in the polluted streams of the Transvaal highveld, but also found in pristine streams. Tolerates high levels of ammonium (Grunewald, 1981). Often dominant in the lower (turbid) reaches of rivers in the eastern Cape (Great Kei, Buffalo, Keiskamma & Great Fish Rivers).

A typical impoundment-outlet taxon (Fig. 8.8; Table 8.1). In the Vaal River, they were dominant downstream of the Vaal-Hartz Weir, particularly in winter (de Moor, 1982a; 1986). In the Buffalo River they were common throughout the year in the mid- and lower reaches, particularly below impoundments. They have been found in rivers as large as the Blue Nile (Lewis, 1953), in the splash zone at the edge of Lake Victoria (Gibbins, 1938), and in channels in sugar-cane fields (Johnson et al., 1982). Larvae prefer slow-flowing (0.7 ms^{-1}), perennial streams with small flow fluctuations (Elouard, 1987). Larvae attach onto rocks, trailing vegetation, dead leaves and other submerged vegetation, as well as sandy substrates (Crosskey, 1960a). Mean dry mass of mature (final instar) larvae from the Buffalo River was 0.233±0.009 mg SE (n=18).

Lamonteilerie (1963) found female S. adersi within a few hours after the White Volta began to flow, and suggested that they survive the dry season as adults. In the Buffalo River, eastern Cape, a cohort colonised the downstream reaches of Bridle Drift Dam within 20 days of the dam first overflowing, and after 35 days, larvae of all sizes were found. Females lay about 400 eggs in clusters onto partly submerged stones (de Moor, 1989) or emergent and trailing vegetation (pers. obs.). The eggs are 202 by 135 μm in size (de Moor, 1982a), and take up to 13 days to hatch at 25^{o}C (Begemann, 1980a). Larvae have 7 instars (Elouard, 1978), and pupate within

17 days at 20þ1°C (Begemann, 1980a). Adults form mating swarms near prominent markers such as trees (de Moor, 1989), and are attracted to hosts both visually (Begemann, 1980b) and by CO_2 (Fallis & Raybould, 1975). Females are ornithophilic (Crisp, 1956; Fallis & Raybould, 1975), but also feed on sheep, goats and humans (Gibbins, 1934). In South Africa they are the main human-biter along the Vaal River (Begemann, 1980a), but do not bite along the Buffalo River, eastern Cape. When feeding on humans, they tend to bite either around the the legs (in Tanzania: Raybould, 1967), or the head and ears (Lake Victoria: Gibbins, 1934). In West Africa they transmit diseases among poultry, and have been implicated as a possible vector of human onchocerciasis (Wegesa, 1970).

S. (Pomeroyellum) alcocki Pomeroy, 1922

Fig. 8.21

Fairly common in small, clear streams. Absent from the Orange and lower Vaal Rivers. Often found in temporary streams, and can tolerate moderate pollution. Larvae attach onto dead leaves and trailing vegetation where the current is slow (0.3-0.8 ms^{-1}: Grenier et al., 1960). In the Vaal River they were found throughout the year in eroding zones (Chutter, 1970). Females are ornithophilic, and pests of poultry in West Africa (Gibbins, 1938, 1941; Disney, 1972).

S. (Nevermannia) brachium Gibbins, 1936a

Fig. 8.18

Seldom recorded in southern Africa, although larvae are practically indistinguishable from, and pupae similar to, those of S. nigritarse. s.s, and their occurrence may be underestimated. The two species are sympatric in the Buffalo River, eastern Cape. Immature S. brachium are most often found in shaded mountain streams. Immatures attach onto rocks and trailing vegetation in cascades and small waterfalls where the current is fast (1.0-1.3 ms^{-1}: Fain & Elsen 1973). In the eastern Cape they were found on a small earth spillway, and downstream of a small cement dam near the Hogsback (Table 8.1). Females presumably ornithophilic. The taxonomy of the S. nigritarse complex (to which S. brachium belongs) has been reviewed by Fain and du Jardin

(1983).

S. (Pomeroyellum) impukane de Meillon, 1936

Fig. 8.25

Fairly common in small, temporary streams. Immatures attach onto small stones, trailing vegetation and dead leaves in slow or fast current. Roberts (1986) found that larvae preferred to attach onto dead leaves than to trailing vegetation or rocks. In the Great Berg River, immatures were present throughout the year (Harrison & Elsworth, 1958), and in the Vaal River, they were found in winter and early dry summer (Chutter, 1970). Population densities seldom high. Females were found laying eggs onto submerged stones in a small (and nearly dry) slow-flowing tributary of the Mkuze River in the Mkuze Game Reserve. They have been recorded in the tailwaters of Loskop Dam, Transvaal, but this is unusual (Fig. 8.25). Females ornithophilic, and in Tanzania they have been implicated in the spread of the sporozoan blood parasite, Leucocytozoon schoutedeni, among poultry (Fallis et al., 1973).

S. (Metomphalus) medusaeforme Pomeroy, 1920

Fig. 8.13

One of the most common blackfly in southern Africa. Widely distributed throughout the region, although largely absent from the Orange and lower Vaal Rivers. Immatures are found in cascades and small waterfalls, usually where the current is fast (0.8-1.5 ms^{-1}: Fain & Elsen, 1973). Very common in mountain foothill streams, although also present in rivers up to 6th order (Great Fish River). Larvae attach onto rocks, and to a lesser extend trailing vegetation, mud or algae. Found in pristine to moderately polluted water.

A typical impoundment-outlet taxon (Fig. 8.13; Table 8.1). Very common in the Buffalo River, eastern Cape, particularly downstream of impoundments. Near Swellendam, southern Cape, immatures were found in high numbers at a dam spillway on a thick carpet of moss. In the upper Vaal River they were found throughout the year on a carpet of moss in a number of habitats, including polluted water, marginal vegetation [in-current] and stones [in-current](Chutter, 1970).

In the Great Berg River they were the most common blackfly in the mid- and upper reaches throughout the year, and were absent from the lower reaches (Harrison & Elsworth, 1958). Females mammalophilic.

S. (Nevermannia) nigritarse Coquillett, 1902

Fig. 8.19

One of the most common blackflies in southern Africa, although larvae are practically indistinguishable from, and pupae similar to, those of S. brachium, and so their occurrence may be overestimated. The two species are sympatric in the Buffalo River, eastern Cape. Absent from the Orange River. Immatures are usually found in small streams where the flow is gentle. They prefer slow currents, and are most often found on the underside of rocks, or on trailing vegetation. They are often found in polluted water.

In the Great Berg River they were found in the mid-reaches, usually in spring and summer (Harrison & Elsworth, 1958). In the the Vaal River they were widely distributed, and common throughout the year (Chutter, 1970). They were the dominant blackfly in the Great Fish River, particularly during low flow, but were replaced by S. chutteri in the mid- and lower reaches after the introduction of Orange River water in 1976 (Coetzee, 1982; O'Keeffe & de Moor, 1988). In an artificial stream, larvae failed to feed under turbulent flow conditions (Reynolds number > 1,300), and this may explain their partial disappearance from the mid- and lower reaches of the Great Fish River since 1976 (Barber, 1985).

Simulium nigritarse s.s. is a typical impoundment-outlet species (Fig. 8.19), and is quick to colonize new habitats: In the Great Fish River larvae were found 24 days after resumption of flow (Chutter, 1972a). Females are anautogenous (Takaoka, 1988), and lay eggs onto submerged stones, or emergent and trailing vegetation (Chutter, 1972a & b; Begemann, 1980b). Ovaries contain about 800 follicles (Chutter, 1972b). Eggs take one week to hatch (Chutter, 1972a & b), or up to 13 days at 25°C (Begemann, 1980a). Eggs are not resistant to desiccation (de Moor, 1989). Larvae have 7 instars which take about 24 days to pupate (Chutter, 1972a & b), or at least 20 days at 20°C (Begemann, 1980a). Pupae hatch after 47 h (at 25°C) or 23.7 days (at 6°C) (Begemann, 1980a). Temperatures exceeding 30°C are lethal to immatures (Begemann, 1980a). The emergence of adults at Carlisle Bridge, in the Great Fish River, showed peaks every 2 to 3 weeks, ascribed to density-dependant cannabilism of early instars by larger larvae (Chutter, 1972a & b).

Females are ornithophilic: Steenkamp (1972) reports a 30-50% reduction in egg production from chickens caused by these flies near Parys, along the Vaal River. In southern Africa they have been implicated in the spread of the sporozoan blood parasite, Leucocytozoon smithi, among turkeys (Huchzermeyer & Sutherland, 1978). They are reported to bite humans in the south-western Cape (Freeman & de Meillon, 1953: 216), although this is unusual (Bequaert, 1938; de Meillon, 1955; Crisp, 1956). Fain & du Jardin (1983) revise the taxonomy of the S. nigritarse complex, and give keys to 19 species within the complex.

S. (Nevermannia) rutherfoordi de Meillon, 1937

Fig. 8.17

Fairly common in small, cool and shaded mountain streams. Absent from the Orange, Vaal, and Great Fish Rivers. Larvae attached onto dead leaves, trailing vegetation and rocks where the flow is gentle. Very common in the upper reaches of the Buffalo River, eastern Cape; Emergence occurred throughout the year, with particularly high numbers in September and October. Other Females not known to bite man or livestock (Meeser, 1942), presumably ornithophilic.

S. (Pomeroyellum) unicornutum Pomeroy, 1920

Fig. 8.28

Fairly common, although absent from the Orange, Great Fish and Vaal Rivers. Immatures are found in a variety of breeding places, from small trickles to large rivers, and in slow or fast currents (Gibbins, 1937a; 1941; Crosskey, 1960a). Immatures are also found in temporary streams, and survive moderately polluted conditions. Larvae attach onto dead leaves in preference to trailing vegetation or rocks (Roberts, 1986). In the Great Berg River they where found mainly in the mid-reaches during summer and autumn (Harrison & Elsworth, 1958). In the Tugela River they were restricted to the source zone, and were dominant during late summer (February; Oliff, 1960). In the Vaal River they were found during winter and early dry summer in eroding and stable depositing zones (Chutter, 1970). Eggs are laid onto a substrate (Obeng, 1967). Females ornithophilic (Disney, 1972).

S. (Metomphalus) vorax Pomeroy, 1922

Fig. 8.14

Fairly common in strongly flowing, clear or turbid rivers. Absent from the Orange and lower Vaal Rivers. Immatures attach onto rocks and trailing vegetation in rapids and waterfalls where the current is fast. Females feed on mammals, including humans and occasionally, and poultry. They have been implicated as possible vectors of human onchocerciasis (Wegesa, 1967), bovine onchocerciasis (Mwaiko, 1981), and and poultry diseases (Fallis et al., 1973).

1. Cool, acid streams

S. (Pomeroyellum) harrisoni Freeman & de Meillon, 1953

Fig. 8.24

Restricted to the mountains of the south-western Cape, and a single record from Zambia (Freeman & de Meillon, 1953: 86). In the Great Berg River they were abundant throughout the year in the mid- and upper zones in spring (Harrison & Elsworth, 1958), and in the Breede River they were abundant in the middle and lower reaches of the river (NEC, Stellenbosch, unpubl. data). Immatures found on trailing vegetation. Females presumably ornithophilic.

S. (Freemanellum) hessei Gibbins, 1941

Fig. 8.7

Rare. Restricted and endemic to the cool, clear-water mountain streams of the southern and south-western Cape. Immatures attach onto rocks in very shallow water (1-2 cm), where the current is very fast. In the Great Berg River they were found in the upper reaches during winter and summer (Harrison & Elsworth, 1958: 269). Females not known to bite people or livestock (Freeman & de Meillon, 1953), presumably ornithophilic.

S. (Pomeroyellum) merops de Meillon, 1950

Fig. 8.6

Fairly common, although restricted to the cool, acidic waters of the southern and south-western Cape. Records of S. merops from Zaire (Hallot et al., 1965), Tanzania (Häusermann, 1966), the Okavango Swamps (de Meillon, 1955), and Zambia (SAIMR) are likely to have been mistaken for S. evillense (Fain et al., 1966). Immatures are found in small, shaded streams attached onto dead leaves, trailing vegetation and rocks where the flow is gentle. Fairly common although numbers are seldom high. Females presumably ornithophilic.

2. Mountain streams

S. (Freemanellum) debegene de Meillon, 1934

Fig. 8.6

The most common member of the Subgenus Freemanellum in southern Africa. Fairly common in mountainous regions of the Transvaal, Natal, Transkei and the eastern Cape. Immatures attach onto rocks in cool (6-20°C), pristine (NTU 10 and conductivity 10 msm^{-1}), forested streams (orders 1 & 2), in waterfalls where the current is fast. Mature (final instar) larvae are up to 12 mm in length, with a mean dry mass of 2.819±0.101 mg SE (n=27). Often occur at high densities. Univoltine. In the Buffalo River, eastern Cape, high numbers of larvae (but no pupae) were found in a waterfall in winter (August), and emergence occurred in spring (September). In the Tugela River they were restricted to foothill torrent and foothill sand-bed reaches (Oliff, 1960: 382). Females presumably ornithophilic.

S. (Anasolen) dentulosum Roubaud, 1915

Fig. 8.4

Common in mountainous regions throughout southern Africa. Usually found at altitudes above 1,000 m, although also found as low as 400 m. Immatures are confined to waterfalls and cascades where the current speed is very fast. Mature larvae up to 12 mm in length. They usually attach onto rocks, but are also found on trailing vegetation. In the Buffalo River, eastern Cape, high numbers of larvae (but no pupae) were common in the upper reaches in winter (May to July), and emergence occurred in spring and summer (October to March).

Females presumably ornithophilic, although occasionally they bite humans (Freeman & de Meillon, 1953: 142). They may be annoying by flying around the head and crawling into hair and eyes (Gibbins, 1941; Cunningham van Someren, 1944; Lewis, 1957).

S. (Freemanellum) empopomae de Meillon, 1937

Fig. 8.7

Very rare. Known only from the type locality near Eshowe, Zululand. Associated with S. debegene, with which they may be synonomous (Freeman & de Meillon, 1953: 156). Females presumably ornithophilic.

S. (Freemanellum) hirsutilateris de Meillon, 1937

Fig. 8.6

Very rare.Known only from the type locality near Eshowe, Zululand. Found in small streams on rocks in very fast current. Associated with S. debegene. Females presumably ornithophilic.

S. (Metomphalus) letabum de Meillon, 1935

Fig. 8.12

Rare. Endemic to mountainous regions in southern Africa. Larvae are similar to those of S. vorax, S. medusaeforme and S. hargreavesi, and so their occurrence may have been underestimated. Immatures are found on rocks where the current is fast. In the Buffalo River they were largely restricted to the upper reaches (altitude 530-1,120 m), and were found at high population densities in March and April in two consecutive years. They are most likely univoltine, and perhaps not as rare as thought. Females presumably mammalophilic, although not known to bite.

S. (Metomphalus) natalense de Meillon, 1950

Fig. 8.12

Very rare. Known only from the Drakensburg and a single record from the upper reaches of the Buffalo River. Immatures attach onto rocks in fast-flowing water. Females presumably mammalophilic.

3. Warm, alkaline streams

S. (Pomeroyellum) bequaerti Gibbins, 1936b

Fig. 8.22

Fairly common in small, clear streams. Absent from the south-western Cape, the Great Fish and the lower Vaal Rivers, and most of the Orange River. In Kenya they have been found at altitudes of 1600-2350 m (Bafort et al., 1977), and in southern Africa they have been found at altitudes of 10-2000 m. Immatures attach on dead leaves, trailing grass and rocks in current speeds ranging from slow to very fast (Meeser, 1942; Freeman & de Meillon, 1953; Bafort et al., 1977). Often found in temporary streams. Common in the mid-reaches of the Buffalo River, particularly in spring and summer. Females not known to bite people or livestock (Bequaert, 1938; Meeser, 1942). Presumably ornithophilic.

S. (Pomeroyellum) cervicornutum Pomeroy, 1920

Fig. 8.23

Fairly common in small to medium-sized, clear streams, particularly in Natal and the eastern Transvaal. Absent from the south-western Cape. Immatures found in a variety of breeding places, from pristine to moderately polluted water, and from slow (0.1-0.3 ms^{-1}: Roberts & Okafor, 1987) to fast flowing water (up to 1.9 ms^{-1}: Fain & Elsen, 1973). Larvae attach onto dead leaves in preference to trailing vegetation or rocks (Roberts, 1986). In Natal they were found in high numbers in a clear, slow-moving stream in a mangrove swamp. They have been recorded in the tailwaters of Loskop Dam, Transvaal, but this is unusual. Females ornithophilic (Crosskey, 1969).

S. (Edwardsellum) damnosum Theobald, 1903 (complex of species)

Fig. 8.5

One of the most common blackflies in warm and wet regions of southern Africa. Absent from the south-western Cape. Distribution extends as far south as the Tsitsikamma Forest. Larvae attach onto trailing vegetation and rocks, and have a preference for fast-flowing water (around 1 ms^{-1}: Lewis, 1948; Grenier et al. 1960; Burton & McRae, 1965; Le Berre, 1966; Elouard, 1987). Often dominant in the lower (turbid) reaches of rivers in the eastern Cape (Sundays, Great Fish, Keiskamma, Buffalo and Great Kei), although they are also present in clear, pristine streams, as well as polluted streams. They are typical impoundment-outlet taxa (Fig. 8.5; Table 8.1), and often dominated the tailwaters of Bridle Drift Dam (B4), in the Buffalo River, particularly when water was discharged from a low-level outlet. In the Vaal River, they were found in high numbers in winter where the river is wide and fringed by marginal vegetation (de Moor, 1982a). It is likely that females prefer to oviposit onto emergent or trailing vegetation rather than rocks (de Moor, 1982a). In the Tugela River, they were restricted to the mid- and lower reach sand-bed zones (Oliff, 1960).

The S. damnosum complex comprises at least 30 cytologically distinct members, many of which are important disease vectors in Central and West Africa (Crosskey, 1987c). In southern Africa, there are at least three cytologically distinct members (Crosskey, 1987c), none of which are known to bite humans. Females in southern Africa are zoophilic. In the Buffalo River Catchment they fed readily on cattle, and were not attracted to flowers or fowls. Likewise, along the Vaal River they are pests of livestock (Steenkamp, 1972). In West Africa, a member of the S. damnosum complex transmits Onchocerca ochengi, a parasitic nematode infecting cattle (Omar et al., 1979).

S. (Metomphalus) hargreavesi Gibbins, 1934a

Fig. 8.11

Uncommon in southern Africa, and absent from the south-western Cape. Widespread and very common in the rest of tropical Africa, particularly in the savanna areas (Crosskey & Büttiker, 1982). In the Buffalo River, eastern Cape, they were common, and sympatric throughout the river with the closely related S. medusaeforme. In the Vaal River, they were generally rare, but appeared, sometimes in high numbers, during clear-water conditions (de Moor, 1982a; 1986; Car & de Moor, 1984), although not found in a previous detailed study of the Vaal River (Chutter, 1968; 1970).

Larvae prefer turbulent conditions in cascades and small waterfalls where the current is fast (1.5 to 1.8 ms^{-1}: Roberts & Okafor, 1987). Usually found in mountain foothills, and in pristine to moderately polluted water. They tolerate high levels of ammonium (Grunewald, 1981). Larvae attach onto trailing vegetation, dead leaves or rocks (Roberts, 1986). A typical impoundment-outlet species (Fig. 8.11; Table 8.1): They have been reported at dam spillways in Ethiopia, West Africa, and southern Africa (Cunningham van Someren, 1944; de Meillon, 1936; Crisp, 1956: 98), and were often dominant downstream of impoundments in the Buffalo River. Burton (1973) found large numbers at a dam spillway in northern Ghana, feeding exclusively by grazing on a filamentous green algae. In Saudi Arabia they are restricted to permanent streams (Crosskey & Büttiker, 1982).

Females feed on mammals, particularly cattle, occasionally including humans (Johnson et al., 1982). They bite mainly around the head and face (Lewis, 1965). In Kenya they became a pest during high rainfall in summer (Lewis, 1964a; 1965). Johnson et al. (1982) suggests they may be autogenous in Nigeria. Eggs are laid in clusters onto wet or submerged rocks, or onto emergent or trailing vegetation (Meeser, 1942; Davies, 1962; Begemann, 1980b).

S. (Pomeroyellum) rotundum Gibbins, 1936a

Fig. 28

Fairly common in southern Africa, although absent from south-western and southern Cape, the

Orange, Great Fish and lower Vaal Rivers. Immatures are found in slow (Williams & Hynes, 1971) to fast flowing water (Gibbins, 1937b; Bafort et al., 1977). Females presumably ornithophilic.

4. Large rivers

S. (Metomphalus) bovis de Meillon, 1930

Fig. 8.10

Fairly common, particularly in the Transkei, Natal, and eastern Transvaal. Absent from the Orange River, and possibly the Vaal River. Immatures are found in large rivers in slow to fast flow (de Meillon, 1935; Crosskey, 1960a; Fain & Elsen, 1973). Larvae attach to rocks or trailing vegetation (de Meillon, 1935). Particularly high numbers were found in the Great Kei River, near East London, in December 1989. They were the only species present in the turbid Umfolozi River near Monzi in December 1989; where immatures attached onto Phragmites reeds. In the Great Berg River they were restricted to the lower reaches, but were found throughout the year, particularly in autumn (Harrison & Elsworth, 1958). In the Tugela River they were restricted to the lower reaches (Oliff, 1960), and in the Vaal River they were found in the eroding zone (Chutter, 1970). They are usually not present in impoundment spillways, although there is one such record from Zimbabwe (Meeser, 1942).

Females feed on cattle (de Meillon, 1930; 1955; Gibbins, 1938; 1941) but also bite humans, particularly the legs (Luna de Carvalho, 1962). They are troublesome at times in Biedouw Valley, south-western Cape (Picker, pers. comm.). In Nigeria they have been implicated as a possible vector of human onchocerciasis (Crosskey, 1957a, 1960a).

S. (Metomphalus) chutteri Lewis, 1965

Fig. 8.10

Very common (since river regulation) in large (greater than 4th order), open rivers in southern

Africa (particularly the Vaal, Orange, and Great Fish Rivers). Present in the Buffalo River, eastern Cape, although very rarely. Endemic to southern Africa.

Early instar larvae are found in slow-flowing reaches upstream of rapids (de Moor et al., 1986). Later instars attach onto rocks in rapids where the current speed is fast (1.0 to 1.2 ms^{-1}: Fig. 6.2; de Moor, 1982a; de Moor et al., 1986). Mean mass of mature larvae 0.289±0.009 mg SE (n=24). Larvae have 7 instars, and take 10 to 13 days to pupate at 18 to $20^{o}C$ (de Moor, 1982a & b). Pupae hatch after 1 to 3 days at $22^{o}C$, or 5 to 7 days at $15^{o}C$ (de Moor, 1982a: 95). Cooler temperatures result in larger and more fecund females than warmer temperatures, and the coexistence of early winter and late summer generations may lead to sudden population outbreaks when synchronous emergence occurs in spring (de Moor, 1982a). In the Vaal River, highest densities were found where the river was narrow, and flow fluctuation greatest (Chutter, 1968). Larval drift had peaks in the early morning and late afternoon, and was higher at night that during the day (de Moor, 1982a; de Moor et al., 1986). In the Orange River, the drift at Marksdrift comprised 98.7% S. chutteri (Car, 1983b). High numbers are often associated with turbid water, and during extended periods of clear conditions, they are replaced by other blackfly species (Car & de Moor, 1984).

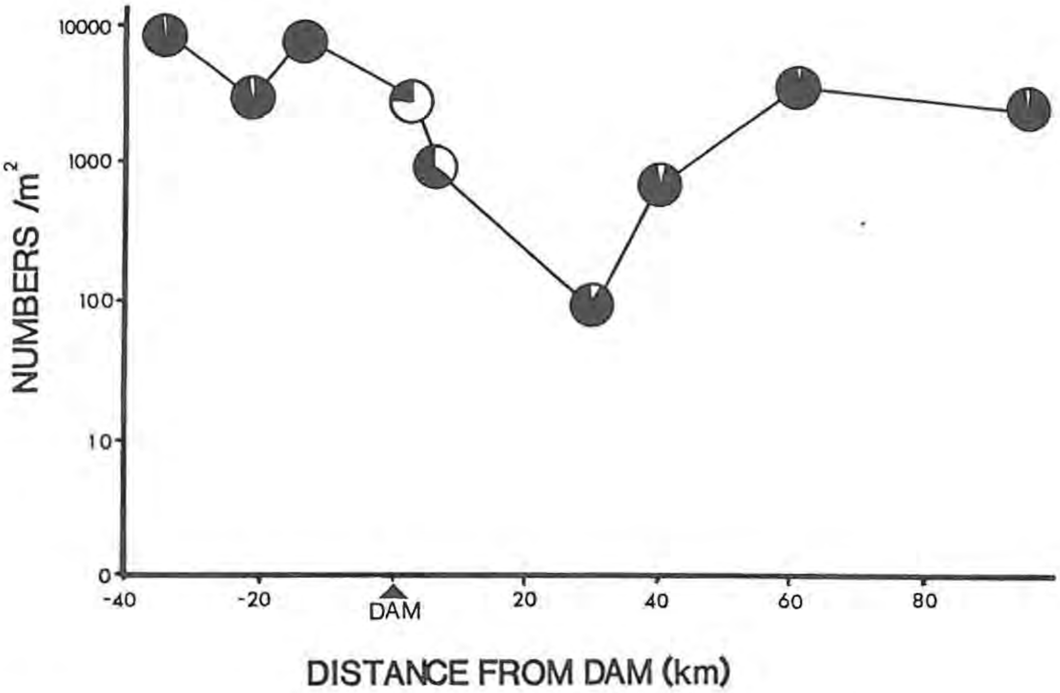


Fig. 8.1 Relative abundance of blackflies (per m^2) upstream and downstream of Elandsdrift Dam in the Great Fish River during five visits in 1986. The shaded portion of the circles represent the pest S. chutteri, whereas the unshaded portion represents other blackfly taxa.

Females are mammalophilic, and feed mainly on sheep, goats and cattle, although they also feed on birds and humans (Chutter, 1968; Begemann, 1980b; Howell et al., 1981). Along the Orange River they are particularly troublesome in spring (September to November; Jordaan & Van Ark, 1990). The fly accounts for an estimated R 22.4 million annual loss in animal production along a 800 km stretch of the Orange River (Nevill, unpubl. data). In 1977 the problem spread to the Great Fish River after the introduction of Orange River water by canal (Coetzee, 1982; O'Keeffe, 1985). The dominant blackfly in the Great Fish River before 1977 was S. nigritarse s.l. (Chutter, 1972a & b; Coetzee, 1982), the larvae of which prefer slow-flowing water. Although S. chutteri (incorrectly identified as S. bovis; de Moor, pers. comm.) were present in the Great Fish River before the opening of the tunnel, their numbers were low, and they were not considered a pest (Chutter, 1972b). The introduction of Orange River water has converted the once seasonal Great Fish River into a perennial river (O'Keeffe & de Moor, 1988). A detailed survey of the Great Fish River (Palmer & O'Keeffe, 1990) showed that S. chutteri were largely absent in a 25-86 km stretch of river downstream of Elandsdrift Dam, and were replaced by other blackfly taxa (S. nigritarse s.l., S. medusaeforme, S. adersi and S. damnosum s.l.; Fig. 8.1). Likewise, in the Vaal River, S. chutteri were scarce in a 8 km stretch downstream of the Vaal-Hartz Weir (Chutter, 1968; de Moor, 1986; de Moor et al., 1986).

Males form mating swarms over fast-flowing water at the lips of rapids (de Moor, 1982a; Begemann, 1986). Newly emerged females enter such swarms and copulation is sometimes completed on the water surface (Begemann, 1980b). Their distribution in the Vaal River is restricted by oviposition requirements of the adult female: Females require long stretches of slow-flowing water upstream of cascades where they drop eggs onto water surface while in flight (de Moor, et al., 1986; de Moor, 1986). Eggs take 4 to 7 days to hatch at 30 and 25°C, and 21 to 25 days to hatch at 10°C (Begemann, 1986). Eggs settle in the sediments, which probably accounts for their tolerance of fluctuating water levels, and the rapid appearance of larvae after floods (de Moor, 1982a). Between 40 and 292 eggs are produced between gonotrophic cycle. Follicular development starts before emergence (de Moor, 1982a, Begamann, 1986), and and may be inhibited by mermithid nematode infections (Chutter, 1967). Females emerging in winter may be autogenous (Begemann, 1986; de Moor, pers. comm.) It is not known how long eggs remain viable, although the eggs of a species from Australia with a similar biology (Austrosimulium pestilens), survived storage for 2½ years (Colbo & Moorhouse, 1974).

Simulium chutteri are sometimes troublesome up to 76 km from the Orange River (Jordaan & Van Ark, 1990), and up to 30 km from the Great Fish River. Programmes to control S. chutteri began in late 1960's, and involved the spraying of organochlorides (DDT) at the breeding sites (Nevill, pers. comm.). Subsequent control methods have involved the use of water-level manipulation and the bacterium Bacillus thuringiensis var. israelensis (Howell et al., 1981; Car, 1983b; Car & de Moor, 1984; de Moor & Car, 1986). Control is best achieved by reducing the aquatic population in winter (July) (de Moor, 1982a; Car, 1983b).

S. (Afrosimulium) gariepense de Meillon, 1953

Fig. 8.3

Fairly common. Endemic to southern Africa. Common along the Orange River before the building of dams (Agnew, 1965). Present in the Vaal, the Great Fish and Sundays Rivers. Immatures attach onto rocks where the current speed is fast (de Meillon, 1950). Population densities often high. Apparently a nuisance along the Orange River during the building of the H. F. Verwoerd Dam (Chutter, 1972a). Females are ornithophilic.

S. (Byssodon) griseicolle Becker, 1903

Fig. 8.3

Rare in southern Africa: known only from the Vaal and Great Kei Rivers. Found in large rivers throughout tropical Africa, including the Nile River (Crosskey, 1987a: 445). Larvae attach onto trailing vegetation, but are also found on dead leaves, rocks and mud. Found in a wide range of current speeds, from 0.2 to 1.1 ms^{-1} (Wanson, 1947; Lewis, 1956). In the Vaal River, immatures were found in stones-in-current and marginal vegetation in summer (Chutter, 1970a).

Females mainly ornithophilic, but also feed on mammals, including humans (Austen, 1909; King, 1923; Disney & Boreham, 1969). They may be annoying by flying around the head (Gibbins, 1938). In tropical Africa they are a serious poultry pest, particularly along the Niger and Nile Rivers (Lewis, 1948; Garside & Darling, 1951; Crosskey, 1960a; El Bashir et al., 1976). Annual outbreaks in Dongola (Sudan) usually occur in February and March (Lewis, 1956). Smoke fires and darkened shelters protect cattle and horses (Lewis, 1956). Large population outbreaks are usually short-lived, lasting a few weeks only (Lewis, 1956). Both sexes feed on nectar, and Lewis (1956) suggests they may also be autogenous. Lamontellerie (1963) suggests that they survive the dry season in Upper Volta as adults.

S. (Pomeroyellum) mcmahoni de Meillon, 1940

Fig. 8.26

Fairly common, particularly in the Vaal and Orange Rivers. Not recorded from the Transkei, the south-western, southern and eastern Cape. Larvae attach onto trailing vegetation, but prefer dead leaves (Roberts & Okafor, 1987) or stones (de Moor, 1982a). Immatures found in slow flowing water (0.3-1.3 ms^{-1}: Bafort et al., 1977; Roberts & Okafor, 1987). Found in impoundment tailwaters (Table 8.1). In the Vaal River they were present throughout the year in a variety of breeding places, occasionally in high numbers (Chutter, 1970a; de Moor, 1986). Females presumably ornithophilic.

5. Temporary streams

S. (Nevermannia) ruficorne Macquart, 1838

Fig. 8.20

Very common, particularly in the drier regions (including Namibia), as well as the more polluted areas (such as the Witwatersrand). Their biology and taxonomy has been reviewed in detail by Crosskey and Büttiker (1982). They are by far the most widespread blackfly in Africa. Immature stages tolerate high water temperatures and poor water quality, although they are also found in pristine streams.

They are found in small trickles (including plastic water pipes) to large rivers (Cunningham van Someren, 1944; Crosskey, 1960a; Crosskey, 1957b). Larvae attach onto dead leaves, trailing vegetation, rocks or algae. They are usually found in slow-flowing water (including stagnant pools), although they have also been recorded in current speeds of up to 1.4 ms^{-1} (Fain & Elsen, 1973). They have been found at altitudes from -200 m (in the Jordan Valley, Palestine) to 1,200 m (in Uganda: Gibbins, 1936a; 1938). They have been recorded at dam spillways in Senegal (Larivière & Abonnenc, 1956), Namibia, and at high numbers on a small earth spillway in the eastern Cape. In North Cameroon they were found in high numbers at a dam spillway in when the flow had stopped, and there was just seepage (Steveny et al., 1981; Table 8.1). In the Buffalo River, eastern Cape, they were encountered where industrial and domestic pollution enters the river, although they were also found in pristine parts of the river during low flow. Chutter (1972a) found them to be common in the Sundays and Great Fish Rivers during low flow. They were common in temporary seepage areas created by mining activities in the sandy soils near Richards Bay, where water quality was good (Conductivity 56 mSm^{-1}; NTU 12).

They are one of the first species to colonize new habitats, and were found within a week after a drought in a stream in Zimbabwe (Harrison, 1966), and within 24 days in the Great Fish River (Chutter, 1972a). Harrison (1966) found that they took 2 weeks to develop into pupae. Crosskey & Büttiker (1982) suggests that they may survive dry periods as eggs deposited in sediments (similar to S. chutteri), and that this accounts for their rapid appearance after floods. However, Begemann (1980b) found females laying eggs onto submerged stones, and Larivière and Abonnenc (1956) also state that they oviposit onto a substrate.

Females are anautogenous (Takaoka, 1988), and feed on birds including poultry (Orian, 1962) and Francolin (Freeman & de Meillon, 1953: 99).

Rare taxa

S. (Meilloniellum) hirsutum Pomeroy, 1922

Fig. 8.9

Rare in southern Africa, although larvae are easily confused with those of S. adersi, and their occurrence may be underestimated. Common in clear, forested streams in the Transkei. Larvae attach onto dead leaves and trailing vegetation, and sometimes rocks. Found in current speeds ranging from slow to fast. They are able to tolerate severely polluted water. Females ornithophilic (Duke, 1962).

S. (Nevermannia) katangae Fain, 1951

Fig. 8.16

In southern Africa they have been recorded from Pretoria (de Meillon, 1955), the Umlaas River, Natal, and the Bulolo River, Port St. Johns. In the rest of Africa they are known from Zaire (Fain, 1951; Lewis & Raybould, 1974a), and the Cameroon (Fain & Elsen, 1973). In Zaire a single pupa was found at high altitude (1,766 m) on a rock where the current was fast (Lewis & Raybould, 1974a). The Bulolo River was a clear-water stream of about 2 m width, with at a water temperature of 22^{o}C.

S. (Nevermannia) narcaeum de Meillon, 1950

Fig. 8.16

Known from two localities in southern Africa. Found in fast flowing water attached onto rocks in rapids.

S. (Metomphalus) wellmanni Roubaud, 1906

Fig. 8.15

Rare. Known from Natal, Transkei, the eastern Transvaal lowveld and the upper reaches of the Vaal River. Immatures usually found in mountainous regions in waterfalls and cascades where the current is fast, although they also occur in slow current (Freeman & de Meillon, 1953: 206). In the Vaal River, they were found in winter and early dry summer (Chutter, 1970a). Females are mammalophilic. Early records of them biting humans (Austen, 1909) are likely to have been mistaken (Freeman & de Meillon, 1953: 206).

8.4 DISCUSSION

The distribution of blackflies in southern Africa reflect a longitudinal zonation, from temporary streams and trickles, mountain streams, to large rivers. Regional differences (determined by pH and temperature) are superimposed upon this zonation. The blackfly fauna in the Buffalo River was typical of (1) mountain streams (Sites 0 & 1, upstream of all impoundments), and (2) warm, alkaline streams (Sites 2b to 13) in the rest of southern Africa. Blackfly taxa which were rare in the Buffalo River fell into two categories: (1) those which made seasonal appearances in the upper reaches of the river (e.g., *S. letabum* and *S. debegene*) and (2) those which made aseasonal appearances in any part of the river (e.g., *S. chutteri* and *S. ruficorne*). The former are likely to be univoltine species present in the Buffalo River catchment throughout the year (but as not larvae or pupae), whereas the latter are likely to have been blown in as gravid females from adjacent rivers. For example, *S. chutteri* is typically found in large and turbid rivers, and is common in the nearby Great Fish River, although they were found in the pristine, upper reaches (Site 2b) of the Buffalo River. Likewise, *S. ruficorne*, which is associated with temporary and often polluted streams, was found in the upper, pristine reaches of the Buffalo River on one occasion. Although the population densities of these taxa in atypical conditions was always low, their presence may lead to rapid changes in species composition if environmental conditions should change. At times, the Buffalo River contained representative blackflies of four of the five blackfly stream types in southern Africa. Not one species typical of cool, acid streams was found in the Buffalo River.

The five most common blackfly taxa in the Buffalo River were common and widespread in medium-sized rivers in the rest of southern Africa (with the exceptions of *S. hargreavesi* and *S. damnosum* s.l., which were absent from the south-western Cape); All five can be classed as typical 'outlet' taxa (Table 8.1). This suggests that impoundments in the Buffalo River have shifted the distribution of blackfly species upstream (*sensu* Ward & Stanford, 1983); Species which would normally only be found in the middle and lower reaches of the river (where levels of transported material are naturally high), are now found in the upper reaches of the river (downstream of Maden (B1), and have displaced clear-water, upper-reach species. Impoundments in the middle and lower reaches of the Buffalo River have had a negligible effect on blackfly species distributions.

Common features of outlet taxa are that they are small (final instar larvae with a mass of less than 0.4 mg), multivoltine, and adult females feed on sheep and cattle (*S. damnosum* s.l., *S. medusaeforme*, and *S. hargreavesi*) and poultry (*S. adersi* and *S. nigritarse*) (Steenkamp, 1972; Begemann, 1980b; Huchzemeyer & Sutherland, 1975). Whether or not blood-feeding is obligatory is not known, but it appears that the life-histories of southern African impoundment-outlet blackflies are different from those reported in Holarctic regions, where several species are autogenous (Wotton, 1982a, 1987a). Most impoundments in southern Africa, including those in the Buffalo River, are used for water storage, and release minimal compensatory flows, if at all. Sudden drying of impoundment tailwaters is likely to select taxa with rapid development of aquatic stages.

Impoundment-outlet blackflies are conspicuously rare in the turbid

Orange River, which is dominated for most of its length by *S. chutteri*. This species was replaced by typical impoundment outlet species downstream of impoundments in the Vaal and Great Fish Rivers. One reason for the change in blackfly dominance downstream of impoundments may lie in the different methods of simuliid oviposition: *S. chutteri* scatter their eggs onto the water surface, whereas *S. nigritarse* and other common 'outlet' taxa in southern Africa, secure their eggs onto substrates (de Moor, 1986; de Moor et al., 1986; Golini & Davies, 1987). This could mean dams act as barriers to downstream colonisation of *S. chutteri* eggs, and explain their relative scarcity downstream of impoundments (de Moor, pers. comm.). However, there are numerous blackfly taxa which are common in impoundment and lake outlets elswhere, which also scatter their eggs onto the water surface (e.g., *Cnephia dacotensis*, *Simulium decorum*, *S. tuberosum*, *S. venustum*, *S. vernum*, *S. vittatum*; Imhof & Smith, 1979; Golini & Davies, 1987; Lake & Burger, 1983; Wotton, 1987a). Differences in oviposition behaviour therefore do not fully explain these observations. An alternative explanation centres on differences in cephalic fan structure, and the hydrodynamic conditions downstream of impoundments. Larvae of *S. chutteri* have characteristic cephalic fans (Fig. 6.7), which differ considerably from the generalised microtrichial structure shared by all impoundment outlet taxa (Chap. 6). Water discharged from the surface of Elandsdrift Dam carried less suspended material than inflowing water, and the diversion of water from Elandsdrift Dam into the neighbouring Sundays River reduced the flows downstream of the dam (Palmer & O'Keeffe, 1990). It is possible therefore that the relatively clear and lower water levels downstream of Elandsdrift Dam, may effectively simulate natural flow conditions, which were present in the Great Fish River prior to the introduction of Orange

River water, and so favour those taxa (such as *S. nigritarse* s.l.) whose larvae are better adapted to clear, slow-flowing conditions. This hypothesis is supported by the observation that *S chutteri* was replaced by other species during prolonged periods of clear water in the Orange River. The association between larval habitats and blackfly cephalic fan structure (Table 6.1) is too close and predictable to be fortuitous.

Table 8.1 Records of blackflies in impoundment outlets in southern Africa. Taxa are listed alphabetically. Stars (*) indicate taxa which are regarded as typical of impoundment outlets.

Taxon	Locality	Reference/Catalogue
* *S. adersi*	Transvaal: Vaal-Hartz Wier	(de Moor, 1986)
	Emmerentia Dam	Paterson (SAIMR)
	Florida Lake	(Cat. VAL 9a)
	Natal: Jozini Dam	This project
	Umlalazi Weir	Meeser (SAIMR)
	O.F.S: Allemanskraal Dam	(Cat. HRG 5j)
	Hoofstad Weir	(Cat. HRG 81)
	Eastern Cape: Elandsdrift Dam	(Palmer & O'Keeffe, 1990)
	Lake Mentz	This project
	Groot River (weir)	" "
	Buffalo River dams	" "
	Bulk River Dam	" "
	small earth-wall dam	" "
S. brachium	Eastern Cape: small dam near Hogsback	This project
	small earth-wall dam	" "
* *S. damnosum* s.l.	Transvaal: Loskop Dam	(Cat. OKS 126x)
	Vaalhartz Weir	(de Moor, 1986)
	Vaal Barrage	(AM Cat. VAL 139a)
	Natal: Jozini Dam	This project
	O.F.S: Allemanskraal Dam	(Cat. HRG 5a)
	Erfenis Dam	(Cat. HRG 7a)
	Orange River: Verwoerd Dam	This project
	Boegoeberg Dam	" "
	Eastern Cape: Elandsdrift Dam	(Palmer & O'Keeffe, 1990)
	Lake Mentz	This project
	Buffalo River dams	" "
	Groot River (weir)	" "
* *S. hargreavesi*	Zululand: weir	(de Meillon, 1953)
	Natal: Jozini Dam	This project
	Eastern Cape: Buffalo River dams	" "
	small dam near Hogsback	" "
S. mcmahoni	Transvaal: Vaal-Hartz Weir	(de Moor, 1982a; 1986)
	Vaal Barrage	(Chutter, 1963)
	Loskop Dam	(Cat. OKS 126bb)
	Orange River: Boegoeberg Dam	This project
* *S. medusaeforme*	Zululand: weir	(de Meillon, 1953)
	Transvaal: Emmerentai Dam	Patterson (SAIMR)
	Doorndraai Dam	"
	Loskop Dam	(Cat. OKS 122n)
	Southern Cape: Buffelsjags Dam	This project
	Orange River: Verwoerd Dam	" "
	Eastern Cape: Elandsdrift Dam	(Palmer & O'Keeffe, 1990)
	Buffalo River dams	This project
	Bulk River Dam	" "
	Groot River (weir)	" "

Table 8.1 (Continued)

* *S. nigritarse* s.s	Transvaal:	Loskop Dam	(Cat. OKS 126y)
		Florida Lake	(Cat. VAL 9a)
	Eastern Cape:	Elandsdrift Dam	(Palmer & O'Keeffe, 1990)
		Buffalo River dams	This project
		Bulk River Dam	" "
		small dam near Hogsback	" "

8.5 DISTRIBUTION RECORDS

[Maps are arranged as in Appendix A, except where more than one taxon shares a map.]

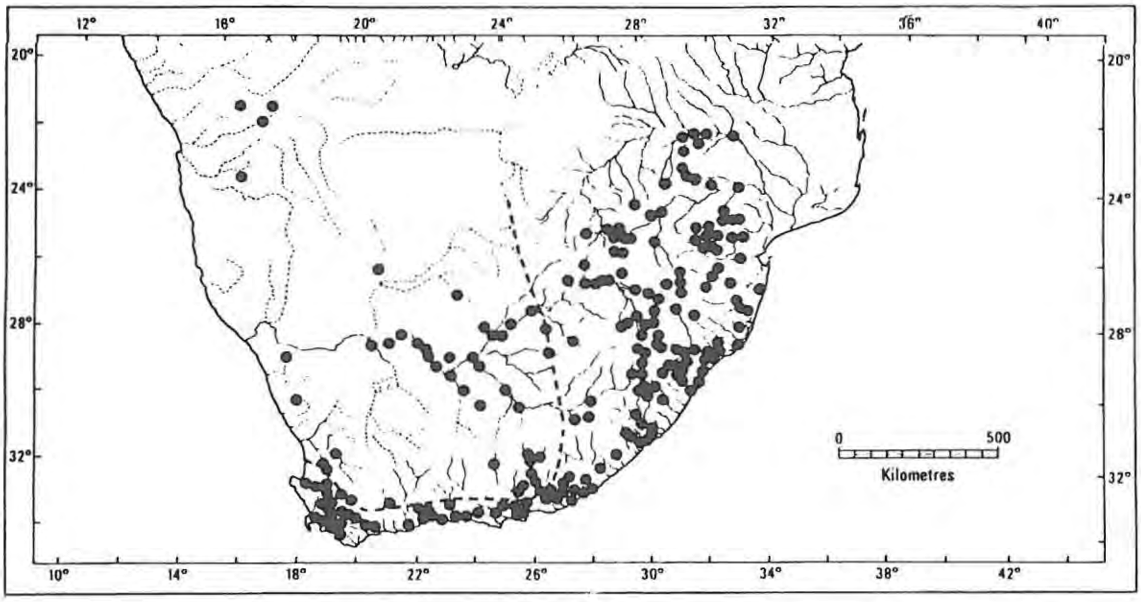


Fig. 8.2 Map of southern Africa showing the distribution of blackfly records. Dashes (- - -) indicate the 500 mm per annum rainfall isohyet (Department of Water Affairs, South Africa, 1986).

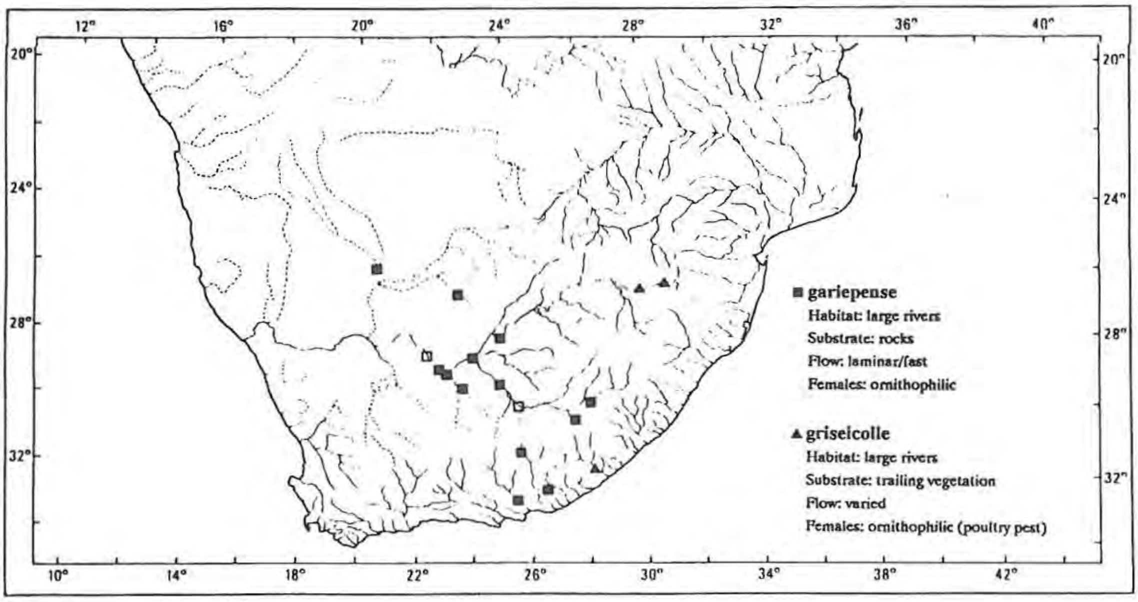


Fig. 8.3 Distribution records of *S. gariepense* and *S. griseicolle* in southern Africa. Open symbols indicate records from impoundment tailwaters.

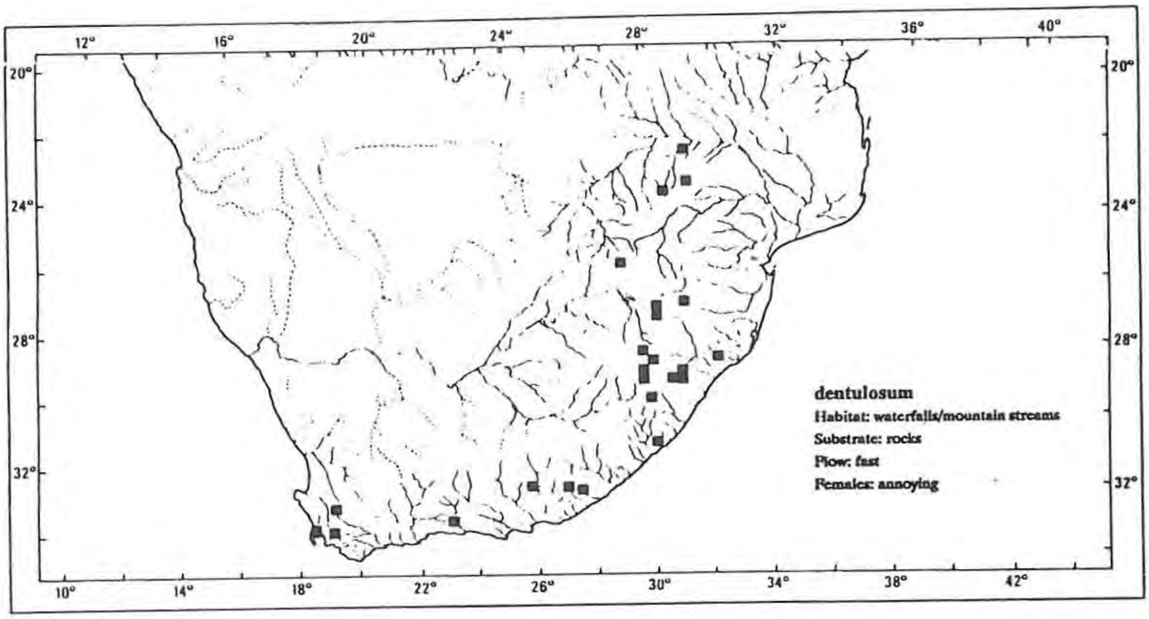


Fig. 8.4 Distribution records of *S. dentulosum* in southern Africa.

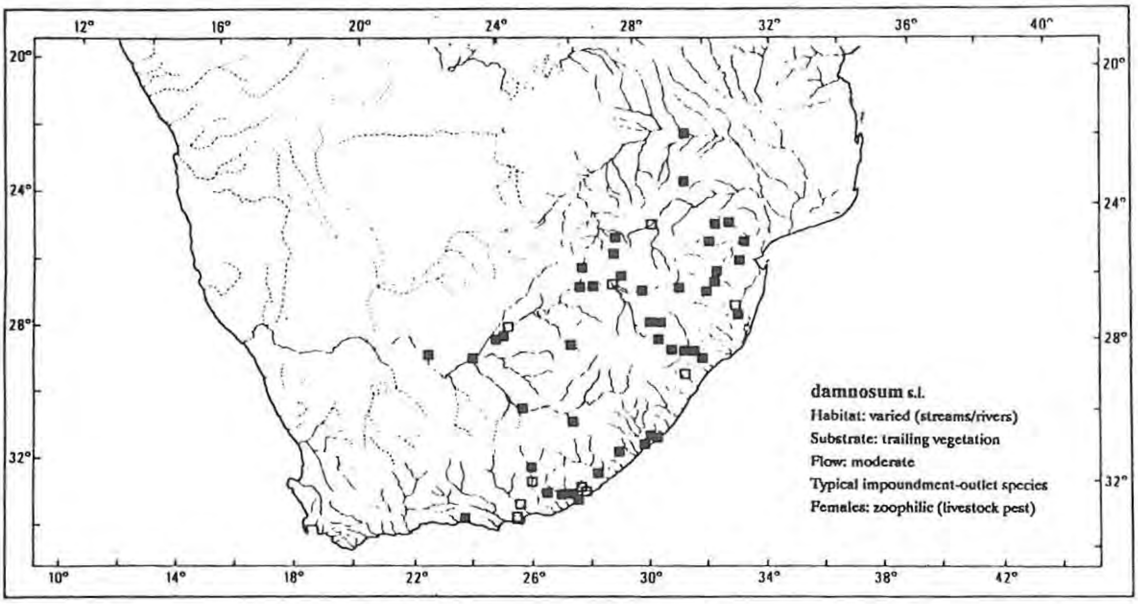


Fig. 8.5 Distribution records of *S. damnosum* s.l. in southern Africa. Open symbols indicate records from impoundment tailwaters.

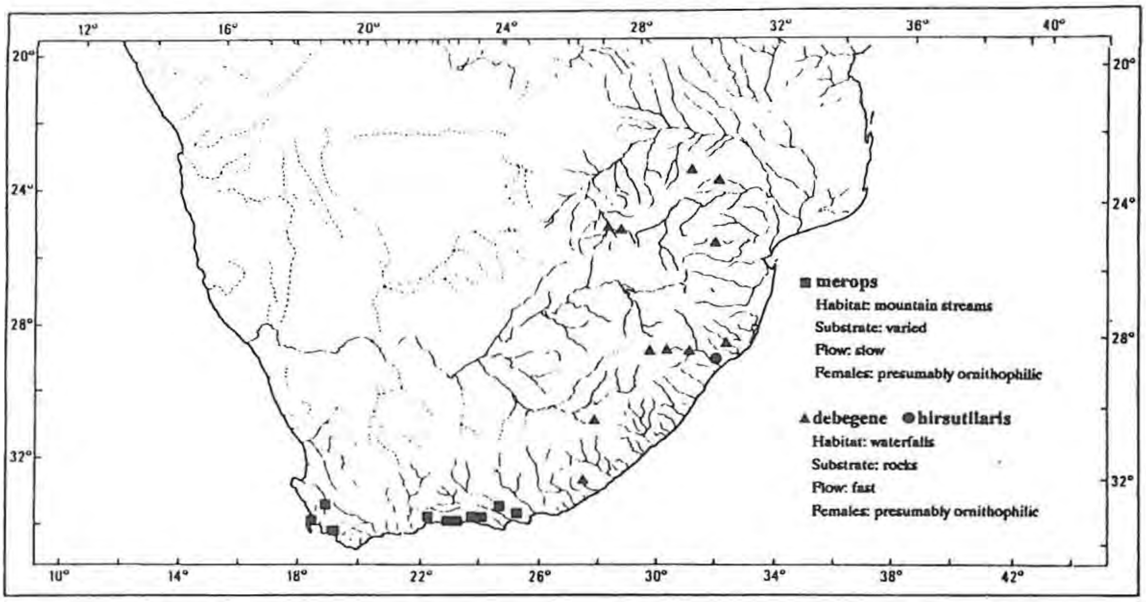


Fig. 8.6 Distribution records of *S. merops*, *S. debegene* and *S. hirsutilaris* in southern Africa.

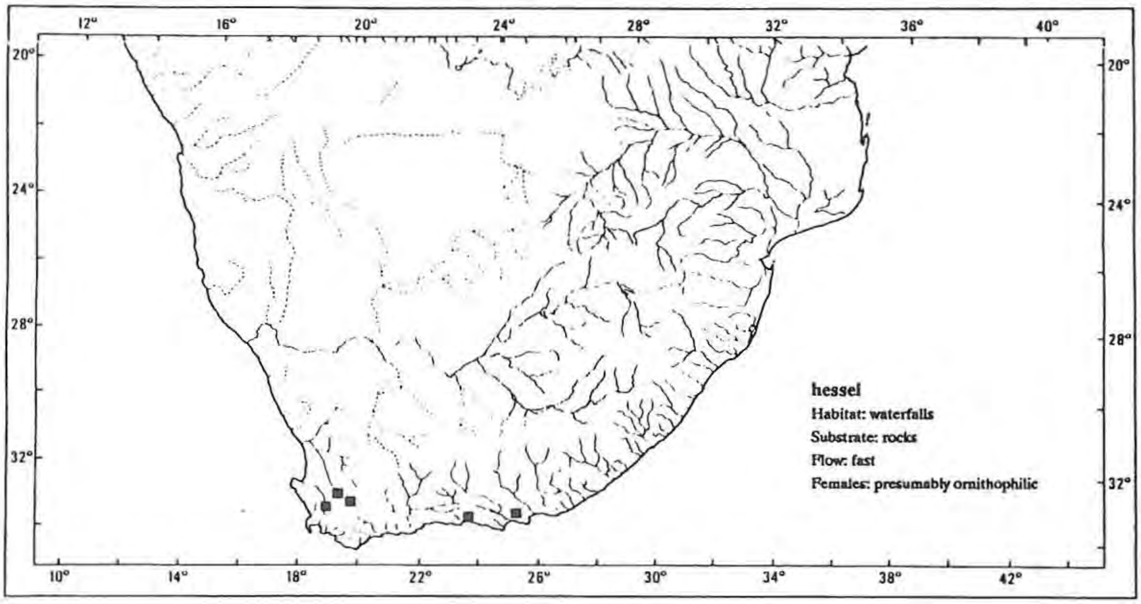


Fig. 8.7 Distribution records of *S. hessei* and *S. empopomae* in southern Africa.

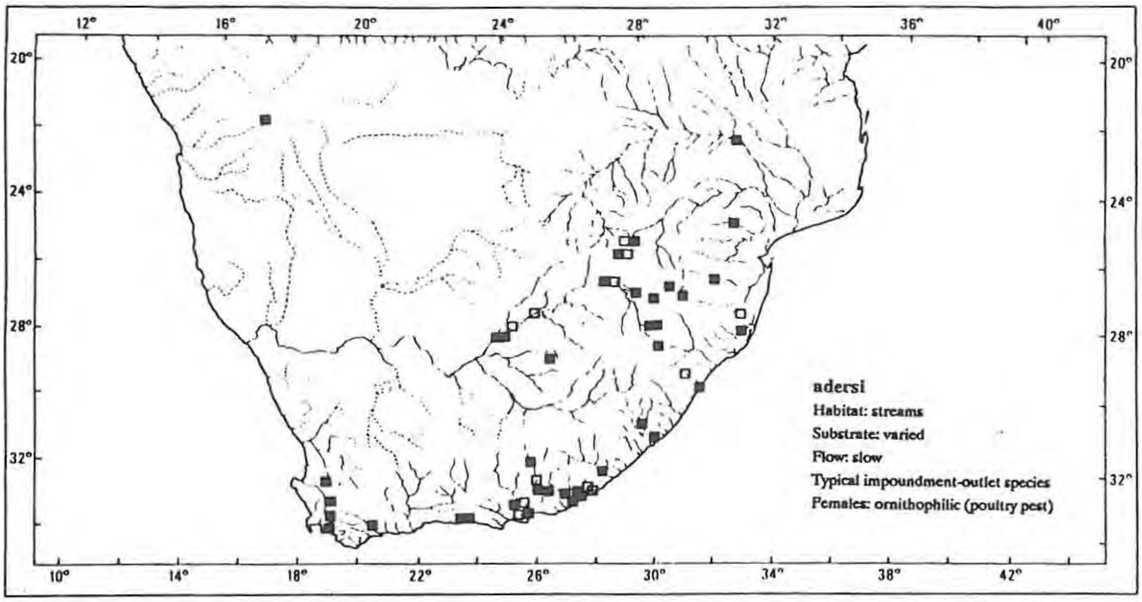


Fig. 8.8 Distribution records of *S. adersi* in southern Africa. Larvae are easily confused with those of *S. hirsutum*, and their occurrence may have been overestimated. Open symbols indicate records from impoundment tailwaters.

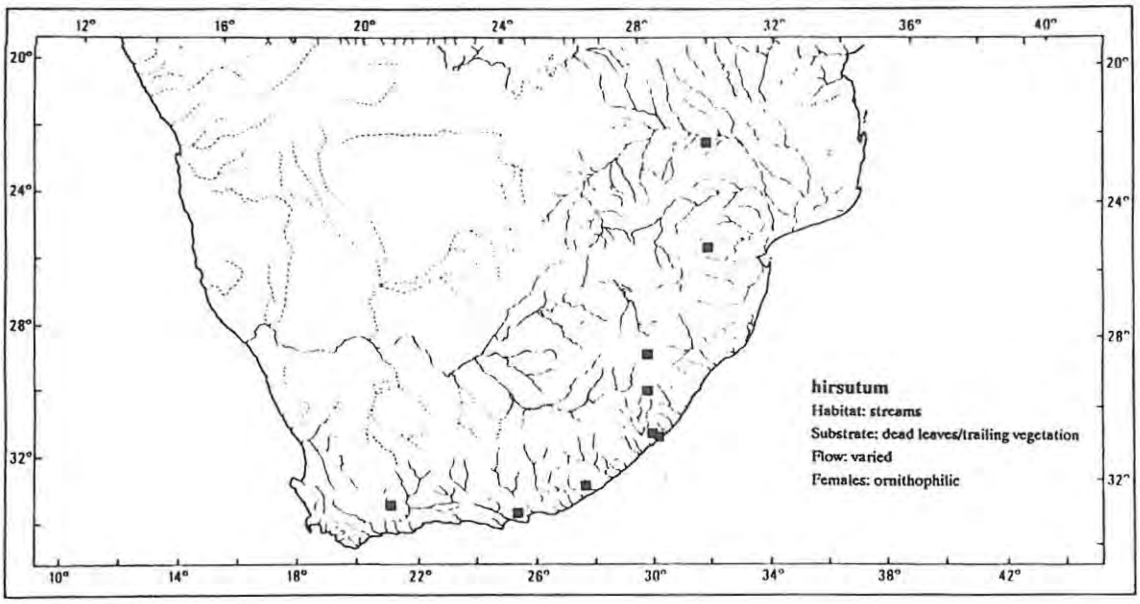


Fig. 8.9 Distribution records of *S. hirsutum* in southern Africa. Larvae are easily confused with those of *S. adersi*, and their occurrence may have been underestimated.

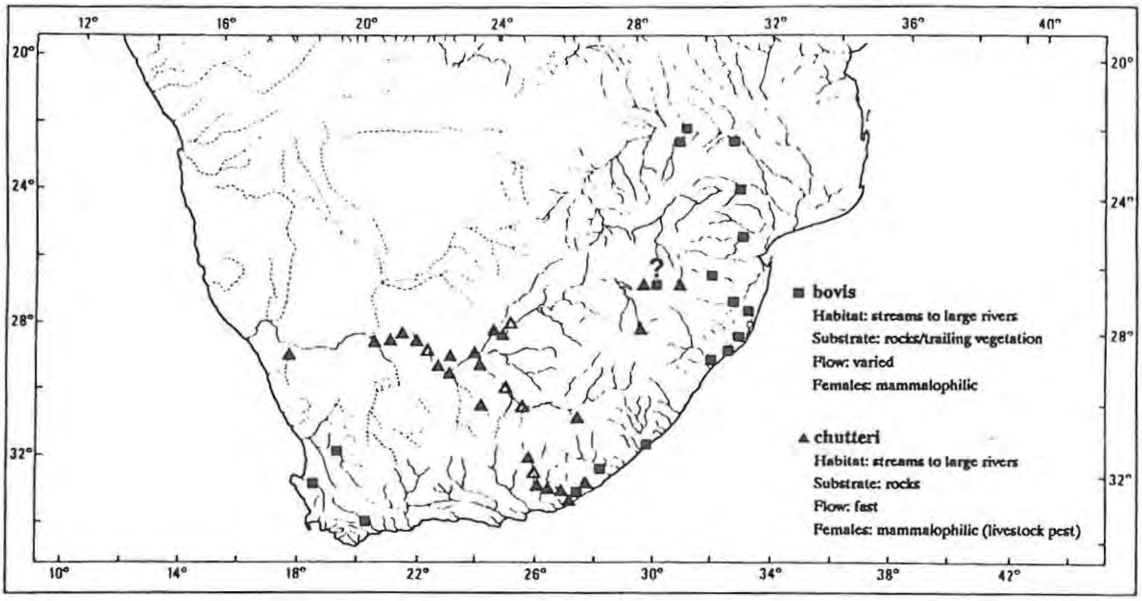


Fig. 8.10 Distribution records of *S. bovis* and *S. chutteri* in southern Africa. Open symbols indicate records from impoundment tailwaters.

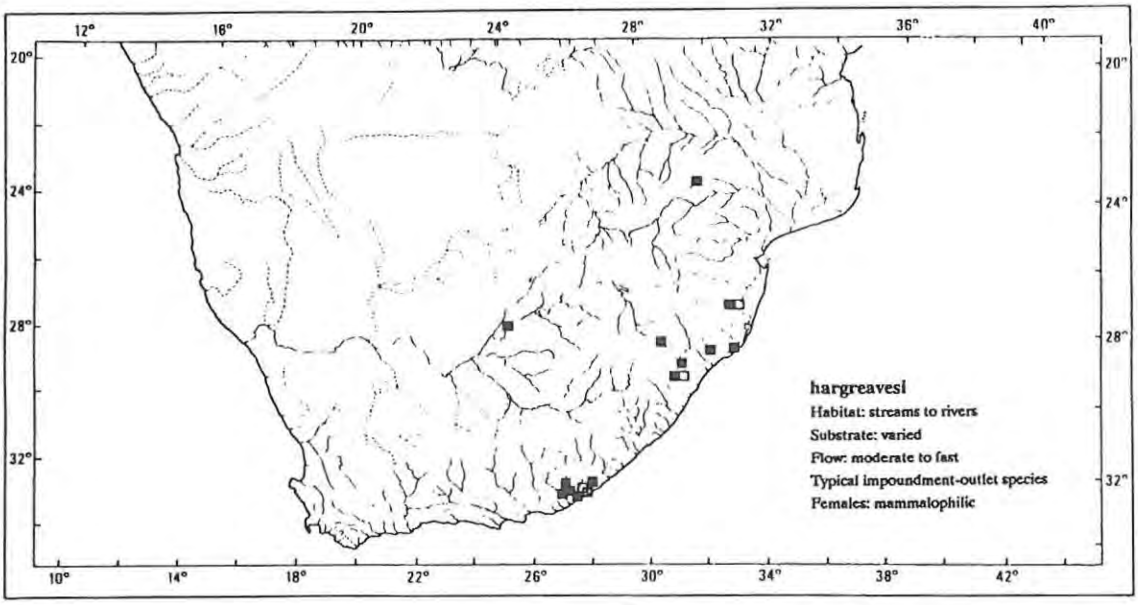


Fig. 8.11 Distribution records of *S. hargreavesi* in southern Africa. Open symbols indicate records from impoundment tailwaters.

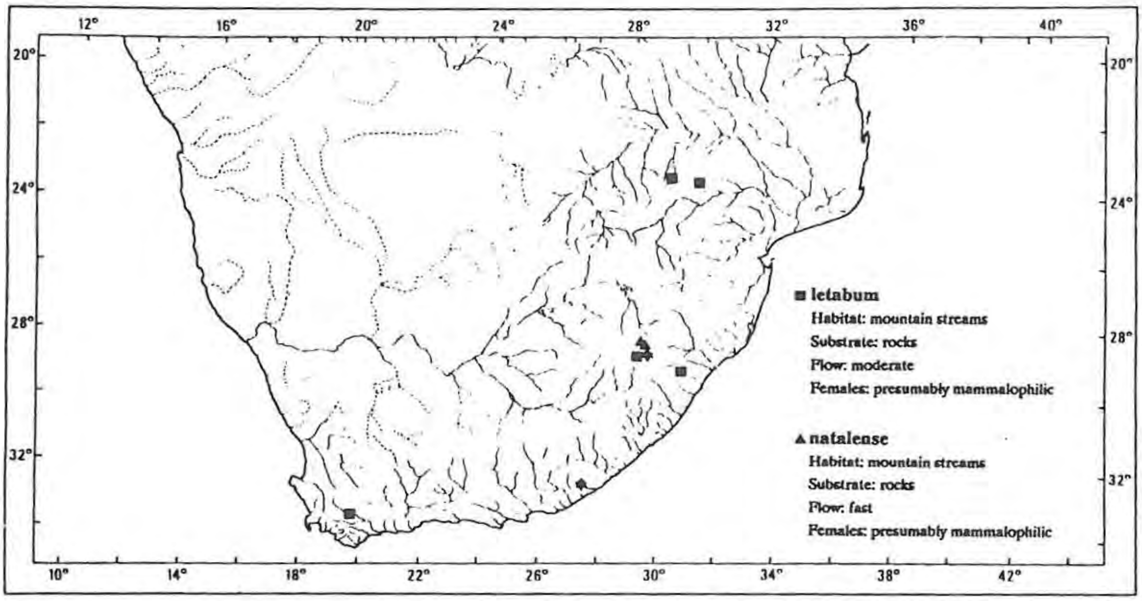


Fig. 8.12 Distribution records of *S. letabum* and *S. natalense* in southern Africa. Stars indicate the presence of both species.

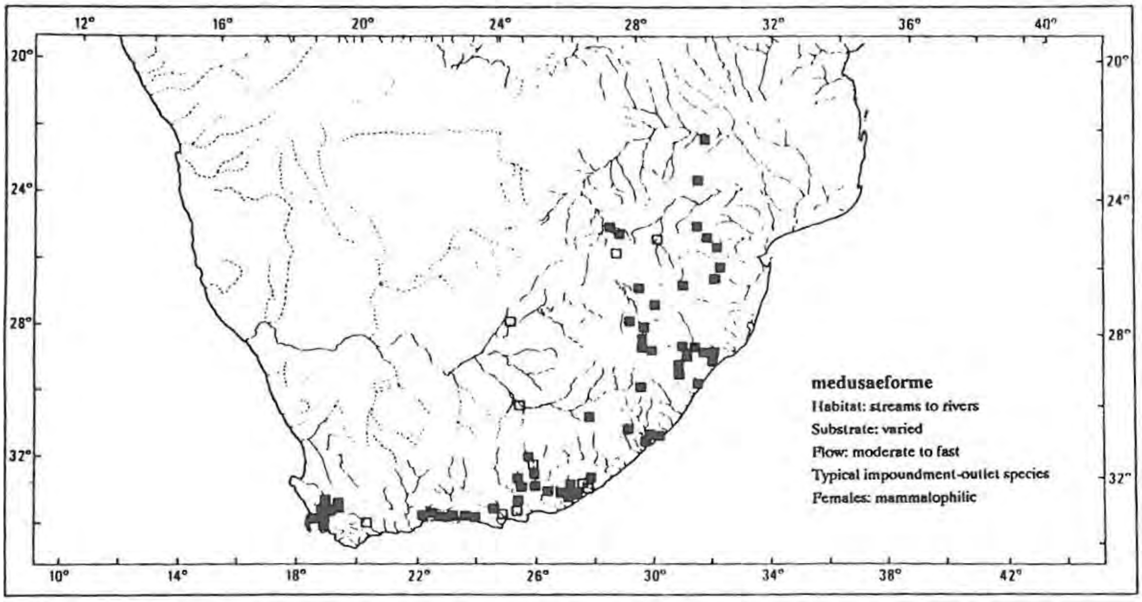


Fig. 8.13 Distribution records of *S. medusaeforme* in southern Africa. Open symbols indicate records from impoundment tailwaters.

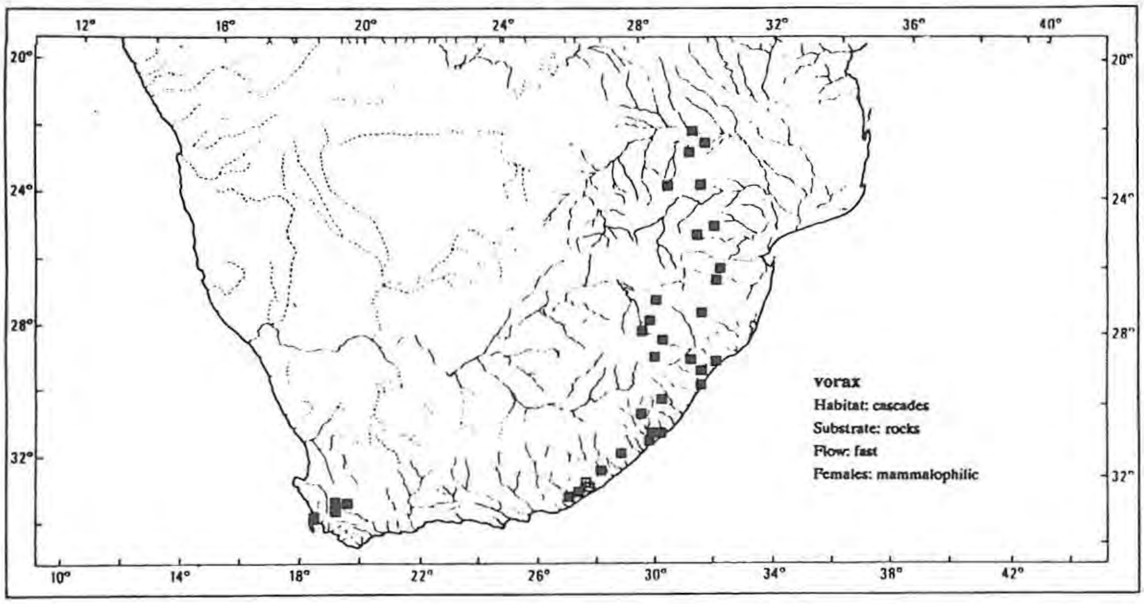


Fig. 8.14 Distribution records of *S. vorax* in southern Africa. Open symbols indicate records from impoundment tailwaters.

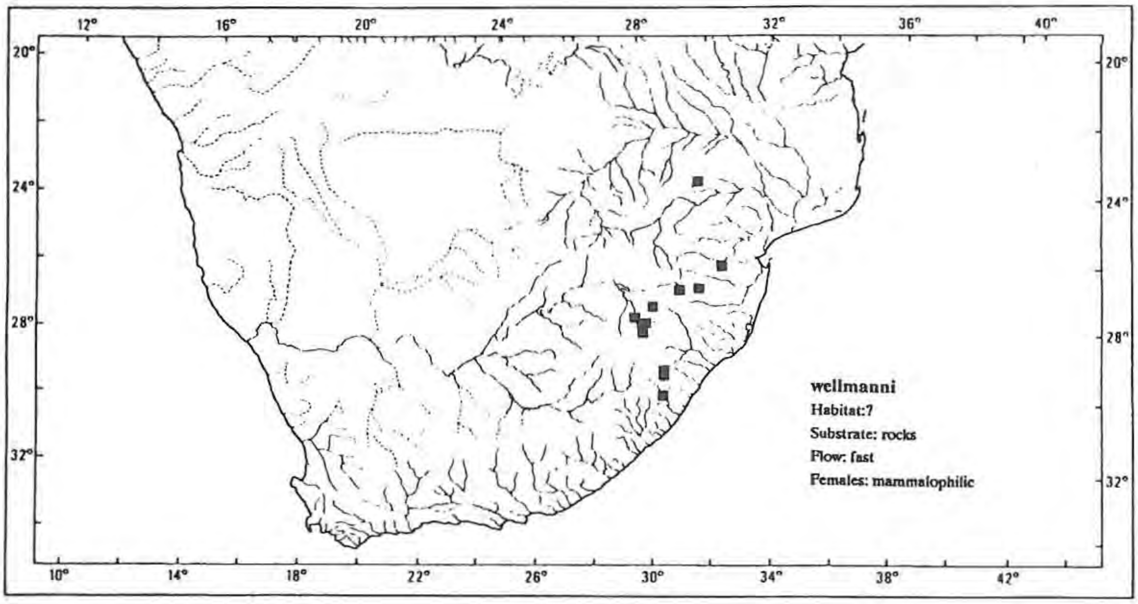


Fig. 8.15 Distribution records of *S. wellmanni* in southern Africa.

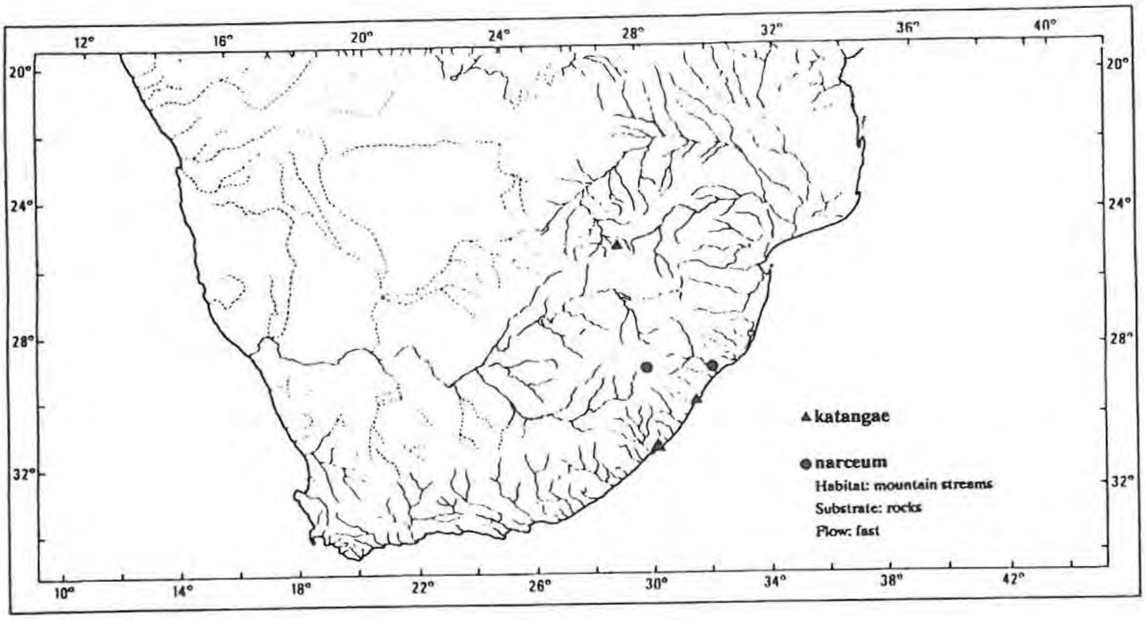


Fig. 8.16 Distribution records of *S. katangae* and *S. narcaeum* in southern Africa.

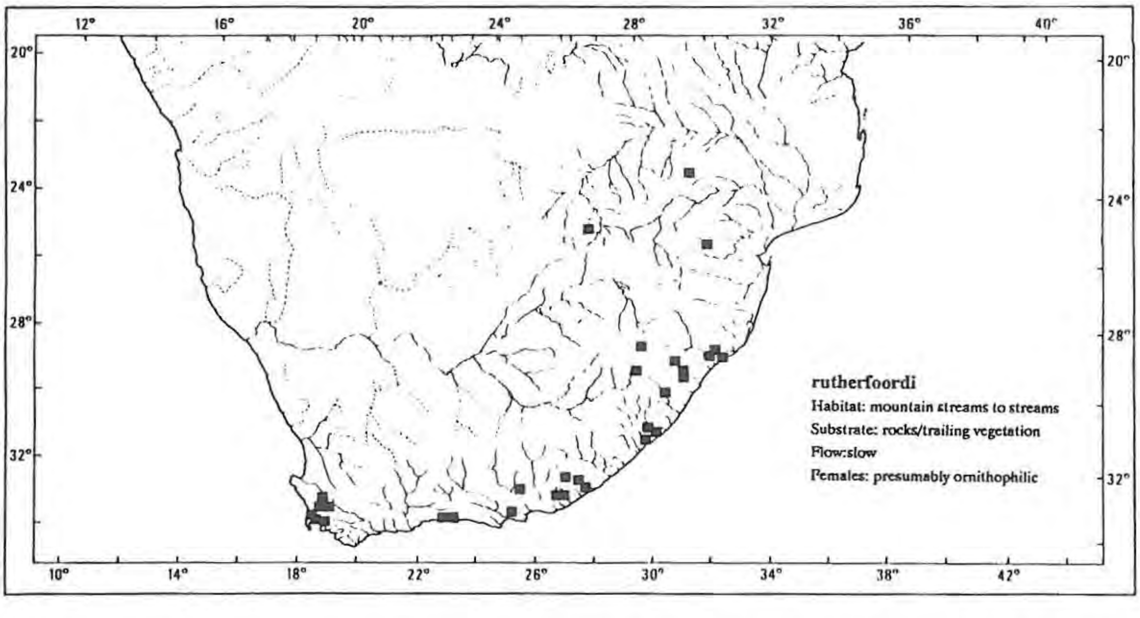


Fig. 8.17 Distribution records of *S. rutherfoordi* in southern Africa.

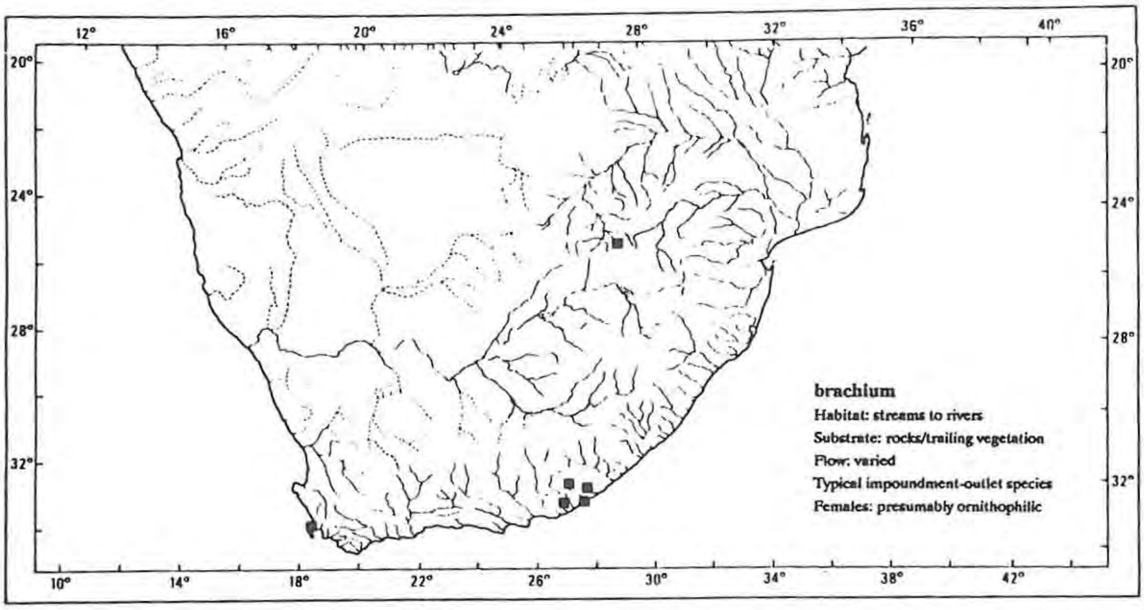


Fig. 8.18 Distribution records of *S. brachium* in southern Africa. Larvae are indistinguishable from those of *S. nigritarse* s.s, and their occurrence may have been undrestimated. Open symbols indicate records from impoundment tailwaters.

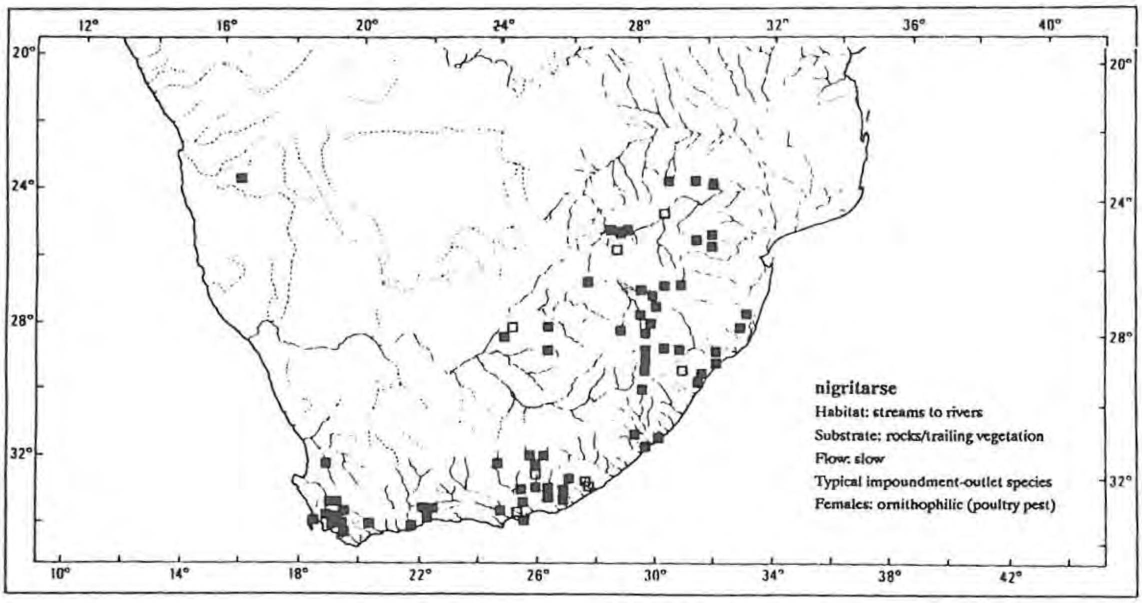


Fig. 8.19 Distribution records of *S. nigritarse* in southern Africa. Larvae are indistinguishable from those of *S. brachium*, and their occurrence may have been overestimated. Open symbols indicate records from impoundment tailwaters.

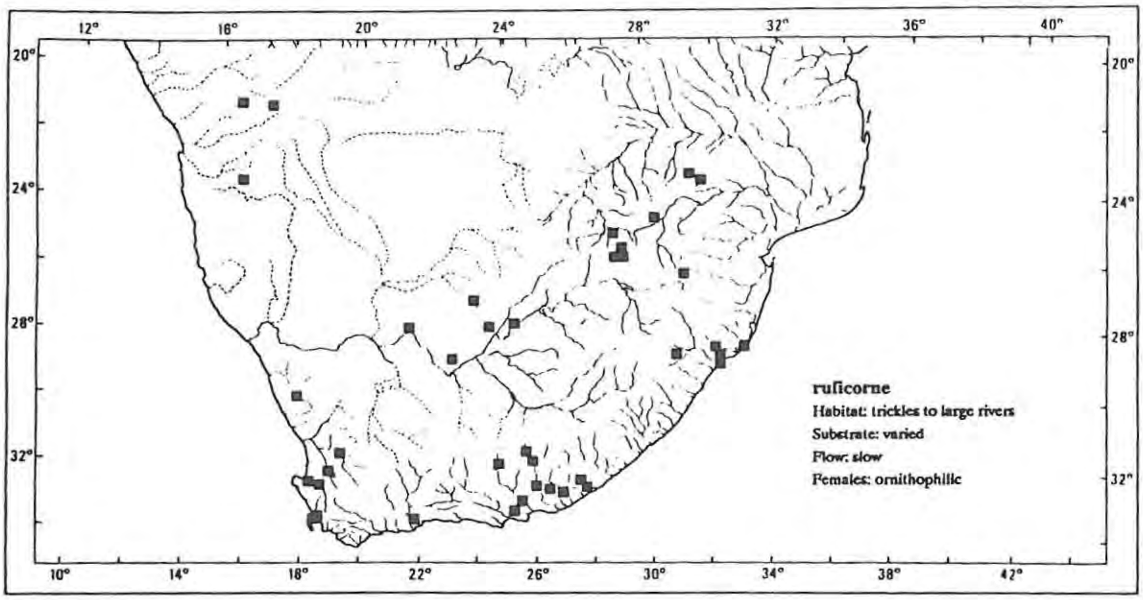


Fig. 8.20 Distribution records of *S. ruficorne* in southern Africa. Open symbols indicate records from impoundment tailwaters.

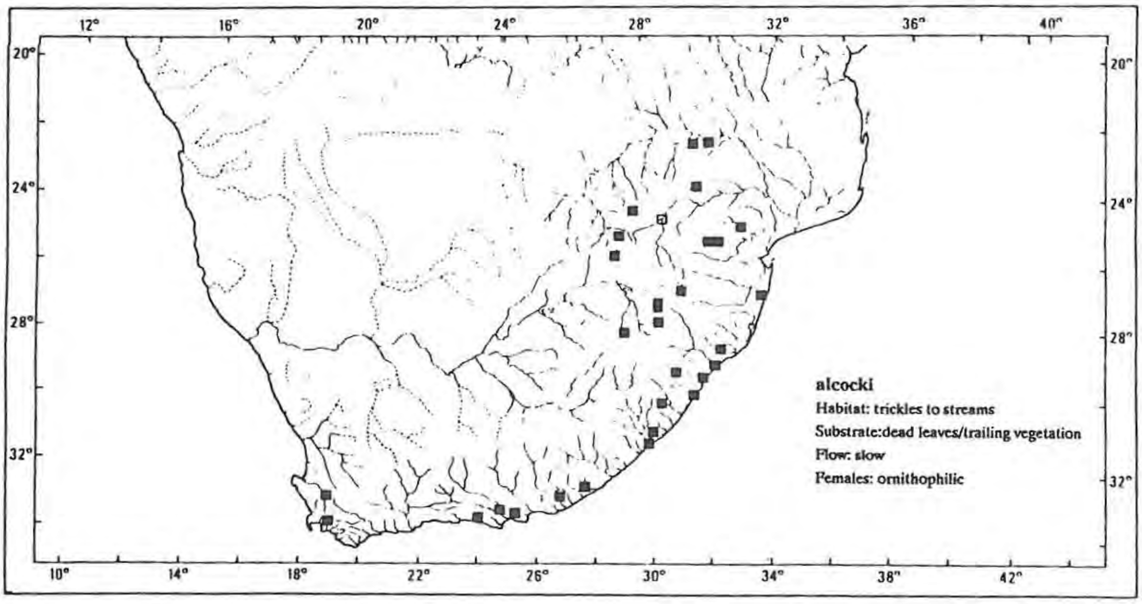


Fig. 8.21 Distribution records of *S. alcocki* in southern Africa. Open symbols indicate records from impoundment tailwaters.

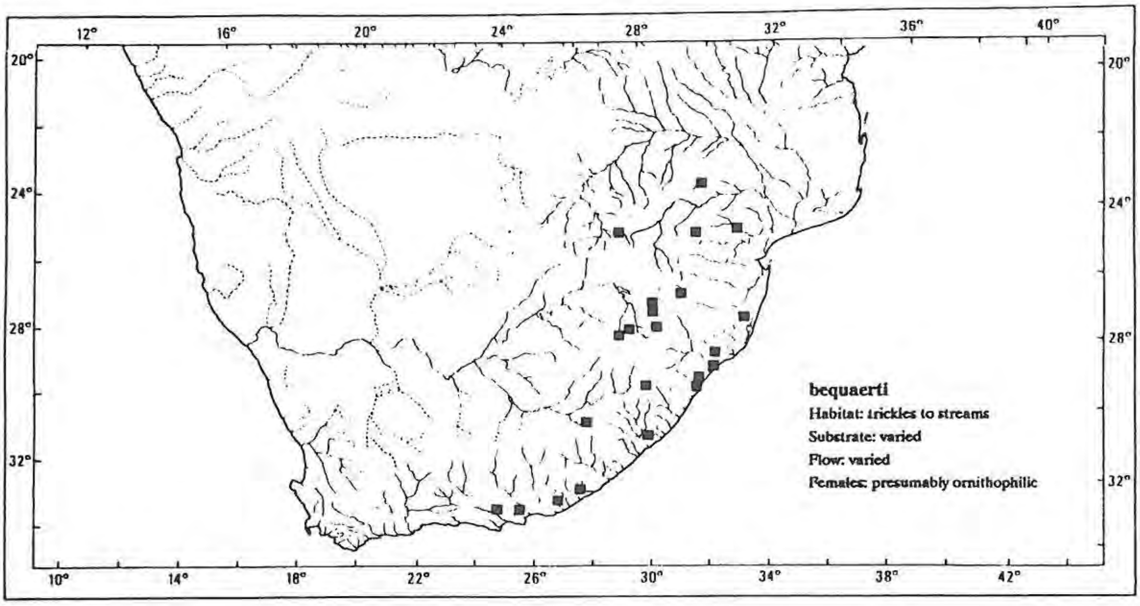


Fig. 8.22 Distribution records of *S. bequaerti* in southern Africa.

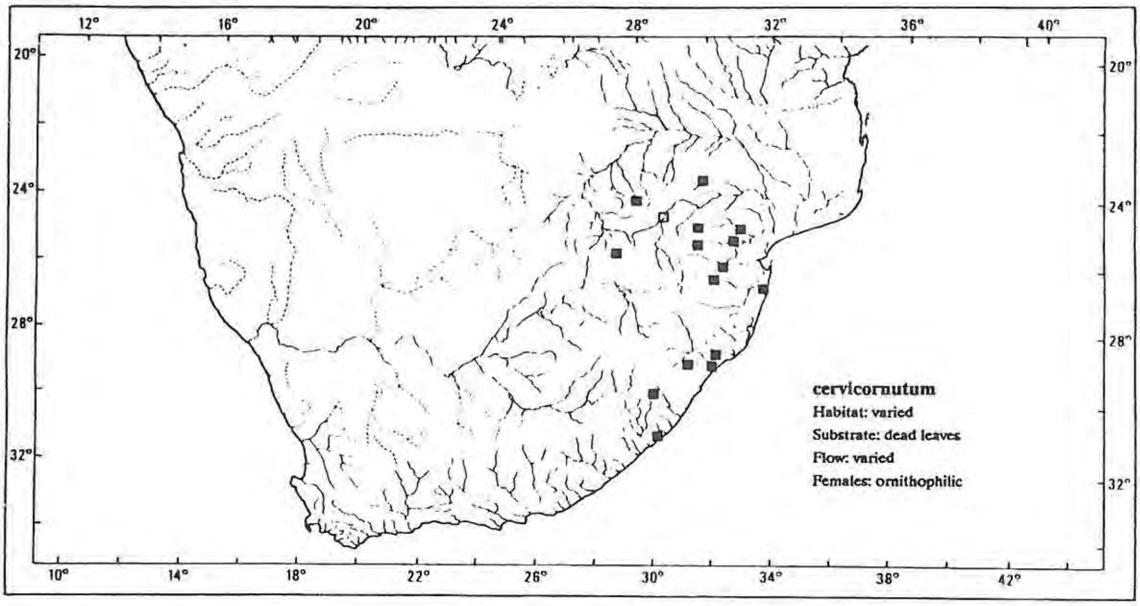


Fig. 8.23 Distribution records of *S. cervicornutum* in southern Africa. Open symbols indicate records from impoundment tailwaters.

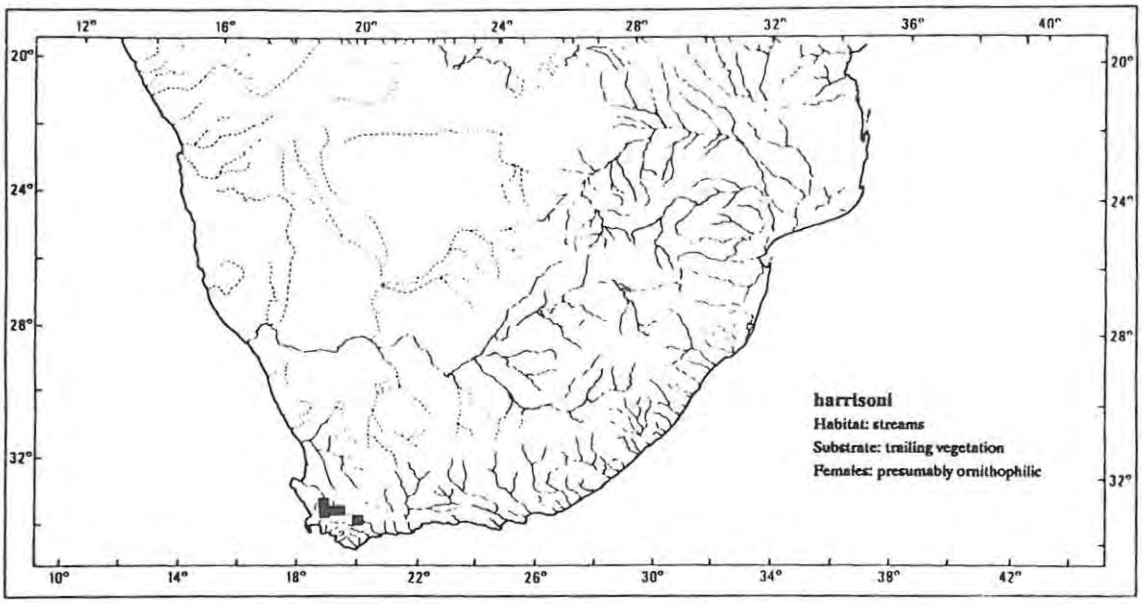


Fig. 8.24 Distribution records of *S. harrisoni* in southern Africa.

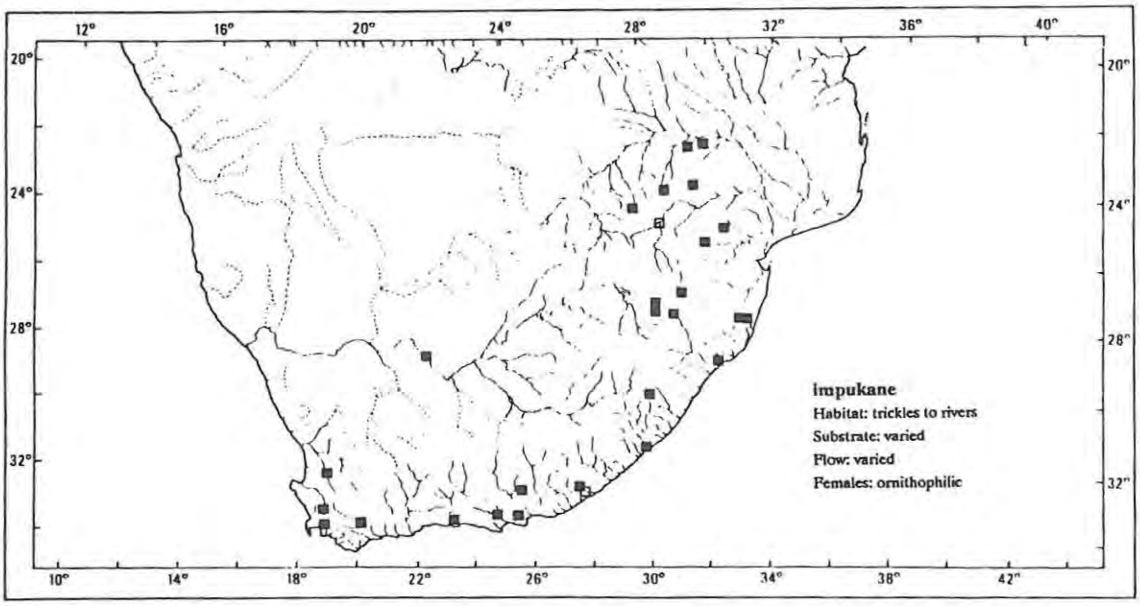


Fig. 8.25 Distribution records of *S. impukane* in southern Africa. Open symbols indicate records from impoundment tailwaters.

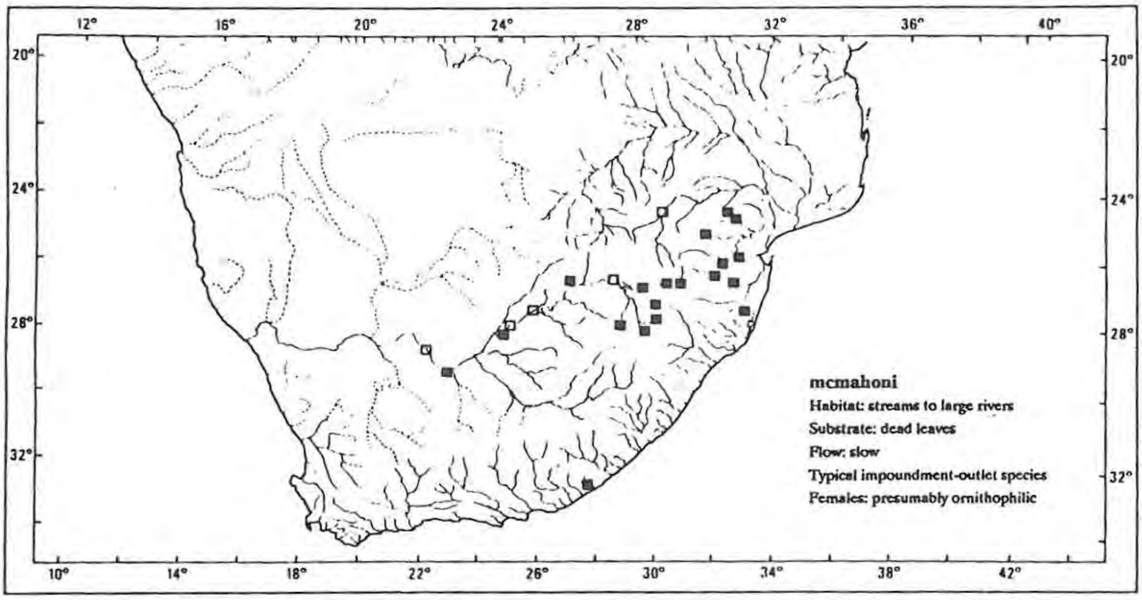


Fig. 8.26 Distribution records of *S. mcmahoni* in southern Africa. Open symbols indicate records from impoundment tailwaters.

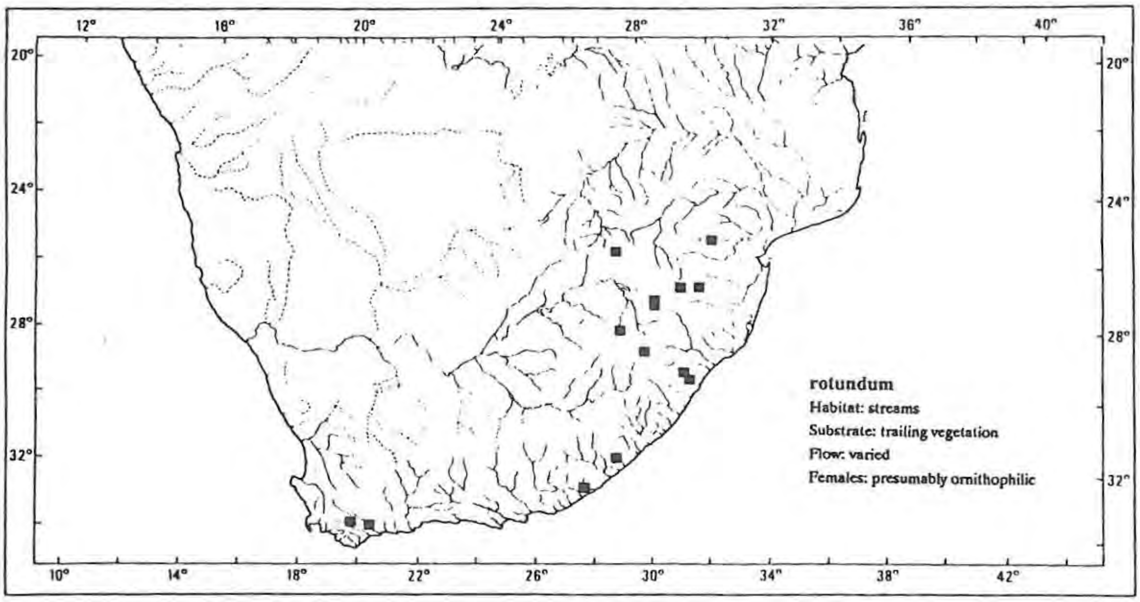


Fig. 8.27 Distribution records of *S. rotundum* in southern Africa.

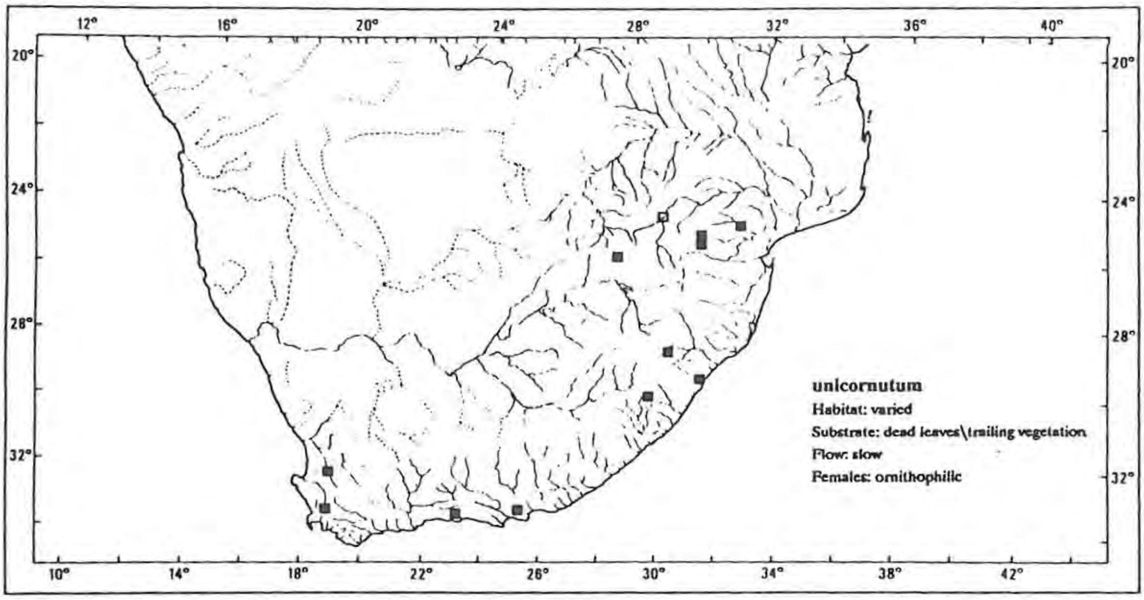


Fig. 8.28 Distribution records of *S. unicornutum* in southern Africa. Open symbols indicate records from impoundment tailwaters.

CONCLUSIONS

This study has provided quantified evidence of the downstream effects of impoundments on the physical, chemical and biotic conditions in the Buffalo River. These effects depended largely on the variable examined, the position of the impoundment along the river profile, the depth from which water was released, and the quality of the inflowing water.

A review of impoundment studies worldwide revealed a logarithmic relationship between river discharge and downstream thermal recovery, and provides a useful tool for predicting the thermal effects of impoundments.

Impoundments which received water from a near-pristine upper catchment, Maden (B1) and Rooikrans (B2), caused alterations of the water quality which were consistent with the Serial Discontinuity Concept (Ward & Stanford, 1983), and recovery to riverine conditions was within 2.6 to 18.4 km, depending on flow. Impoundments which received agricultural runoff and urban effluents, Laing (B3) and Bridle Drift (B4), improved the water quality of the downstream reaches (with the exception of nitrate concentrations, which were higher in the tailwaters compared to inflowing water). Impoundments with polluted inflows therefore "reset" the river towards its natural condition. This represents a reversal of the Serial Discontinuity Concept described for pristine rivers. Most of the downstream changes in transported organic matter in the Buffalo River were due to inflows of agricultural and urban effluent. These disturbances to the river caused greater perturbations than did the impoundments. The downstream effects of impoundments on water chemistry and transported material therefore depend on the relative impact of other catchment perturbations. These disturbances become more severe during low flow, and it is during this time that the impoundments have the greatest effect on the river.

The ratio of CPOM:FPOM (1000-4000:250-1000 μm) in transport in the Buffalo River decreased with increasing stream order as a result of inputs of FPOM from pollution sources and from plankton blooms discharged from reservoirs. More than 95% of the dissolved and particulate material in transport was ultra fine (<80 μm). It is concluded that too much emphasis has been placed on coarse material (>1 mm) in theories of river ecosystem functioning.

Taxonomy is the foundation of any biological study because it identifies the fundamental units, and their variation, which are the basis of evolutionary change. The records of several species of blackflies in southern Africa are now believed to be mistaken identities. Seven blackfly taxa were found in impoundment outlets in southern Africa, of which five can be classed as typical 'outlet' taxa. Three of these (*S. damnosum* s.l., *S. medusaeforme*, and *S. hargreavesi*) are pests of sheep and cattle, and two (*S. adersi* and *S. nigritarse*) are pests of poultry. The association of pest blackflies with impoundment outlets has been reported in other parts of Africa, and in some instances, this has been overcome by releasing insecticides from the dam (Barnley, 1953; 1958; Crisp, 1956). The fact that the most common blackflies in southern Africa are those found in impoundment outlets, suggests that the distribution of blackflies in southern Africa is very different today than it was prior to the building of the first dams. Impoundments have favoured species of blackflies that would normally only be found in the middle and lower reaches of a river. Impoundments have therefore shifted the blackfly distribution upstream (*sensu* Ward & Stanford, 1983), and in doing so, have reduced the habitat available for clear-water species. Impoundments in the upper reaches of the

Buffalo River had a more severe impact on the distribution of blackfly species than impoundments further downstream. Taxa which are likely to have reduced in abundance in recent years are members of the subgenus *Pomeroyellum*, usually found in clear, foothill streams. With the increasing human population and changing land-use patterns in southern Africa, rivers are becoming increasingly regulated (Petijean & Davies, 1988). It is likely therefore that problems with blackflies will be aggravated in the future. Species which are likely to succeed in future are those which can withstand polluted conditions and temporary drying (e.g., *S. ruficorne* and *S. nigritarse*), and those which are adapted to turbid conditions (e.g., *S. chutteri*).

The rapid development of resistance to insecticides among blackflies (Adiamah et al., 1986; Kurtak et al., 1987), suggests that the widespread occurrence of sibling species may be a recent development, and that blackflies may be undergoing a phase of emergent speciation, probably tracking environmental changes which have occurred in historical times. The role of competition for limited resources as a catalyst in speciation may therefore be of secondary importance to that of adaptation to changing environmental conditions. An implication of this is that studies of species' environmental requirements are more likely to provide an understanding of blackfly distribution, than studies which examine biotic interactions.

It is recommended that all new impoundments should incorporate variable-depth water outlets, and that planners and engineers should take account of downstream effects and recovery distances when choosing impoundment sites, so that downstream damage to sensitive ecosystems can be avoided or ameliorated. In the Great Fish River, reservoir releases should aim to simulate natural flow conditions, and in doing so, create conditions which are unsuitable for the pest blackfly, *S. chutteri*.

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APPENDICES

Appendix A

CHECKLIST OF SIMULIIDAE FOUND IN SOUTHERN AFRICA

[Adapted from Crosskey (1987a). The list includes all simuliid species known south of (and including) the Limpopo and Orange River catchments. Valid names are printed in bold text, and recognised synonyms are indented and printed in italics. Life cycle stages which are known and described are indicated as follows: **m** = adult male; **f** = adult female; **p** = pupa; **l** = larva.]

PROSIMULIUM Roubaud, 1906

Subg. PARACNEPHIA Rubtsov, 1962
- **barnardi** (Gibbins, 1938) (**m, p**)
- **brincki** (de Meillon, 1955) (**m, f, p, l**)
- **harrisoni** (Freeman & de Meillon, 1953) (**m, f, p**)
- **muspratti** (Freeman & de Meillon, 1953) (**m, f, p, l**)
- **thornei** (de Meillon, 1955) (**m, f, p, l**)
- **turneri** (Gibbins, 1938) (**f**)

SIMULIUM Latreille, 1802

Subg. AFROSIMULIUM Crosskey, 1969
- **gariepense** de Meillon, 1953 (**m, f, p, l**)

Subg. ANASOLEN Enderlein, 1930
- **dentulosum** Roubaud, 1915 (**m, f, p, l**)
  - *gilvipes* Pomeroy, 1920
  - *adolffriedericianum* Enderlein, 1930
  - *ruwenzoriense* Gibbins, 1934
  - *emfulae* de Meillon, 1937
  - *britannicum* Davies, 1966
  - *altissimum* Fain, Bafort & Silberstein, 1977
  - *bambusicola* Fain, Bafort & Silberstein, 1977
  - *trifurcatum* Fain, Bafort & Silberstein, 1976

Subg. BYSSODON Enderlein, 1925

Group 1: GRISEICOLLE species-group
- **griseicolle** Becker, 1903 (**m, f, p, l**)
  - *scapulatum* (Enderlein, 1935)
  - *dentulatum* Wanson & Henrard, 1944

Subg. EDWARDSELLUM Enderlein, 1921
- **damnosum** Theobald, 1903 (**m, f, p, l**)(complex)
  - *cingulatum* (Enderlein, 1921)

Subg. FREEMANELLUM Crosskey, 1969
  debegene de Meillon, 1934 (m, f, p, l)
  empopomae de Meillon, 1937 (m, p)
  hessei Gibbins, 1941 (m, f, p, l)
  hirsutilateris de Meillon, 1937 (m, p)

Subg. MEILLONIELLUM Rubtsov, 1962
  adersi Pomeroy, 1922 (m, f, p, l)
  hirsutum Pomeroy, 1922 (m, f, p, l)
    dubium Pomeroy, 1922

Subg. METOMPHALUS Enderlein, 1935
  bovis de Meillon, 1930 (m, f, p, l)
    faini Wanson, 1947
    ulangae Lewis & Raybould, 1974
  chutteri Lewis, 1965 (m, f, p, l)
  hargreavesi Gibbins, 1934 (m, f, p, l)
    elgonense Gibbins, 1934
    tisiphone de Meillon, 1936
    loangolense Roubaud & Grenier, 1943
  letabum de Meillon, 1935 (m, f, p, l)
  medusaeforme Pomeroy, 1920 (m, f, p, l)
    ugandae Gibbins, 1934
    capense (Enderlein, 1935)
    caffrum (Enderlein, 1935)
    pseudomedusaeforme de Meillon, 1936
    angolense Abreu, 1961
  natalense de Meillon, 1950 (m, f, p)
  vorax Pomeroy, 1922 (m, f, p, l)
    limbatum Enderlein, 1921
    lepidum de Meillon, 1935
    tangae Smart, 1944
  wellmanni Roubaud, 1906 (m, f, p, l)
    magoebae de Meillon, 1935

Subg. NEVERMANNIA Enderlein, 1921

Group 2: LOUTETENSE species-group
  narcaeum de Meillon, 1950 (m, f, p)
  rutherfoordi de Meillon, 1937 (m, f, p, l)

Group 3: RUFICORNE species-group
  brachium Gibbins, 1936 (m, f, p, l)
  katangae Fain, 1951 (m, f, p, l)
  nigritarse Coquillett, 1902 (m, f, p, l)
    caffraricum (Enderlein, 1935)
  ruficorne Macquart, 1838 (m, f, p, l)
    beckeri Roubaud, 1906
    annulipes Becker, 1908
    divergens Pomeroy, 1922
    diversipes Edwards, 1923

Subg. POMEROYELLUM Rubtsov, 1962
alcocki Pomeroy, 1922 (**m, f, p, l**)
kenyanum Sguy, 1938
henrardi Gibbins, 1941
bequaerti Gibbins, 1936 (**m, f, p, l**)
phoroniforme de Meillon, 1937
cervicornutum Pomeroy, 1920 (**m, f, p, l**)
harrisoni Freeman & de Meillon, 1953 (**m, f, p, l**)
impukane de Meillon, 1936 (**m, f, p, l**)
mcmahoni de Meillon, 1940 (**m, f, p, l**)
altipartitum Roubaud & Grenier, 1943
merops de Meillon, 1950 (**m, f, p, l**)
rotundum Gibbins, 1936 (**m, f, p, l**)
unicornutum Pomeroy, 1920 (**m, f, p, l**)
monoceros Roubaud & Grenier, 1943
wolfsi Wanson & Henrard, 1944
bertrandi Luna de Carvalho, 1962

Uncertain Records

PROSIMULIUM Roubaud, 1906

Subg. PARACNEPHIA Rubtsov, 1962
herero (Enderlein, 1935) (**f**)
[Only known from a single locality in Namibia (Freeman & de Meillon, 1953).]

Subg. PROCNEPHIA Crosskey, 1969
damarense (de Meillon & Hardy, 1951) (**m, f, p**)
[Only known from the Brandberg, Namibia (Freeman & de Meillon, 1953).]

rhodesianum Crosskey, 1968 (**m, f, p, l**)
[Only known from a single locality in Zimbabwe.]

SIMULIUM Latreille, 1802

Subg. ANASOLEN Enderlein, 1930

rhodesiense de Meillon, 1942 (**m, f, p**)
[Only known from a single locality in Zimbabwe.]

Subg. METOMPHALUS Enderlein, 1935
arnoldi Gibbins, 1937 (**m, f, p, l**)
[Known as far south as the Victoria Falls (Gibbins, 1937a; Lewis, 1964b; de Meillon, 1955). Records from Natal (Gibbins, 1938) are likely to have been misidentified *S. bovis*.]

Subg. NEVERMANNIA Enderlein, 1921
simplex Gibbins, 1936 (**m, f, p, l**)
elgonicum Sguy, 1938
[Known from Uganda, Kenya, and Zaire (Fain & du Jardin, 1983). Although recorded in Zimbabwe by Meeser (1942) and in the Cape Peninsula by Gibbins (1938), the larvae of this species are easily confused with *S. nigritarse*, *S. brachium*, and *S. rutherfoordi*.]

Subg. PHORETOMYIA Crosskey, 1969
lumbwanum de Meillon, 1944 (**m, f, p, l**)
lerabanum Gouteux, 1979

[Recorded as far south as the Victoria Falls (Freeman & de Meillon, 1953) and the Okavango River (Windhoek State Museum).]

Subg. POMEROYELLUM Rubtsov, 1962
evillense Fain, Hallot & Bafort, 1966 (**f, p**)

[Recorded as far south as the Okavango Swamps (Johnson et al., 1982).]

garmsi Crosskey, 1969 (**m, f, p, l**)
violaceum Pomeroy, 1922 (preocc.)
occidentale Freeman & de Meillon, 1953 (preocc.)

[A West African species recorded in the Coleford Nature Reserve by Paterson (1979), and in the Vaal catchment (as *S. alcocki occidentale*) by Chutter (1970). It is easily confused with *S. alcocki*.]

tentaculum Gibbins, 1936 (**m, f, p, l**)

[Recorded by Gibbins (1938) from Orange Kloof, Cape Peninsula, although most likely misidentified *S. merops*.]

Appendix B

Specifications of sampling sites in the Buffalo River. Stream order was based on 1:50,000 scale topographical maps (Strahler, 1957). Stream width (m) was taken as bankfull width, 'D/S' refers to distance from source (km) and 'D/I' refers to distance from upstream impoundment (km). The positions of the four mainstream impoundments (**B1** to **B4**) are indicated.

Site	Alt. (m)	Order	Width (m)	D/S (km)	D/I (km)	Grid Ref. South	Grid Ref. East	Name	
0	1120	1	1	0.9	-6.0	32.43.00	27.14.50	Evelyn Valley	
1	530	3	14	6.9	-1.0	32.44.00	27.17.45	Weir R2M01	
									B1
2b	518	3	14	8.1	0.2	32.44.28	27.18.06	Below Maden Dam	
2c	515	3	14	9.4	1.4	32.44.55	17.18.18	Above Rooikrans Dam	
									B2
3	492	3	6	12.8	0.3	32.45.30	27.19.32	Below Rooikrans Dam	
4	470	3	17	15.0	2.6	32.45.45	27.20.52	Cecilia Farm	
5	450	3	10	18.0	6.4	32.46.15	27.21.45	Two Rivers Farm	
6	410	4	11	30.8	18.4	32.49.15	27.22.45	Ciskei Defence Force	
7	370	4	12	39.1	27.1	32.51.22	27.23.08	Still Water Farm	
8	310	4	32	58.0	44.1	32.56.22	27.27.42	Weir R2M10	
									B3
9	270	4	43	66.4	0.5	32.58.10	27.29.25	Below Laing Dam	
10a	210	4	23	81.4	15.5	32.56.36	27.34.15	Dongwe	
10b	156	4	13	95.0	29.0	32.59.28	27.38.30	Potsdam	
									B4
11	109	4	23	109.0	0.1	32.59.30	27.43.45	Below Bridle Drift Dam	
12	50	4	26	116.0	7.0	32.59.28	27.46.38	Amanzi Farm, below wier	
13	25	4	?	123.0	14.5	32.59.45	27.47.45	Buffalo Pass bridge	

Appendix C

Publications

Palmer, R. W. & O'Keeffe, J. H. 1989. Temperature characteristics of an impounded river. Arch. Hydrobiol. **116**(4): 471-485.

Palmer, R. W. & O'Keeffe, J. H. 1990. Downstream effects of impoundments on the water chemistry of the Buffalo River (Eastern Cape), South Africa. Hydrobiologia. **202:** 71-83.

Palmer, R. W. & O'Keeffe, J. H. 1990. Transported material in a small river with multiple impoundments. Freshwater Biology. **24:** 563-575.

Palmer, R. W. and O'Keeffe, J. H. 1990. Downstream effects of a small impoundment on a turbid river. Arch. Hydrobiol. **119(4)**: 457-473.

O'Keeffe, J. H., Palmer, R. W., Byren, B. A., & Davies, B. R. 1990. The effects of impoundment on the physicochemistry of two contrasting southern African river systems. Regulated Rivers: Research and Management **5**: 97-110.

Palmer. R. W. 1991. Descriptions of the larvae of seven species of blackflies (Diptera: Simuliidae) from South Africa, and a regional checklist of the family. J. ent. Soc. sth. Afr. **54(2)**: 000-000.

"Ecological effects of impoundments..."

[Ammendements to PhD thesis by R. W. Palmer, 1991.]

Addendum:

Glossary

CPOM	Coarse particulate organic matter: The mass of suspended organic (combustable) material which is retained by a 1 mm mesh sieve.
Cfbl	Humid temperate climate: C = At least one month with mean temperature below 18°C and at least eight months with mean temperature above 1°C; coldest month above -3°C; f = Precipitation during the driest month exceeds one-tenth that of the wettest month; b = Mean temperature of warmest month below 22°C; l = Mean temperatures of all months between 10 and 22°C (Schülze 1965).
Cfwb	Same as above; w = Dry season in winter.
FPOM	Fine particulate organic material: The mass of suspended organic (combustable) material within the size range 250 - 1000 µm.
POM	Particulate organic material: The mass of suspended organic (combustable) material retained by a Whatman^{R} GF/C filter (pore size approximately 0.6 µm).
Recovery	That length of stream which is required for any parameter to return to values close to those measured at the inflow to an impoundment, or to achieve a new dynamic equilibrium.
Riverine conditions	Unperturbed: where organic material is derived from natural in-stream and/or riparian sources, as described by the River Continuum Concept (Vannote & Sweeney, 1980).
Total suspended solids	The mass of organic and inorganic material suspended in the water coloumn which is retained by a Whatman^{R} GF/C filter (pore size approximately 0.6 µm).

Errata

piii. first line: Distribution and abundance of blackflies in the Buffalo River (insert of).

piv. line 23: No hyphen in "upperreaches".

p2. para. 1, line 8: Publication date for Lillelhammer & Saltviet 1984 (not 1982).

p3. line 19: Howell et al 1981 (insert l).

p37. para. 2, line 1: Water samples were collected at roughly monthly intervals between April 1986 and April 1988 (insert 1986).

p42. Table 4.1: Median composition of major ions in the Buffalo River, expressed as a percentage of their total molarities, at Site 0, and the range of median values at Sites 1 to 13 (insert underlined text).

p57. Table 5.2: The percentage of total suspended material...... (replace "transported" with "suspended).

p175. line 1: 20b1°C should read 20±1°C.

p226. 2nd last line: Publication date for Lillelhammer & Saltviet 1984 (not 1982).

Appendix D. Summary statistics of chemical data collected at 16 sites in the Buffalo River at roughly monthly intervals between April 1986 and April 1988. The positions of impoundments (B1 to B4) are indicated. [Med=median, Av=arithmetic mean, SD=standard deviation, n=sample size.]

	Conductivity (mS/m)					
Site	Med	Av	SD	n	min	max
0	3	3	1	16	2	7
1	7	9	2	23	4	13
---B1						
2b	7	10	6	25	5	28
2c	8	9	4	18	5	18
---B2						
3	9	9	2	28	6	17
4	12	12	4	22	6	21
5	12	12	3	24	6	19
6	37	36	17	27	11	74
7	37	39	19	16	12	71
8	75	74	40	24	18	160
---B3						
9	55	55	11	23	39	78
10a	58	58	12	23	39	75
10b	66	69	24	16	39	118
---B4						
11	52	52	6	23	40	62
12	53	53	4	21	47	65
13	70	75	31	21	46	200

	Turbidity (NTU)					
Site	Med	Av	SD	n	min	max
0	4	5	2	15	2	8
1	2	3	2	21	2	8
---B1						
2b	4	5	4	21	2	18
2c	4	5	4	21	2	17
---B2						
3	5	8	15	24	2	78
4	6	8	7	23	2	39
5	7	8	4	22	3	22
6	7	16	18	23	2	65
7	7	14	14	17	2	45
8	16	43	63	23	5	290
---B3						
9	36	37	22	22	4	80
10a	38	44	26	21	17	125
10b	28	32	19	16	6	70
---B4						
11	65	66	35	22	17	140
12	54	57	29	21	17	130
13	14	23	21	20	4	74

	pH					
Site	Med	Av	SD	n	min	max
0	6.1	6.1	0.5	15	5.3	7.3
1	7.2	7.0	0.4	21	6.3	7.6
---B1						
2b	7.1	7.1	0.5	24	6.4	8.7
2c	7.1	6.9	0.3	19	6.2	7.4
---B2						
3	7.2	7.2	0.4	26	6.5	8.5
4	7.2	7.2	0.5	20	6.3	8.4
5	7.2	7.3	0.4	23	6.6	8.3
6	7.6	7.6	0.3	25	7.0	8.2
7	8.0	7.9	0.4	15	7.1	8.4
8	7.8	7.8	0.6	23	6.7	9.6
---B3						
9	8.1	8.2	0.5	21	7.5	9.5
10a	8.2	8.2	0.5	22	7.0	9.5
10b	8.3	8.2	0.4	15	7.1	8.7
---B4						
11	7.9	7.9	0.4	22	7.0	8.6
12	8.3	8.2	0.4	19	7.6	8.9
13	7.8	7.8	0.5	22	6.9	9.2

	Alkalinity (mg/l)					
Site	Med	Av	SD	n	min	max
0	5	5	2	15	3	10
1	15	17	6	23	11	30
---B1						
2b	18	24	16	26	10	70
2c	14	16	5	21	11	26
---B2						
3	19	21	13	29	13	86
4	26	28	12	22	16	59
5	26	28	8	24	17	49
6	82	81	42	27	28	196
7	72	74	32	16	28	124
8	113	126	68	24	42	275
---B3						
9	86	91	20	23	52	137
10a	98	97	20	23	52	139
10b	98	97	19	16	51	123
---B4						
11	80	81	7	22	72	98
12	81	81	5	21	73	94
13	77	72	17	23	42	106

Appendix D (cont.)

Site	Chlorophyll a (µg/l) Med	Av	SD	n	min	max	
0	0.1	0.1	0.1	14	0.0	0.4	
1	0.1	0.2	0.1	18	0.0	0.6	
							B1
2b	0.7	0.8	0.4	18	0.2	1.9	
2c	0.7	0.9	0.7	20	0.1	2.9	
							B2
3	1.4	1.6	0.9	19	0.3	3.6	
4	0.7	1.2	0.9	18	0.2	3.7	
5	1.0	1.3	1.2	18	0.1	4.0	
6	2.2	2.2	1.6	18	0.3	6.2	
7	1.6	2.0	1.8	17	0.1	5.5	
8	13.1	18.3	16.5	20	0.5	54.0	
							B3
9	2.3	7.9	10.4	19	0.3	40.0	
10a	4.5	7.2	8.1	19	0.5	26.6	
10b	3.2	5.1	4.5	17	0.2	16.6	
							B4
11	1.7	2.1	1.8	18	0.0	8.5	
12	1.2	2.0	1.9	19	0.1	7.6	
13	5.6	10.5	14.1	18	0.4	54.5	

Site	Nitrite (µmol/l) Med	Av	SD	n	min	max	
0	0.11	0.33	0.31	15	0.02	0.80	
1	0.16	0.40	0.48	22	0.01	1.96	
							B1
2b	0.22	0.43	0.50	23	0.08	2.11	
2c	0.13	0.36	0.52	21	0.03	2.16	
							B2
3	0.22	0.35	0.37	25	0.03	1.40	
4	0.27	0.45	0.57	21	0.06	2.60	
5	0.23	0.46	0.56	23	0.08	2.60	
6	0.51	0.72	0.68	25	0.12	2.70	
7	0.57	0.68	0.64	16	0.13	2.50	
8	12.80	24.95	27.55	24	0.17	84.00	
							B3
9	0.29	0.39	0.28	23	0.04	0.86	
10a	0.21	0.34	0.29	23	0.04	1.23	
10b	0.30	0.46	0.47	16	0.04	1.75	
							B4
11	0.40	0.77	1.41	23	0.04	6.80	
12	0.48	0.54	0.43	21	0.04	1.50	
13	14.50	34.42	57.15	23	0.08	255.00	

Site	Nitrate (µmol/l) Med	Av	SD	n	min	max	
0	6.0	5.6	2.1	15	1.0	8.3	
1	6.7	7.1	3.0	22	1.9	12.8	
							B1
2b	4.4	5.4	3.8	23	0.4	15.0	
2c	4.1	4.5	3.2	21	0.0	11.3	
							B2
3	2.0	4.1	5.2	28	0.2	20.0	
4	2.8	7.1	10.4	21	0.4	41.6	
5	5.5	8.8	11.1	23	0.5	49.0	
6	11.2	20.2	18.2	25	2.0	73.0	
7	8.9	12.4	11.3	16	3.5	46.3	
8	111.5	126.4	130.8	24	15.5	526.0	
							B3
9	43.0	42.2	31.5	23	0.2	136.0	
10a	30.1	27.3	25.3	23	0.0	72.0	
10b	2.7	14.9	18.8	16	0.1	52.0	
							B4
11	52.0	57.3	27.1	23	22.0	150.0	
12	55.0	54.0	16.1	21	28.1	78.0	
13	330.0	412.6	287.6	21	78.0	896.0	

Site	Ammonium (µmol/l) Med	Av	SD	n	min	max	
0	0.48	0.58	0.62	15	0.02	2.50	
1	0.33	0.57	0.58	22	0.02	2.30	
							B1
2b	1.20	1.56	2.72	23	0.02	13.60	
2c	0.34	0.51	0.45	21	0.03	1.40	
							B2
3	0.90	0.97	0.76	25	0.04	2.75	
4	0.55	0.72	0.64	21	0.03	2.30	
5	0.82	0.96	0.91	23	0.03	3.30	
6	1.30	3.03	6.45	25	0.03	26.00	
7	0.71	1.05	0.81	16	0.04	2.40	
8	18.80	88.20	177.55	24	0.06	800.00	
							B3
9	0.94	9.20	36.61	23	0.28	177.00	
10a	0.72	2.06	4.47	23	0.17	22.00	
10b	0.90	1.11	0.77	16	0.17	2.50	
							B4
11	0.90	4.04	8.23	23	0.11	30.00	
12	0.94	1.02	0.73	20	0.12	2.20	
13	32.00	46.18	57.94	23	0.30	236.00	

Appendix D (cont.)

Site	Soluble reactive phosphate (µmol/l) Med	Av	SD	n	min	max
0	0.5	0.5	0.3	15	0.0	1.0
1	0.5	0.9	1.3	22	0.0	6.0
---B1						
2b	0.7	2.9	7.4	23	0.1	35.0
2c	0.7	6.3	24.7	21	0.0	114.0
---B2						
3	0.4	1.0	2.0	25	0.0	10.0
4	0.6	0.7	0.6	22	0.0	3.0
5	0.5	0.9	1.8	23	0.0	9.2
6	0.7	0.9	1.0	25	0.0	5.0
7	0.8	0.8	0.3	16	0.0	1.3
8	30.6	45.3	68.9	23	0.6	338.0
---B3						
9	1.5	4.6	13.2	23	0.1	65.0
10a	1.1	1.3	1.1	23	0.1	5.0
10b	1.0	0.9	0.5	16	0.1	2.2
---B4						
11	1.0	1.5	2.1	23	0.2	10.5
12	1.2	1.3	1.0	21	0.2	3.6
13	103.0	101.7	79.8	23	0.3	292.0

Site	Oxygen (% saturation) Med	Av	SD	n	min	max
0	72	87	31	13	50	153
1	95	94	17	18	64	122
---B1						
2b	97	92	19	17	56	118
2c	88	86	16	20	57	112
---B2						
3	100	101	19	20	75	160
4	88	92	25	19	59	152
5	79	88	25	19	59	154
6	91	94	26	20	64	162
7	92	102	24	16	73	156
8	88	89	23	20	57	160
---B3						
9	99	98	33	19	6	168
10a	104	104	17	19	68	131
10b	98	101	23	14	73	148
---B4						
11	93	93	20	18	40	125
12	98	102	25	20	70	160
13	101	110	34	18	71	187

Site	Chloride (mg/l) Med	Av	SD	n	min	max
0	11	12	1	15	10	15
1	15	16	3	20	13	24
---B1						
2b	16	20	9	21	13	43
2c	15	17	5	20	11	30
---B2						
3	16	17	2	25	14	24
4	18	19	4	22	15	30
5	19	20	4	22	15	30
6	49	47	19	23	22	73
7	49	59	30	17	24	106
8	101	101	51	21	29	195
---B3						
9	80	83	21	19	49	125
10a	93	91	24	20	53	135
10b	114	122	56	16	54	250
---B4						
11	84	82	6	20	71	93
12	83	83	5	21	73	92
13	117	132	89	19	78	490

Site	Magnesium (mg/l) Med	Av	SD	n	min	max
0	0.4	0.4	0.1	14	0.1	0.6
1	1.6	1.7	0.6	21	0.8	3.2
---B1						
2b	1.9	2.5	2.1	23	0.9	8.4
2c	1.5	1.8	0.7	20	0.8	3.6
---B2						
3	2.0	1.8	0.5	25	0.3	3.0
4	2.1	2.2	0.9	23	0.2	4.0
5	2.4	2.5	0.7	22	1.1	4.0
6	10.9	10.4	6.6	25	1.5	27.0
7	9.5	10.7	6.1	15	2.8	19.4
8	13.0	12.7	6.4	23	3.6	28.0
---B3						
9	11.1	10.9	3.8	22	3.2	21.5
10a	12.2	11.6	4.1	22	4.5	18.2
10b	13.7	13.6	5.3	14	5.4	21.4
---B4						
11	9.9	9.1	2.9	21	2.8	13.3
12	9.9	9.2	2.5	20	3.3	12.4
13	12.4	12.3	2.2	23	4.8	15.6

	Calcium (mg/l)						
Site	Med	Av	SD	n	min	max	
0	0.1	0.2	0.2	14	0.0	0.7	
1	1.7	1.8	1.1	21	0.2	4.8	
							B1
2b	2.8	3.7	3.4	23	0.2	12.1	
2c	1.8	1.7	0.8	19	0.1	3.3	
							B2
3	2.4	2.5	1.1	25	0.6	5.0	
4	2.6	3.1	1.7	23	0.2	7.3	
5	3.1	3.6	1.5	22	2.0	6.8	
6	10.7	11.9	7.1	26	3.0	28.0	
7	11.8	12.6	6.7	15	4.4	25.0	
8	19.0	19.3	11.0	23	5.6	48.0	
							B3
9	13.9	14.1	3.3	22	8.7	22.0	
10a	15.5	15.7	4.7	22	8.2	25.6	
10b	18.0	18.5	8.2	15	8.7	42.5	
							B4
11	12.0	12.3	3.0	21	6.1	17.9	
12	12.2	12.1	2.4	20	8.1	16.8	
13	18.0	17.1	3.4	23	9.7	23.0	

	Sodium (mg/l)						
Site	Med	Av	SD	n	min	max	
0	3	3	1	14	2	4	
1	6	7	2	21	4	11	
							B1
2b	6	8	5	23	3	22	
2c	6	6	2	20	4	11	
							B2
3	7	7	3	28	2	22	
4	9	10	5	22	1	24	
5	10	11	4	23	6	20	
6	30	31	19	25	8	80	
7	30	30	14	15	9	51	
8	71	79	61	23	17	240	
							B3
9	52	50	21	21	21	92	
10a	62	55	24	22	24	94	
10b	76	64	29	15	26	104	
							B4
11	45	40	14	21	17	61	
12	44	40	14	20	20	63	
13	69	72	53	21	23	280	

	Potassium (mg/l)						
Site	Med	Av	SD	n	min	max	
0	0.2	0.2	0.1	13	0.1	0.3	
1	0.4	0.4	0.2	20	0.1	1.1	
							B1
2b	0.4	0.5	0.2	22	0.1	1.2	
2c	0.4	0.5	0.3	20	0.2	1.4	
							B2
3	0.5	0.5	0.3	25	0.1	1.9	
4	0.5	0.6	0.2	22	0.2	0.9	
5	0.6	0.6	0.2	22	0.3	1.0	
6	1.1	1.1	0.4	24	0.5	2.1	
7	1.2	1.2	0.5	15	0.6	2.2	
8	4.4	8.6	14.9	23	1.1	68.0	
							B3
9	2.5	4.5	6.3	21	1.7	24.0	
10a	2.3	2.4	0.5	22	1.6	3.3	
10b	2.4	2.4	0.5	15	1.6	3.3	
							B4
11	2.9	2.9	0.9	21	1.3	4.6	
12	2.6	2.8	0.7	20	1.6	4.3	
13	9.3	8.6	3.5	23	1.9	14.3	