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Michael Hubbard

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Edited by

M. J. A. WERGER

with the assistance of
A. C. VAN BRUGGEN
for the zoological chapters

FRESHWATER INVERTEBRATES
(EXCEPT MOLLUSCS)

by

A. D. HARRISON



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4 Freshwater invertebrates (except molluscs)

A. D. Harrison

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1. Introduction

A study of the biogeography of freshwater invertebrates of the African continent below the latitude of 10°S requires a consideration of global implications. In this chapter discussion is mainly of riverine forms and attempts to elucidate their origin and to place them into useful ecological categories.

Many biogeographers follow Darwin in postulating that a new species of organism comes into being in one relatively small spot on the earth's surface and then radiates outwards from this centre of origin along suitable dispersal routes to colonize new regions, some, perhaps, ultimately very far from the source. Subsequent new species are thought to arise when the dispersal routes which link the origin with the new colonies are broken and genetic exchange ceases. This type of long distance dispersal undoubtedly has occurred often, in both plants and animals, especially in those groups which have strong fliers or resistant, wind-borne propagules. This theory implies that any given species must have had its ancestral home somewhere else.

However, an opposite theory can be advanced for any species in any place, namely, that it is descended from an ancestral line which has been in the same place, more or less, through many geological ages. As no species can be completely divorced from the biota to which it belongs, it follows that such an entire biota may have ancient ancestral roots of this same type.

Also, it should be remembered that many individual species of organisms are not limited to small areas but are each spread over wide regions of the earth's surface. A slow gene-flow keeps each of these widespread species either fairly uniform or evolving in the same direction in all parts of its range, even although distinguishable clines or races may appear. When the range of such a widespread single species is broken up by a new major physical or other type of barrier, many parallel or allopatric populations may be cut off and from these new species may develop. These new species may found a new higher taxon which already starts off with a wide distribution without the need of long distance migration along special dispersal routes for every species. This fraternal ('allopatric' or 'vicariant') speciation is discussed in detail by Croizat et al. (1974) and Rosen (1975). They point out that a whole ancestral biota can be fragmented in this way into a number of allopatric or vicariant biotas.

2. Fauna of continental southern Africa

The freshwater invertebrate fauna of southern Africa (Harrison 1965b) appears to consist of elements which have reached their present position both by long distance dispersal from such regions as the Palaearctic and by allopatric speciation with the rest of the biota following the breakup of Gondwanaland. This fauna consists of two major groupings, the South Temperate Gondwanian and the Pan-Ethiopian.

2.1 *South Temperate Gondwanian fauna*

K. H. Barnard (1927), writing on freshwater isopods and amphipods from the Southwestern Cape region, first referred to the usefulness of Wegener's Continental Drift theory in explaining the relationships between the freshwater faunas of the southernmost tips of the southern continents. Similar relationships have been established by subsequent workers, who have noted also that the faunas of southern South America and southern Australia are more closely related to each other than they are to that of South Africa.

Modern theories of plate tectonics suggest that Africa, in early Jurassic times, lay well to the south of its present position and was joined to a more northerly-lying Antarctica as well as to South America and Australasia. Madagascar, India and other fragments formed parts of the same Gondwanaland-complex (Dietz & Holden 1970). Therefore large parts of southern Africa must have been in south-temperate regions, with the south coast being very much cooler and wetter than it is today (see Axelrod & Raven Chapter 5). Northwards, Africa was connected to South America through the whole temperate zone, the sub-tropics and the tropics. Therefore tropical Gondwanaland, which finally broke up in the Cretaceous, must have been a very large land mass, larger than any tropical land mass existing at present.

During later Jurassic times Africa and South America moved northward and Africa broke away from south-temperate Gondwanaland before the further break-up of the latter into the remaining present southern land masses and India. The south-temperate freshwater faunas of southern Africa and the Gondwanaland remainder thus became allopatric, and divergent evolution was reinforced by the fact that Africa was moving northward into warmer climatic zones. In fact, it appears that much of the original south-temperate zone actually moved into the subtropics and the subtropical zone moved into the tropics proper.

It is clear therefore that in southern Africa many cold-adapted species, in fact whole groups of cold-adapted organisms, must have become extinct. An obvious example is that of the Siphonuridae (Ephemeroptera), a primitive group which radiated early throughout Pangea (Edmunds 1972) and is still well established in the other southern continents and the Holarctic. It must once have existed in southern Africa but is now absent.

The same thing seems to have happened with the southern stoneflies. The Antarctoperlaria and Notonemouridae (Plecoptera) are very characteristic south-temperate forms (Illies 1960, 1965, Zwick 1973), but only the Notonemouridae are still to be found in South Africa and refugial regions in Madagascar.

Some cold-adapted Gondwanian groups are still extant and are part of what Stuckenberg (1962) calls the palaeogenic fauna. Most of these probably only survived because of the tectonic uplift of the subcontinent, the formation of the eastern escarpment mountains and later the Cape Fold belt, each occurring in time to give them the high altitudes of mountain refugia. These freshwater invertebrates are typical of the upper zones of montane rivers and streams, the 'rithron' of Illies (1961a) and Harrison (1965a).

Examples of these surviving Gondwanian forms include the Leptophlebiidae (Ephemeroptera), which have been worked out well by Tsui & Peters (1975). They consider that the following southern African genera fall into this group: *Adenophlebia*, *Adenophlebiodes* (*Adenophlebiodes*), *A.* (*Hyalophlebia*) and

Aprionyx. Adenophlebia and *Aprionyx* have cold, stenothermal species which must have been widespread in the Mesozoic when the climate of the subcontinent was probably cooler (Balinsky 1962) but which eventually could exist only in the cooler montane streams, preferably tree-shaded, where they are found at present.

The two subgenera of *Adenophlebiodes* form a hardier, more eurythermal line which can stand higher maximum temperatures and more silt in the environment. These are found in warmer and slower-flowing streams from northern South Africa into the tropics. This seems to have been a rather rare performance by a southern Gondwanian group, but it is not unique.

According to Ball (1974) the Dugesiidae (Platyhelminthes: Turbellaria) also had an austral origin in southern Gondwanaland and thence radiated into the southern continents. The subgenus *Dugesia* (of the genus *Dugesia*) arose in Africa after its separation; it then spread widely over the continent and, after the closing of the Tethys Sea, was able to colonize the Palearctic and move eastwards into India and southeastern Asia.

Another more eurythermal group includes species of the ostracod genus *Gomphocythere* (Limnocytherinae) which are found in all the southern continents but are not limited to colder regions and in Africa are found as far north as Ethiopia (McKenzie & Hussainy 1968).

Harrison (1965b) lists a number of palaeo-endemic, montane forms, some of which appear to be Gondwanian in origin. In addition to the Leptophlebiidae, other groups which have been compared in detail to Gondwanian groups from other continents are the Notonemouridae (Plecoptera) (Illies 1961b, 1966, Zwick 1973), and the Podonomiidae (Diptera: Chironomidae) (Brundin 1966).

Altogether all these species account for very little of the southern African freshwater fauna.

2.2 Pan-Ethiopian fauna

The bulk of the freshwater fauna of southern Africa is closely related to that of the whole of tropical Africa and forms a truly Pan-Ethiopian (Sub-Saharan) element (Harrison 1965b). Nevertheless, it is now obvious that its affinities are more complicated than previously suggested and that it probably comes from two main sources.

First, there is the original biota of the vast tropical Gondwanaland which broke up, apparently, during the Cretaceous. Krömmelbein (1966) presents interesting evidence of the original sympatry of South American and African freshwater ostracods from what are, apparently, upper Jurassic strata. He concludes that specimens collected from northeastern Brazil and West Africa are parts of one original assemblage in one basin with completely free interchange.

Edmunds (1972), reviewing the biogeography and evolution of the Ephemeroptera states, 'the distribution of many groups of mayflies suggests a tropical connection or near-connection of Africa and South America persisting at a later date than the detachment of Africa from Gondwanaland in the south. Some of the Neotropical mayfly fauna invaded Central and North America, and there are numerous invasions of the Oriental Region (and to a lesser extent of the Palearctic and Australian regions) by Ethiopian mayflies'. Far more must have invaded the southern African region as it moved north into warmer climatic zones. Edmunds lists six families and the *Hexagenia-Eatonica* complex whose

ancestral lines became allopatric when Africa and South America separated. Some of these, such as the Baetidae, Tricorythidae and Oligoneuridae, have common and abundant species in southern Africa.

Other aquatic groups show similar distributions: the caddis genus *Leptonema* which is known from tropical America and Africa; the freshwater snail genus *Biomphalaria* (Pulmonata: Planorbidae) which is known from circum-Caribbean countries, the West Indies, tropical South America, Africa and Madagascar; and the Torridincolidae (Coleoptera) which are found in Brazil, southern Africa and Madagascar (Steffan 1973). There are also the examples of the freshwater fishes covered in Chapter 36 of this volume.

Many other similar allopatric distribution patterns are shown by terrestrial organisms such as the Peripitinae (Onychophora) (Croizat 1958). Detailed taxonomic studies of other groups will doubtless reveal further examples. Often in the past it has been assumed that some freshwater groups have invaded Africa from the palaeartic region, but Edmunds (1972) emphasizes that the reverse could be the case.

Second, a large segment of the Pan-Ethiopian fauna consists of those groups that entered Africa from the north after the closing of the Tethys Sea and after India became joined to the main Asiatic mainland. In wetter periods there seems to have been the possibility of an interchange of fauna between Africa, Asia, the Malay-Indonesian and even the Australian Regions as well as, of course, the Palaeartic. This is the same route postulated by Smith (1973) for the entry of many flowering plants into Africa from a region of development in south-east Asia.

However, this was not, nor is it yet, a one-way route for the freshwater fauna. Therefore one has to have a world picture of the groups in order to decide on their main direction of dispersal. Bowmaker et al. in Chapter 36 show that this was the main dispersal route of the cyprinid fishes.

Freshwater invertebrate groups which may have received some of their members along this route are the Heteroptera, Dytiscidae and Hydrophilidae (Coleoptera), Odonata and many of the Diptera including the Chironomidae. As already mentioned, a few of the Chironomidae originated from the south-temperate Gondwanian fauna. They also contain one possible candidate for the tropical Gondwanian group, *Harrisonina petricola* (Orthocladinae: Harrisonini), but most of them belong to genera widespread in the Holarctic and which reach further afield into Australia and South America. At the moment it is not possible to say whether some of these, such as the Tanypodinae, followed the baetid pattern suggested by Edmunds of origin in tropical Gondwanaland and spread to other parts of the globe or whether they followed the cyprinid pattern of origin in the palaeartic and south-east Asia and spread to Africa when the present land connexions were made.

It should be noted that the chironomid fauna of Israel includes many 'African' species (Kugler & Wool 1968). Kugler & Reiss (1973) report that the *triangularis* group of *Tanytarsus* (Chironomidae: Tanytarsini) which is so well represented in Africa and Madagascar also ranges over Europe, Israel and the Arabian Peninsula. Reiss (1971) reports that the chironomid fauna of Nepal, collected between altitudes of 400 m and 4000 m above sea level, shows relationships to that of the Ethiopian Region.

Ecologically, the Pan-Ethiopian element, whatever its origins, can be divided

into a number of sub-groups, mainly on the temperature tolerance of species, but there is much overlapping (Harrison 1965b).

2.2.1 Widespread, hardy species

These are to a greater or lesser extent eurythermal and most inhabit marginal or trailing vegetation. Some exploit almost all rivers and streams, for example *Baetis bellus*. The connexion between hardness of species and this type of habitat is discussed by Chutter (1963).

2.2.2 Tropical or warm stenothermal species

Tropical riverine and standing-water invertebrates follow a southward distribution pattern from central Africa, extending into warm lowlands and avoiding the Highveld with its cool summers and cold winters. Few reach the Natal coastal belt (30°S) and none the lower Buffalo River, eastern Cape (33°S). Some may extend southwards up the Upper Limpopo valley in a similar way to the frogs described by Poynton (1962), or through Botswana in wetter periods to reach the lower Orange River. Species which have reached the Transvaal middle veld (1000 m to 1300 m) appear constantly to attempt invasion of adjacent highveld regions, as illustrated by observations on dragonflies (Balinsky 1962). Dejoux (1974) classifies many of the tropical chironomid midges as 'Nilotic Fauna'.

However, the proportion of tropical, warm-adapted species which show this southward distribution into the subtropics is small. The fish (see Chapter 36) also follow this invertebrate pattern.

2.2.3 Highveld or warm temperate climate species

These species are characteristic of elevated highlands in the South African Transvaal, Natal and Orange Free State regions, and to some extent in Rhodesia. In the Cape Province many extend down to sea level, forming the greatest part of the lower-zone fauna of streams and rivers (Harrison & Elsworth 1958, Harrison & Agnew 1962). Comprehensive lists are given by Oliff (1960) and Chutter (1970).

2.2.4 Cold stenothermal, montane species

Many species belong to typically montane genera or families found often elsewhere in the world, but others, such as *Baetis* spp. (Ephemeroptera) to genera which are also found in lower riverine zones. In the high latitudes of the southwestern Cape some species are even found near sea level. Most are typically montane and restricted to mountains with high rainfall and permanent streams as in the Cape Fold belt and the ranges of the eastern escarpment. Mutual extinction as a result of competition must have occurred between the species of this group and those of the south temperate Gondwanian element.

Distribution of this group is influenced largely by low maximum temperatures but some species which seem to be more eurythermal are in fact limited to perennial, silt-free streams. Some have a surprisingly extensive distribution, considering the large gaps separating suitable habitats. For instance *Centroptilum*

sudafricanum Lestage is found from Cape Town to the eastern mountains of Southern Rhodesia and probably further north, jumping the "Limpopo Gap" which is about 400 miles across' (Harrison 1965b). Regional endemicity follows a similar pattern to that of the south temperate Gondwanian fauna.

2.2.5 Temporary mountain stream species

These species show a high degree of specialization for their exacting but refugial habitats which are subjected to the rigours of an annual dry season, when no rain may fall in some areas for at least three consecutive months. Such habitats are characteristic of Balinsky's (1962) 'drought corridor', a vast area stretching down from Somalia, Kenya and Tanzania to a wide belt across almost the whole of Zambia and Rhodesia down to South West Africa and Botswana, then on into South Africa particularly the western Orange Free State, western and northern edges of the Transvaal and most of Cape Province north and east of Cape Town (Chapter 9, Fig. 1). South of the Zambezi River perennial mountain streams are limited to mountains of the eastern escarpment, the Drakensberg and outliers, and the Cape Fold belt.

The southern tropical and subtropical parts of the corridor have a group of species characteristic of temporary mountain streams (Harrison 1965b), for example the beetle *Torrindicola rhodesica*, the chironomid midge *Harrisonina petricola* and simuliid midges belonging to the same group as *Prosimulium damarensis*.

3. Fauna of Madagascar

Madagascar should be considered along with continental southern Africa as it also has two ancestral elements in its freshwater fauna, the temperate Gondwanian in its mountains and a larger Pan-Ethiopian.

Gondwanian species have been listed for the following groups: Notonemouridae (Plecoptera), by Illies (1961b) and Zwick (1973); Blepharoceridae (Diptera) by Stuckenberg (1958); Leptophlebiidae (Ephemeroptera) by Tsui & Peters (1975). Stuckenberg and Tsui & Peters found that there is a closer affinity with the Gondwanian fauna of Australasia or India-Sri Lanka than with that of southern Africa. This would suggest that Madagascar had a Jurassic or Cretaceous connexion with the India-Antarctica-Australasia portion of Gondwanaland and that it retained this after its connexion with south-temperate southern Africa was broken. According to McKenzie & Sclater (1973) the early position of Madagascar in Gondwanaland is not yet clear. There must have been continuous mountain building in Madagascar from Cretaceous times for these south-temperate elements to have survived.

The work of Embleton & McElhinny (1975) has established that the latest connexion between Madagascar and continental regions was in the area of Kenya and Tanzania. This must have continued late enough to allow a complete Pan-Ethiopian element to move in, but there was no continuous high montane zone which would allow mixing of south-temperate Gondwanian elements. In fact there appear to be none of these in the East African mountains today.

The strong Pan-Ethiopian aquatic element in Madagascar's fauna is exemplified by the Chironomidae (Freeman 1961) and the freshwater molluscs

(Brown in Chapter 35). Many of these are delicate forms which must have entered Madagascar before the opening of the Moçambique Channel but a few strong fliers among the insects may have made their way across and some may still do so.

4. Ecological zonation of the rivers of southern Africa

Harrison & Elsworth (1958), Oliff (1960), Harrison (1965a), Chutter (1970) and Schoonbee (1973) have all shown that in southern Africa, as in other parts of the world, the benthic faunal communities of rivers show a distinct sequence, based roughly on altitude, from the mountain sources to the mouths.

Illies (1961a) proposed a universal scheme for the classification of rivers into physical zones. Harrison (1965a) applied this classification with minor modifications to rivers in southern Africa from the tropics to temperate regions. As will be discussed later, further modification of Illies' scheme was proposed by Harrison & Rankin (1976) for rivers in the wet tropics.

Illies' zones are shown best in his example of a South American tropical river, the Huallaga–Marañon–Amazonas. The rhithron, composed of torrential mountain streams and rivers lies high in the Andes, much of it starting above the permanent snow line. Low temperature stenotherms and some more widespread eurythermic forms are characteristic of this region, which he further divides into three sub-regions, the epi-, meta- and hyporhithron. The rhithric or cold-stenothermic forms disappear as temperatures rise and habitats are subjected to increasing turbidities and siltation. Illies relates his rhithric lower boundary to altitude, suggesting that near the equator, as in his Amazonian example, it lies at the 2000 m level but that at progressively higher latitudes it drops lower and lower. The potamon comprises the warmer, siltier and less torrential regions of the river and is subdivided into epi-, meta-, and hypopotamon. The epipotamon, in the lower mountain valleys or among foothills, has its torrential sections, with their true stony run fauna, interspersed with slower sandy- or muddy-bottomed sections sometimes with growths of submerged aquatic angiosperms. The two lower subzones of the potamon lie below the last rapids, forming the navigable section of the Amazonas River. These two last zones are difficult to separate in many other rivers.

4.1 *Rhithric and pseudorhithric species*

In tropical Africa zones of true rhithron, with their typical rhithric fauna are very infrequent and most lie north of the equator. Even in the extensive Drakensberg Ranges in South Africa, they are only to be found amongst the higher peaks. As soon as the streams enter agricultural zones, including grazing areas, the true rhithric qualities are destroyed by rising silt content, and the typical fauna is eliminated even where temperatures are still suitable. This was clearly seen by Chutter (1970) working on the upper tributaries of the Vaal River. In streams protected from silting, usually arising from human activities, rhithric communities are found at lower altitudes.

As predicted in Illies' paper the cold stenothermal forms are driven to higher altitudes at lower latitudes. In the southern Cape (34°S), where mountain streams drop straight into the sea, rhithric forms reach the estuaries (Harrison 1965a). In

the Chimanimani Mountains of Rhodesia there are not many left at 1980 m at latitudes of 17° to 18°S (Harrison 1965b). The effect of high montane forests in tropical regions is shown by Statzner (1975) who worked in the Kahuzi–Biega National Park region of Zaire at a latitude of about 2°S. He found a rhithron–potamon boundary at 1700 m, much lower than in Rhodesia, but the river he was studying was in a well-afforested region and temperatures at this altitude do not appear to have risen above 16°C at any time during the year.

Among those rivers which do not have a true rhithron nor a rhithric fauna is the Zambezi River and most of its tributaries, except the short ones from the eastern Rhodesian mountains. The Umgeni River, starting in the coastal mountains of Natal, has only a hint of a rhithron (Schoonbee 1973), with only a few members of the rhithric community. However, the upper Tugela River, arising in the Drakensberg proper, has a rhithron with a fully developed rhithric community as can be seen from records by Oliff (1960).

In the wet tropics (Harrison & Rankin 1976) a special situation exists in rivers arising in mountains whose peaks are below the rhithron–potamon boundaries for those latitudes. Here rain falls throughout the year and temperatures may rise to 23°C but vary very little either annually or diurnally. They noted that in ‘the permanent rain forests of these mountains all streams, whatever their altitude, have similar characteristics: the water is clear with very little turbidity; stones, rocks and other substrata are clean, with very little silt; temperatures are warm but do not exceed 23° and exhibit nightly drops of only a few degrees’. These conditions can in no way be called potamic nor can the fauna be termed cold-adapted rhithric.

Bishop (1973) working in Malaysia, and Hynes (1971) and Harrison & Rankin (1976) in the West Indies, showed that many of the insect groups found in this type of montane region are warm-adapted members of the same families which Illies (1961) and Harrison (1965b) consider as being characteristic of the true cold rhithron. Harrison & Rankin call these true montane zones of tropical and sub-tropical rivers the ‘pseudorhithron’ and their warm-adapted eurythermic fauna the ‘pseudorhithric’ fauna. No tropical rivers of this type have been studied as yet in the rainforest regions of Africa but it is possible that pseudorhithric conditions may be found there also. Such conditions should not be confused with downstream extensions of true cold-adapted rhithric forms permitted by the lowering of the montane forest boundaries in some rivers. The latter has been seen in small, afforested streams, such as the Yarrow Stream (Crass 1947), which arise in the coastal mountains of sub-tropical Natal.

4.2 *Potamic species*

Many potamic species are found throughout southern Africa but others are more limited in their distribution. Four main faunal categories are distinguished by Harrison (1965b) and summarized here:

- (a) Species found throughout almost the whole of the potamon over the whole of southern Africa. *Baetis bellus* is an example which is found in the potamon of the Great Berg River, western Cape (33°S), up to the lower epipotamon of the Zambezi River (15°35'S).
- (b) Species found in the lower epipotamon and in the meta- and hypopotamon

zones all over southern Africa. *Simulium bovis* is an example which is found from the Great Berg River to the Zambezi River.

(c) Species which are less temperature tolerant, either limited to the cooler and upper, or to the warmer and lower parts of the potamon. Harrison (1965a) notes a zonation involving four or five species of *Cheumatopsyche* (Trichoptera: Hydropsyhidae) in rivers with a long epipotamon, especially those in the tropics. Schoonbee (1973) describes a number of mayfly associations which succeed one another in an orderly sequence down the length of the epipotamon of the Umgeni River, Natal.

(d) Species which are rheobiotic and disappear in the meta- and hypopotamon. Many of these are specialized dwellers of stony runs. Species in this category may also fall into (b) and (c).

Very little is known about the invertebrate fauna of the meta- and hypopotamon of the tropical rivers of southern Africa, except that it is rich in decapods such as *Macrobrachium* spp. It is quite likely that species will be found which are largely limited to these lower zones.

As latitudes become lower the montane end of the epipotamic fauna extends to higher and higher altitudes. It is in these regions that the cold stenothermal, true rhithric fauna becomes replaced by more widespread eurythermal species. Some of these are found throughout the whole of the epipotamon at more temperate latitudes but retreat into the montane epipotamon of the tropics. Others may extend to lower altitudes to varying degrees. Harrison (1965a) lists a number of common forms.

In some rivers of the elevated sub-continent the epipotamon is enormously long and commonly manifests the phenomenon of rejuvenation of the stream bed in some reaches. This occurs when the river encounters harder geological strata. At first the river bed flattens out so as to be canal-like, almost metapotamon in nature, then the profile steepens, rock is exposed and soft bottoms give way to stony rapids and runs. This sequence can be repeated a number of times down the length of the river; extreme examples are the Victoria Falls on the Zambezi River and the Augrabies Falls on the Orange River. Oliff (1960) shows that in the Tugela River, Natal, these rocky, rejuvenated sections are colonized by widespread rheobiotic, eurythermal species and not by what Illies (1961a) later called rhithric forms. In tropical rejuvenated regions warm stenothermal, rheobiotic forms may be found in addition to these (Harrison 1965a).

Chutter (1970) points out that Illies' system of classification does not subdivide the epipotamon sufficiently to be useful in long, extensive river systems such as the Vaal-Orange where large quantities of silt and sand may occur in the bed. He suggests dividing the epipotamon into stable and unstable depositing zones, produced over different strata and greatly affecting the composition of faunal communities.

4.3 *Species succession in temporary streams*

An interesting faunal succession is seen in temporary, or intermittent, epipotamic streams which abound in southern Africa because of the seasonal nature of the rainfall over most of the region. Harrison (1958) describes a stony run of the Kuils River, an intermittent tributary of the Great Berg River in the winter rainfall

region of the Cape Province, South Africa. After being dry all summer, flow starts after early autumn rains (April) and a simple faunal succession is observed. Initially the community is dominated by *Simulium ruficorne* (Diptera: Simuliidae), a species characteristic of slow-flowing streams; however, even at this early stage, small numbers of more permanent inhabitants, nymphs of baetid mayflies, have already appeared. During the course of the winter the community becomes more balanced and *S. ruficorne* is largely replaced by another species, *S. adersi*. By spring the community is very similar to that of permanent streams nearby except that some insects, such as Tricorythidae (Ephemeroptera) and Hydropsychidae (Trichoptera) are conspicuously absent.

In Rhodesia (Harrison 1966) a small epipotamic stream is quite dry in early spring but benthic fauna develop rapidly after the flow resumes following late spring rains. Initially a form of *Simulium ruficorne* and *Chironomus satchelli* (Diptera: Chironomidae), a species usually found in ponds, are abundant within most habitats but there is very little else. Within a month elements of the fauna of permanent streams are well established and within two months the benthic community is indistinguishable from that of permanent streams nearby.

It appears that in temporary streams such as these some forms manage to aestivate, notably pulmonate snails and larger oligochaetes, others such as rhabdocoels and small Crustacea survive as resting eggs, but many others, including the Ephemeroptera, Odonata, Trichoptera and Diptera, are derived from eggs laid by flying adults after the resumption of flow.

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