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Geographical distribution of riverine invertebrates in Southern Africa

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The South African Council for Scientific and Industrial Research has organised an extensive programme of research into the biology of South African rivers. This began in the Western Cape Province in 1950, but was later extended to the rest of the country and is still continuing. Much of the accumulated faunistic data has been published and the following discussion has been based largely on this as well as on unpublished records and further data collected by the author in Southern Rhodesia. In addition the valuable work of other investigators has been taken into account.

BRINCK (1955 A and B), in his consideration of the distribution of the Southern African Gyrinidae and Odonata, points out that the species found on the sub-continent are clearly part of the Ethiopian fauna as a whole, but that they can be divided into two groups:

1. An "Old Element", palaeo-endemic and showing its greatest development in the Western Cape Province, largely restricted to refugial regions, mainly montane.
2. A hardy element of lower altitudes or plain regions, more tolerant of higher temperatures, which appears to have invaded the region in comparatively more recent times.

HUTCHINSON (1929 and 1933) noted a similar trend in the distribution of water bugs; in fact this pattern appears over and over again in the distribution of many groups of animals and plants, both aquatic and terrestrial.

BALINSKY (1962), considering the Southern African fauna as a whole, points out that in the Mesozoic most of the sub-continent must have been in a southern temperate zone and occupied by a temperate zone fauna. As the continent moved north and as temperatures rose much of this fauna

was driven into montane regions, except in the Western Cape Province, and its place was taken by species moving south from tropical and subtropical regions. He also points out that this process could have been virtually complete in the Pleistocene and that the present distribution pattern is a stable one. As far as water insects are concerned, they could have spread over their existing range before present day barriers arose. As BRINCK (1960) points out, there was no significant Pleistocene glaciation so it was possible for the ancient fauna to survive.

Accepting these ideas and taking into account the known distribution of numerous aquatic groups, it would appear logical to classify the riverine and stream invertebrate fauna as follows:

1. An Old Element, palaeogenic and palaeo-endemic. This would constitute the remains of the Mesozoic fauna which is now limited largely to montane regions, except in the Western Cape. This element has "Gondwanaland" affinities with relatives in the other southern continents. PLUMSTEAD (1962) cites botanical evidence that Southern Africa broke away from the rest of the southern continental mass in the late Jurassic, so that close similarity to Australasian and South American forms cannot be expected.

STUCKENBERG (1962) deals with the distribution of the members of this group (see Appendix 1) and shows that its greatest development is in the South Western Cape which is still practically a temperate region. Elements of the group are then distributed east and northwards along the Drakensberg and adjacent ranges but discontinuity of suitable habitats has led to the development of endemic regions. However, some species are found in most these mountains. The last outpost appears to be the eastern mountains of Southern Rhodesia where only one species has been found so far, *Chlorolestes elegans* PINHEY (PINHEY 1951 and BRINCK 1955 B). See Appendix 2.

Apart from affinities with the Australasian and South American forms, some members of this group have obvious, but possibly very ancient affinities with the fauna of the Holarctic region.

The acid stream endemic fauna of the Southern and Western Cape, HARRISON and AGNEW (1962), consists of species from this Old Element and from 2d, below.

2. A truly Pan-Ethiopian (Sub-Saharan) element. This group has obvious Palaeartic and Oriental affinities and contributes the bulk of the Southern African riverine fauna. The constituent species can be divided into a number of sub-groups, based largely on temperature tolerance, but there is much overlapping.

a. Widespread, hardy species which are to a greater or lesser extent eurythermal. Some are found in almost all rivers and permanent streams, except in the truly montane zones (epi- and metarhithron) and most of

them inhabit marginal or trailing vegetation, e. g., *Baetis bellus* BARNARD. CHUTTER (1963) discusses the connection between hardy species and this type of habitat.

b. Tropical or warm stenothermal species. POYNTON (1962) discussing Southern African frogs, describes a group which follows a "tropical pattern" of distribution. Some of these frogs extend southward from Central Africa into warm lowland and coastal regions, avoiding the highveld where the summers are cooler and the winters cold. One arm of their range extends through Moçambique and the lowveld of the Transvaal and Swaziland into Zululand and the coastal regions of Natal; the other, smaller arm extends south up the upper Limpopo valley and some reach the Mafeking region. Tropical riverine species follow a similar southward distribution pattern but few reach the Natal coastal belt (lat. 30° S) and none has been found in the lower Buffalo River, Eastern Cape (lat. 33° S). It is possible that some have moved up the upper Limpopo valley, or through Bechuanaland in wetter periods to reach the lower Orange River, but the fauna here has not been studied. Some species reach the Middle Veld of the Transvaal (1000 to 1300 m) and there appear to be constant, but temporary invasions of the adjacent Highveld, as indicated by colonies of dragonflies observed by BALINSKY (1962).

It should be realised that only a proportion of tropical, warm adapted species show this southward, sub-tropical distribution.

c. Highveld — temperate climate species. These are characteristic of elevated "highveld" regions of the Transvaal, Natal and Orange Free State, but also of Southern Rhodesia. Many extend south into the Cape Province where they are found at sea level. There is some falling off of these species in the temperate South Western Cape but those still present form the bulk of the fauna of the lower zones of streams and rivers there (HARRISON and ELSWORTH 1958 and HARRISON and AGNEW 1962).

d. Cold stenothermal, montane species. Many belong to genera characteristic of and largely limited to mountain streams in many parts of the world, but others to genera which also include species found in lower river zones. Some members of this group are found near sea level in the South Western Cape, but otherwise they are typically montane. Like the Old Element they are restricted to mountains with high rainfall and permanent streams, mostly the Cape Fold Belt and Eastern Escarpment ranges. Naturally at lower latitudes they are limited to increasingly higher altitudes.

Although maximum temperature is the most important factor influencing the distribution of this group it is not the only one; some species are more eurythermal than would first appear but are limited to perennial, oligosaprobic, 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. However, there is regional endemicity following much the same pattern as that of the Old Element.

e. Temporary mountain stream species. In Africa, south of the Zambezi River, perennial mountain streams are found only, to any extent, in the mountains of the Eastern Escarpment, the Drakenberg and outliers, and the mountains of the Cape Fold Belt (South Western Cape). In other parts mountain and headwater streams dry up every annual dry season except, in rare cases, where they originate in permanent springs. This is most marked in what BALINSKY (1962) calls the "drought corridor", a large region including most of the Cape Province north and east of Cape Town, South West Africa, Bechuanaland, the western Orange Free State, the western and northern fringes of the Transvaal, and then a broad belt extending north east and including most of Southern and Northern Rhodesia and large parts of Tanganyika, Kenya, Somaliland, etc. In much of the Central African and some of the Transvaal parts of this corridor the annual rainfall is not low, but it is so seasonal that practically no rain falls for at least three consecutive months of the dry season.

From the little information available it appears that there is a group of species characteristic of temporary mountain streams in the Southern African sections of this corridor, but possibly in other parts as well. Species assigned to this group, Appendix 3, could be part of an "old element" but, in most cases their affinities are not at all clear. The habitat is a very exacting one, demanding a high degree of specialisation, but could be considered also to be refugial.

Little is known of the fauna of the lower zones of temporary streams and rivers, specially those of the drought corridor, but these appear to be colonised largely by widespread species also found in permanent streams. In temporary standing waters there are characteristic species, specially crustacea.

It is interesting to note that ILLIES (1964), using the very limited data available to him, has discerned in the distribution of the South American riverine fauna a pattern similar to the Southern African one. In South America there is also a group with Gondwanaland affinities characteristic of high mountains, but with elements at low altitudes in the extreme south (ILLIES 1960 and 1961). Most of the members of this group are fairly closely related to Australasian forms and, with these, probably give an idea of the composition of the aquatic fauna of the old southern continent at a time well after Southern Africa had broken away. It is widely agreed that Australasia and South America remained connected until later times. This

palaeo-endemic group is much stronger in South America than in Southern Africa, probably because the land mass extends much further south into the wet, temperate zone, and because the Andes form a massive, high and continuous refugial region, extending right up the sub-continent.

In warmer regions the palaeo-endemic group is replaced by forms more widely distributed in South America and by cosmopolitan genera. A similar pattern is discernable in the aquatic fauna of Australia and New Zealand as shown by FREEMAN (1961) in his study on the Chironomidae of Australia.

Appendix 1. Old Element, palaeo-endemic forms. The following are suggested:

Crustacea (see BARNARD 1927). Isopoda: *Phreatoicus capensis* BARNARD, *Protojanira prenticei* BARNARD. Amphipoda (Gammaridae): *Paramelita* spp. Insecta. Plecoptera, Capniidae-Notonemourinae: *Aphanicerca* spp., *Aphanicercella* spp., *Aphanicercopsis* spp. and *Desmonemoura pulchella* TILL.; according to ILLIES (1961), the remaining known genera of this sub-family are distributed as follows: South America (Chile) 4; Madagascar 2; Australasia 4.

Ephemeroptera. Leptophlebiidae: *Aprionyx* and *Castanophlebia* have only been found in South African montane or semimontane regions, both have affinities with South American and Australasian forms (BARNARD, 1932); possibly the following genera belonging to the Ephemerellidae can be included here: *Ephemerellina* and *Lithogloea.*

Odonata. Anisoptera: *Presba* spp., related to the Australian *Syncordulia.* Zygoptera: *Chlorolestes* spp. and *Ecchlorolestes* spp., related to the Australian *Synlestes* (BRINCK, 1955B).

Megaloptera. Corydalidae: *Chloroniella peringueyi* ESB.-PET. (Neuromini), *Platychauliodes* spp. and *Taeniochauliodes ochraceopennis* ESB.-PET. (Chauliodini).

Trichoptera. No caddies can be included here with certainty although some genera are limited to the South Western Cape: *Cheimacheramus, Petroplax, Barbarochthon* (Sericostomatidae), *Hydrosalpinx* and *Petrothrincus* (Aequipalpia).

Diptera. Blepharoceridae: *Elporia* spp. (STUCKENBERG, 1962). Chironomidae: the Podonominae *Archaeochlus* sp. (Drakensberg) and *Aphrotenia* sp. (Tsitsikamma) recently found by L. BRUNDIN (private communication).

Rhagionidae: *Trichacantha* spp. and *Pachybates* spp. (STUCKENBERG, 1961).

Coleoptera, Elminthidae: *Leielmis georyssoides* (GROUVELLE), *Peloriolus granulosus* DELÈVE, *Peloriolus costulatipennis* DELÈVE, *Peloriolus parvulus* DELÈVE, *Elpidelmis capensis* (GROUVELLE), *Ctenelmis harrisoni* DELÈVE.

Hydrachnellae: *Diversibates, Ambiguobates, Mideopsellides, Stormaxonella, Africacarus, Karlvietsia.* Some of these appear to have Australasian or South American affinities. See K. VIETS (1956) and K. O. VIETS (1962).

Appendix 2. Recent collections in the Chimanimani Mountains, eastern Southern Rhodesia, in permanent streams between 1670 and 2280 metres, showed that the following were present (N — also found in territories to the north; S — also found in territories to the south):

Perlidae — *Neoperla spio* (NEWMAN) (N, S); Ephemeroptera — *Baetis harrisoni* BARNARD (N, S); *Baetis cataractae* CRASS (N?, S); *Baetis bellus* BARNARD (N?, S); *Pseudocloeon* sp. nov., *Pseudocloeon inzingae* CRASS (S); *Centroptilum sudafricanum* LESTAGE (N?, S); *Centroptilum parvum* CRASS (S); *Dicercomyzon* sp. (genus — N); *Euthraulus* sp. (genus — N, S); *Adenophlebiodes* sp. cf. *masoniella* AGNEW

(S); Heteroptera — *Enithares glauca* Bol. (S); *Anisops debilis* Hutch. (S): Zygoptera — *Chlorolestes elegans* Pinhey (S); Trichoptera — *Goerodes* sp. (genus — N, S); *Helicopsyche* sp. (genus — N); *Hydropsyche* sp. (genus — N, S); *Cheumatopsyche afra* type (N, S); *Cheumatopsyche thomasseti* type (N, S); *Athripsodes* spp. (genus — N, S); *Sortosa (Thylakion)* sp. (genus — N, S); *Afritrichia* sp. (genus — N); *Ugandatrichia* sp. (genus — N); Psephenidae — *Eubrianax* sp. (genus — N, S); Simuliidae — *Simulium dentulosum* Roubaud (N, S); *Simulium medusaeforme* Pomeroy (N, S); *Simulium nigritarsis* (Coquillet (N, S); Chironomidae — *Pentaneura trifascia* Freeman (N, S); *Pentaneura teesdalei* Freeman (N); *Pentaneura nigromarmorata* Goetghebuer (N, S); *Pentaneura interrupta* Goetghebuer (N, S); *Pentaneura comata* Freeman (N, S); *Cricotopus bizonatus* Freeman (S); *Cricotopus* sp. n., *Syncricotopus micans* Kieffer (N, S); *Cardiocladius africanus* Freeman (N, S); *Psectrocladius viridescens* Freeman (S); *Chaetocladius ruwenzoriensis* Freeman (N); *Limnophyes natalensis* Kieffer (N, S); *Smittia conigera* Freeman (N, S); *Corynoneura dewulfi* Goet. (N, S); *Thienemanniella lineola* Fr. (N, S); *Chironomus (Chironomus) satchelli* Freeman (N, S); *Stenochironomus spatuliger* Kief. (N, S); *Stenochironomus polychaetus* Kief. (N, S); *Stenochironomus edwardsi* Freeman (N, S); *Polypedilum (Polypedilum) alticola* Kieffer (N, S); *Polypedilum (Poly.) fuscum* Fr. (S); *Polypedilum (Poly.) annulatipes* Kief. (N, S); *Polypedilum (Poly.) allansoni* Freeman (S); *Polypedilum (Poly.) annulatum* Freeman (N, S); *Polypedilum (Pentapedilum) anale* Freeman *(N, S); Tanytarsus (Tanytarsus)* sp. nov., *Tanytarsus (Cladotanytarsus) pseudomancus* Goet. (N, S); *Stempellina chambiensis* Freeman (N, S); *Zavrelia kribiensis* Kieffer (N, S). The water was very soft; conductivity — 6.8 m.mhos; bicarbonates — 2 mg./l. as $CaCO_3$; pH — 5.6 (Bundi River).

A number of other species of aquatic insects and Hydrachnellae still have to be identified or described. In general the fauna fell into groups 2d, 2c, a few 2a and one species in group 1.

Appendix 3. The temporary mountain stream element includes a beetle *Torridincola rhodesica* Steffan, belonging to the Torridincolidae n. fam. (Sphaerioidea); Simuliidae of the *Prosimulium damarensis* de Meillon and Hardy group, found so far in the Brandberg, S.W. Africa and near Salisbury, Southern Rhodesia. Crosskey (personal communication) says that this species and *Prosimulium damarensis* might have to be placed in a new subgenus. Chironomidae-Podonominae, unidentified species of a new genus found near Salisbury, Southern Rhodesia, and the first record for the Sub-Family in the Ethiopian region, and *Harrisonia petricola* Freeman, a very aberrant member of Orthocladiinae with no close relatives, found near Loskop, Transvaal, and near Salisbury, Southern Rhodesia. In addition there is a mite which appears to be related to non-aquatic groups which is being studied by Dr. I. M. Newell. It was found near Salisbury, Southern Rhodesia.

Summary

Southern African riverine invertebrates can be divided into two main groups, with sub-groups. 1. An Old Element (palaeogenic, palaeo-endemic) of which the species are cold stenothermal and mostly montane, with „Gondwanaland" affinities; these comprise a small proportion of the fauna and are limited mainly to the southern tip of the sub-continent but some extend northward in refugial regions. 2. A truly Pan-Ethiopian element constituting the bulk of the fauna and consisting of (a) widespread species found from tropical climates to highveld and temperate climates; (b) warm stenothermal, tropical species; (c) highveld-temperate climate

species; (d) montane, cold stenothermal species and (e) temporary mountain stream species. The distribution of these various groups is discussed.

Zusammenfassung

Die wirbellosen Tiere der südafrikanischen Flüsse können in zwei Hauptgruppen nebst Untergruppen eingeteilt werden. 1. Altendemische Formen (paläogenische, paläoendemische), deren Gattungen kaltstenotherm und meist montan mit „Gondwanaland"-Affinitäten sind; diese umfassen einen kleinen Anteil der Fauna und sind hauptsächlich auf die Südspitze des Unterkontinents beschränkt, obwohl einige sich nördlich in Zufluchtsregionen vorfinden. 2. Ein echt panäthiopischer Faktor, den Hauptteil der Fauna umfassend und bestehend aus (a) weitverbreiteten, von tropischen Klimaregionen bis auf die Hochfeld- und gemäßigten Klimata vertretenen Gattungen; (b) warmstenothermen, tropischen Gattungen; (c) Gattungen des Hochfelds und eines gemäßigten Klimas; (d) montanen, kaltstenothermen Gattungen und (e) zeitweiligen Bergbachgattungen. Die Verteilung dieser verschiedenen Gruppen wird besprochen.

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