

The biogeography of the Prosopistomatidae, with a particular emphasis on Southern African species

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Abstract

The mayfly family Prosopistomatidae consists of the single genus *Prosopistoma* Latreille. Its known distribution includes species from Africa, Madagascar, the Comores, Europe, the Levant, India, Sri Lanka, China, Vietnam, the Philippines, Malaysia, Sumatra, Java, the Solomon Islands, Papua New Guinea and northern Australia. A tropical Gondwanaland origin of the family has been suggested. No species are currently known from the Neotropical or Nearctic regions, though the family may yet be discovered in northeastern South America, since this region separated from West Africa only c.120 mya. Focussing on southern Africa, several undescribed species have recently been discovered, with interesting implications to the biogeography on a more localised scale. In the western Cape, a prosopistomatid species has been collected in the Olifants River, extending the distribution of this family further south into a more temperate region. Geological evidence indicates that the Olifants River was connected to the Orange River during the Tertiary period. Prosopistomatidae are known from the Orange River today, and the presence of the family in the Olifants River in the western Cape supports the geological evidence of the historical link between these two rivers. Another unexpected discovery was from the Buffalo River in the eastern Cape, at 33°S. A subtropical zone extends along the east coast of South Africa as a result of the warm Agulhas current offshore, allowing the southerly extension of the distribution of more tropical species.

Keywords: *Prosopistoma*, Gondwanaland, Southern Africa, river capture.

Introduction

The Prosopistomatidae are a group that have fascinated biologists since the nymph was first discovered by Geoffroy (1762), who described it as a crustacean. It was not until over a century later that Joly (1871) realised that these animals were in fact members of the Ephemeroptera. The history of their complicated nomenclature has been thoroughly revised by Hubbard (1979).

New species of this small, monogeneric family continue to be discovered from time to time, and Table 1 lists several species that are awaiting description.

The family is not recorded from the Neotropical or Nearctic regions. However, following evidence from studies on other groups, it is not unreasonable to expect Prosopistomatidae in Neotropical areas such as Brazil. For example, Krömmelbein (1966), looking at freshwater ostracod fossils from the Jurassic, concluded that West Africa and northeastern Brazil at one time formed a continuous landmass. South America separated from Africa 127 mya (Dingle *et al.* 1983), while India and Madagascar began to break away earlier than this, around 195mya during the early Jurassic (Scotese, 2001). Since India and Madagascar separated from the Gondwanan landmass before South America did, and seeing that India seems to have played a critical role in the introduction of Prosopistomatidae to Asia, it would be reasonable to expect Prosopistomatidae to occur in at least the northeastern part of South America.

Few adult Prosopistomatidae have been described, being known only in *Prosopistoma africanum* (Gillies, 1954) and *Prosopistoma pennigerum* (Fontaine, 1955; Degrange, 1955). Peters (1967) mentions male imagos being collected in Malaysia, but these have not been described as he was unsure which nymph they may be associated with. Elouard (pers. comm.) has collected both nymphs and adults of three undescribed species from Madagascar. The Prosopistomatidae are reproductive as female subimagos (Edmunds and McCafferty, 1988). It is therefore not surprising that the aerial stage of their life cycle is very short. Fontein (1982) reports that the adults of *P. pennigerum* live for only half an hour after emergence.

Phylogenetically, the family has proved difficult to place. Vayssière (1934) and Gillies (1954) placed the Prosopistomatidae and the North American family the Baetiscidae, as sister lineages, based on nymphal characteristics,

particularly the fused, carapace-like thorax. Fontein (1957) did some detailed anatomical studies of the two families, and concluded that they had too many characteristics in common to be explained purely by convergence. McCafferty and Edmunds (1979) placed them in the Pannota, where the nymphs are characterised by having the forewing pads fused with the thorax so that less than half the wingpad extends beyond this fusion. The carapace of the Prosopistomatidae and Baetiscidae was seen to represent the maximum expression of this fusion. McCafferty (1991), although keeping them both in the Pannota, placed the Prosopistomatidae closer to the Caenidae than to the Baetiscidae in his phylogeny. In contrast to these views, Kluge *et al.* (1995) placed the Baetiscidae and Prosopistomatidae together in a suborder of their own, the Posteritorna, based on forewing venation, and Kluge (1998) elaborates on this theme. McCafferty (1997), Wang *et al.* (1997), and McCafferty and Wang (2000) support the removal of both these families from the Pannota, placing them in a suborder of their own, the Carapacea. Recently, a new genus of Baetiscidae was described from Baltic amber (Staniczek and Beckly, *in press*), showing an originally Holarctic distribution of this family. It is, however, beyond the scope of this paper to discuss the phylogeny of these two apparently closely related families in further detail.

Origin and global distribution of the Prosopistomatidae

Edmunds (1972, 1979) suggested that the Prosopistomatidae had a Gondwanaland origin. McCafferty (1999) lists the Prosopistomatidae amongst the Gondwanan families that are mainly tropical, but not Pantropical. The modern Oriental species may represent a single lineage introduced from Gondwanaland after the Indian Plate completed the split from Africa about 140mya during the late Jurassic era, drifting northwards to collide with Asia about 45mya. Further developing this idea, based on the structure of the mandibles, Koch (1988) proposes that a northern and southern group of the family, separated by the Tethys Sea, must have existed during the Upper Cretaceous. In Central Asia the Northern group became extinct because of cold climatic conditions, but established in what is now Europe, with related species migrating to the middle east (Koch, 1988). Some of this originally northern line also became established in the Phillipines and New Guinea. Considering that the mandible of the

Australian species illustrated by Campbell and Hubbard (1998: 144) has a short thick neck, as does the species recently described from China (Tong and Dudgeon, 2000: 124), both also belong to Koch's northern group. It is interesting to note that the distribution described by Koch (1988) follows Huxley's modification of the Wallace line (Rosen (1988: 445) with Palawan having a different fauna to the main Phillipine Islands. McCafferty (1999) discusses the concept of "stepping stone archipelagos" being available intermittently between South East Asia and Australia, and this may explain the relatively high number of prosopistomatid species in this region (Table 1). The occasional linking and separation of the islands would encourage speciation, with populations being separated long enough for species to differentiate. Some of these would be eliminated with rising sea levels, but the overall effect would be an increase in number of species. The effect of changing land forms on speciation is investigated in a different context later in this text.

The relatively larger number of species found in Africa, Madagascar and Asia (Table 1) seems to support the idea of a tropical Gondwanan origin of the Prosopistomatidae, with what is now Africa being the epicentre of their evolution. During the late Carboniferous - early Permian era, when mayflies are thought to have evolved (Riek, 1970), Gondwanaland was situated much further South (e.g. Scotese, 2001). Prosopistomatidae are clearly not part of the old temperate paleoendemic species which arose at that time, that fauna now being confined in relict populations to the cooler regions of the southwestern and southern Cape, and eastern escarpment mountain chains of southern Africa. The tropical fauna evolving during these times in the warmer, more northern climes of Gondwanaland would have migrated southwards as Gondwanaland began to drift northwards from the Jurassic onwards. The migration of the aquatic species would have been aided by the ancient drainage routes, such as the Trans-Tswana River (Fig. 2b), which flowed from what is now Angola through to what is now the Orange River in South Africa (Dardis *et al.*, 1988; Burke, 1996).

Adult Prosopistomatidae have emergence patterns that are typical of the tropics. They emerge at dawn rather than dusk (personal observation), possibly selected for as a result of predator-avoidance, since many of the crepuscular predators, such as dragonflies and bats, are less active at dawn (personal observation). Prosopistomatidae are poor fliers, and the winds of dawn are generally stiller in tropical areas, so a

dawn emergence would also prevent the mating pairs being blown away from their favoured river sites. As a general rule, if wind is produced by convection (as is often the case in the tropics), then dawn will be calmer and the wind will increase towards mid afternoon. If the wind is associated with a frontal system, time of day is irrelevant to wind pattern, and in such climates, mayflies often emerge during the middle of the day rather than at dawn or dusk (personal observation). If a tropical group invades a

temperate area, they retain their tropical emergence patterns and eggs hatch only when temperatures are adequately warm (Edmunds, 1979). It remains to be seen if the only African *Prospistoma* species known from a semi-temperate climate in the Western Cape (discussed in detail below) may follow this behaviour. Fontaine (1982) reports that the European species *P. pennigerum* flies at dawn, so it is likely that the dawn emergence is a family trait, and supports the idea of a tropical origin.

Table 1 - List of known species, and distribution of *Prospistoma* LATRIELLE 1833 (following the zoogeographic regions of Cranston and Naumann (1991).

Species	Distribution	Comments
PALAEARCTIC		
<i>P. pennigerum</i> (MÜLLER, 1785)	Europe	Adult also known
<i>P. oronti</i> ALOUF, 1977	Israel, Lebanon, Syria	Nymph only
<i>P. phoenicium</i> ALOUF, 1977	Israel, Lebanon, Syria	Nymph only
ORIENTAL		
<i>P. indicum</i> PETERS, 1967	India	Nymph only
<i>P. lieftincki</i> PETERS, 1967	Sri Lanka	Nymph only
<i>P. sinense</i> TONG & DUDGEON, 2000	China (Guangdong Province)	Nymph only
<i>P. funanense</i> SOLDÁN & BRAASCH, 1984	Vietnam	Nymph only
<i>P. annamense</i> SOLDÁN & BRAASCH, 1984	Vietnam	Nymph only
<i>P. boreus</i> PETERS, 1967	Philippines	Nymph only
<i>P. palawana</i> PETERS, 1967	Philippines	Nymph only
<i>P. wouterae</i> LIEFTINCK, 1932	Java	Nymph only
<i>Prospistoma</i> sp. TONG & DUDGEON, 2000	China (Hunan Province)	Nymph only
<i>Prospistoma</i> sp. PETERS, 1967	Malaysia	Adult only
<i>Prospistoma</i> sp. SARTORI & GATTOLLIAT (<i>in press</i>)	Borneo	Nymph only
AUSTRALIAN		
<i>P. sedlaceki</i> PETERS, 1967	New Guinea, Solomon Islands	Nymph only
<i>P. pearsonorum</i> CAMPBELL & HUBBARD, 1998	N. Australia	Nymph only
AFROTROPICAL		
<i>P. deguernei</i> (VAYSSIÈRE, 1893)	Senegal	Nymph only
<i>P. africanum</i> GILLIES, 1954	Tanzania, South Africa	Adult also known
<i>P. crassi</i> GILLIES, 1954	South Africa	Nymph only
<i>P. variegatum</i> LATRIELLE, 1883	Madagascar	Nymph only
<i>P. sp.</i> VAYSSIÈRE, 1936	Kenya	Nymph only
<i>P. sp.</i> BARNARD, 1940	Kenya	Nymph only
<i>P. sp.</i> PAULIAN, 1947	Congo	Nymph only
<i>P. sp.</i> MARLIER, 1954	Congo	Nymph only
<i>P. sp.</i> OLIFF, 1960 (= sp. A below)	Natal	Nymph only
<i>P. sp.</i> PAULIAN, 1961	Comores	Nymph only
<i>P. sp.</i> STANDER, 1963 (= sp. A below)	Natal & Swaziland	Nymph only
<i>P. sp.</i> TAYLOR, 1999	Okavango River	Nymph only
<i>P. sp.</i> TAYLOR, 1999	Zambezi River	Nymph only
<i>P. sp.</i> TAYLOR, 1999	Chobe/Zambezi	Nymph only
<i>P. sp.</i> A	South Africa, widespread	Nymph only
<i>P. sp.</i> B	Buffalo River, Eastern Cape	Nymph only
<i>P. sp.</i> C	Olifants River, Western Cape	Nymph only
<i>P. sp.</i> D	Cunene River, Namibia	Nymph only
<i>P. sp.</i> (Elouard, pers comm.)	Guinea	Nymph only
<i>P. sp.</i> (large sp.) (Elouard, pers comm.)	Madagascar	Adult also known
<i>P. sp.</i> (small sp.) (Elouard, pers comm.)	Madagascar	Adult also known
<i>P. sp.</i> (small sp.) (Elouard, pers comm.)	Madagascar	Adult also known

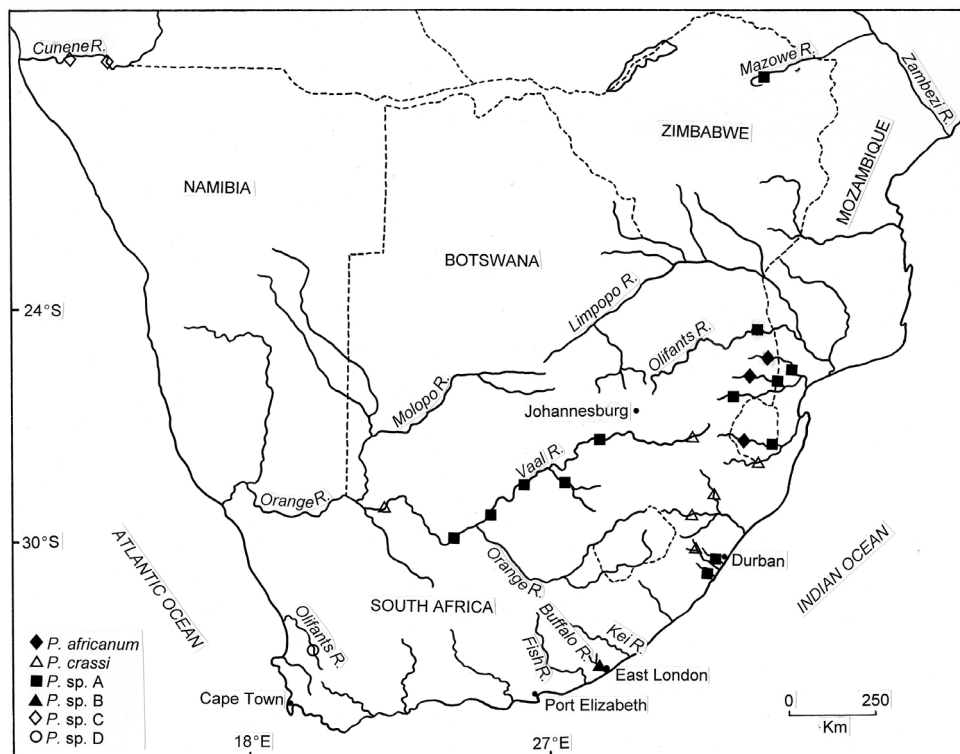


Fig. 1 - Known distribution of Prosopistomatidae in Southern Africa, based on material and records held at the National Collection of Freshwater Invertebrates, Albany Museum, Grahamstown, South Africa.

Focus on southern African Prosopistomatidae

The known distribution of the Prosopistomatidae in southern Africa is indicated in Fig. 1. Early museum records indicated several records of *Prosopistoma deguernei* (VAYSSIÈRE) in South Africa. This species was originally described from Senegal (Vayssière, 1893). However, inspection of this material shows these identifications to be incorrect, and in all cases the material represents an undescribed species, called *Prosopistoma* sp. A in this paper. This species has proved to be widespread in Southern Africa, with records in Malawi and Zimbabwe, as well as extensively in the more tropical northern and eastern rivers of South Africa. This species is superficially similar to *Prosopistoma crassi*, described from material from the Mgeni (Umgeni) and Thukela (Tugela) Rivers in KwaZulu-Natal, South Africa (Gillies, 1954). Unlike *P. crassi*, the antennae of *Prosopistoma* sp. A are longer than the distance between the base of the antennae and anterior margin of the head (following Gillies, 1954), and several other morphological features differ as well. This species will be described in a separate paper.

Oliff (1960), in a detailed study of the Thukela River in KwaZulu-Natal, divided the river into several zones according to altitude, flow type and

substrate type. He observed *P. crassi* in a rejuvenated zone amongst the foothills (Hart's Hill) about one third of the distance from the source of the river, and a second species (which he called *Prosopistoma* sp. 1) in his so-called valley sand bed zone. This work indicated distinct habitat preferences for the two species. Oliff's (1960) *Prosopistoma* sp. 1 is equivalent to *Prosopistoma* sp. A, discussed above.

Prosopistoma africanum also has a widespread distribution in Africa. Originally described from Tanzania (Gillies, 1954), it has also been recorded from several sites in South Africa. Interestingly, the South African material has indicated a preference of the species for sections of river where bedrock is prevalent, possibly representing rejuvenation zones, such as the Sabie River in the Kruger National Park (personal observation) and the Usutu River in Swaziland (Archibald and de Moor, 1981).

Prosopistomatidae have also been recorded in the Orange River near Upington (Palmer, 1996) (Fig. 1). These were rare, and only collected at two sites, despite rigorous sampling of the river over a period of several years. It is possible that this is a direct effect of daily fluctuating water levels in the river as a result of sporadic releases of water from the van der Kloof Dam for hydroelectric power. Unfortunately, little was

know about the Orange River invertebrate fauna before man-induced flow modifications came into effect during the 1970's. Chutter (1968) reports *P. ?crassi* from the lower Vaal River, a major tributary of the Orange River. Agnew (1986) also records a *Prosopistoma* sp. in the lower Vaal River, up to the Orange River confluence. Examination of museum material and records from the late 1950's and early 1960's for the Vaal River and its tributaries indicate that both *Prosopistoma* sp. A, and to a lesser extent *P. crassi*, were widespread, though never abundant. It is interesting to note that Prosopistomatidae nymphs do not appear to occur in large numbers at any site, but rather remain as a dispersed population in the river. W.J. Müller (pers. comm.) reports the presence of Prosopistomatidae in the Vaal River downstream of the Vaal Dam at Engelbrecht drift Weir, observed during water quality studies in 1999. Unlike the van der Kloof Dam, the release from the Vaal Dam is continuous because water has to be released for downstream users, so the presence and abundance of the Prosopistomatidae does not seem to have been affected by the dam. However, no Prosopistomatidae were collected further downstream, below the Vaal Triangle Industrial area, probably indicating sensitivity to pollution. This suggests that the modern distribution of Prosopistomatidae in South Africa has been affected by anthropogenic activities. This is certainly true of the European species too, which is now quite rarely encountered (Haybach, pers. comm.).

In the Eastern Cape, Prosopistomatidae were collected from the Buffalo River near East London (Fig. 1) (R.W. Palmer, pers. comm.). When considered in the light of Stuckenberg's (1969) Effective Temperature hypothesis, which proposes that a tropical influence extends along the east coast of South Africa as far south as East London (Fig. 3), this distribution does not seem anomalous, despite the southerly latitude. Unfortunately, material is not available for identification, and recent collecting in the Buffalo River by Albany Museum staff members has not produced more material. Further collecting endeavours will have to be undertaken to see if this is a known species, or perhaps one new to science.

Until recently, no Prosopistomatidae had been recorded from the south western or southern Cape, where the climate is temperate. However, during surveys carried out on the Olifants River in the western Cape during 1994, a *Prosopistoma*

species was collected by Rebecca Tharme (pers. comm.). This has considerably extended the southern distribution records for Prosopistomatidae in Africa into a region with a cooler, more temperate climate.

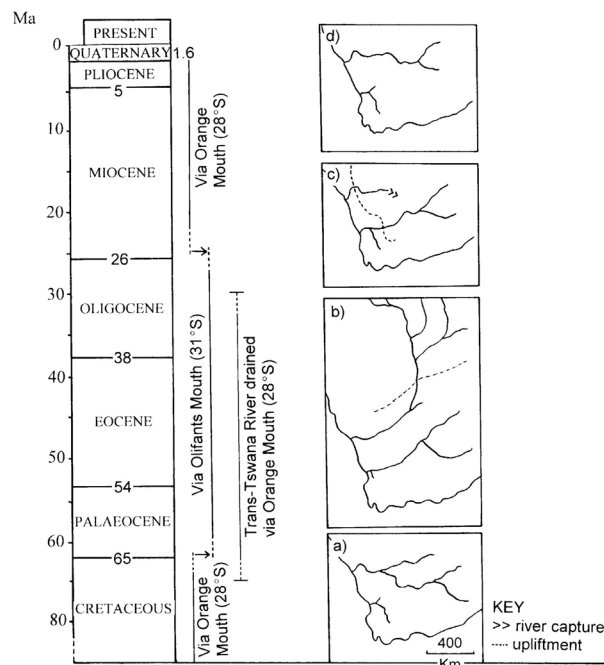


Fig. 2 - Changes in palaeo-drainage patterns in southern Africa since the Cretaceous.

(a) Early Cretaceous. The upper Orange and Vaal Rivers flowed in a similar pattern to that seen today, exiting to the Atlantic Ocean via the Orange River mouth at 28°S (Dingle and Hendey, 1984)

b) Late Cretaceous to Early Tertiary (approx 70-30ma) - the great Trans-Tswana River flowed southwards from what is now Angola, exiting into the Atlantic Ocean via the mouth of the Orange River at 28°S (after Burke, 1999). This connection was finally severed as a result of crustal upliftment. During this period, the rivers from what is presently the upper catchment of the Orange River flowed southeast to exit via the mouth of what is now the Olifants River at 31°S.

c) Oligocene (approx. 38-26 ma) - the rivers from what is presently the upper catchment of the Orange River continued to flow southeast to exit via the mouth of what is now the Olifants River at 31°S. Erosion of the headwaters of the lower Orange, along with crustal upliftment, eventually resulted in river capture (modified after McCarthy *et al.*, 1985).

d) Miocene to present - the lower Orange River has cut back to capture the Orange-Vaal headwaters once again.

Much geological evidence has been presented indicating that the Orange and Olifants rivers were linked during the Tertiary era (Dingle and Hendey, 1984; McCarthy *et al.*, 1985; Partridge and Maud, 1987). Although the details of the

connection between the two systems vary according to different authors, there is strong evidence to indicate that the Orange and Olifants systems were once joined. Dingle and Hendey (1984) show that the upper Orange and Vaal river systems have reached the Atlantic Ocean via two different exits at different times: the current Orange River Mouth (28°S), and via what is presently the Olifants River Mouth (31°S) in the southwestern Cape. This is explained in detail in Fig. 2.

Mayflies were a well-established group by the time these changes in drainage patterns commenced, having originated in the late Carboniferous to early Permian eras, some 270mya (Riek, 1970). It is likely then that the Olifants River species shares a common ancestor with the Orange and Vaal river species, but has become a separate species as the result of a vicariance event, in this case, river capture and tectonic upliftment.

Knowledge of the distribution of living organisms can often confirm geological and geomorphological evidence of historic drainage patterns, and often more than one group of organisms follows a similar pattern. The distribution of *Pseudobarbus* species (the indigenous redbfin minnows) in South Africa, also clearly indicates a paleo-linkage between what are now the Orange and Olifants Rivers (Skelton, 1986, 1994). There are several examples of river capture and tectonic upliftment considerably changing the landscape and flow pattern of rivers over time. Dardis *et al.* (1988) summarise the paleodrainage of southern Africa, and indicate that at one time an extensive river system drained southwards from Angola, the so-called "Trans-Tswana" River, which discharged into the Atlantic Ocean via the Orange River. Gravel and terrace deposits indicate a river four times the current size of the Orange River. This link between South-Central Africa and the south was eventually broken as a result of crustal warping and upliftment.

Recent collecting in the Cunene River along the Namibia/Angola border has produced another new species (Table 1, *Prosopistoma* sp. D). This was found at several sites along the river below the Ruacana Falls (de Moor *et al.*, 2000). Additional records provided by Taylor (1999) have also indicated the presence of the family in the eastern Caprivi area of Namibia in the Okavango, Chobe and Zambezi Rivers, but this material still needs to be examined; these have therefore not been indicated in Fig. 1.

A number of biogeographic models have been proposed for the southern African subregion.

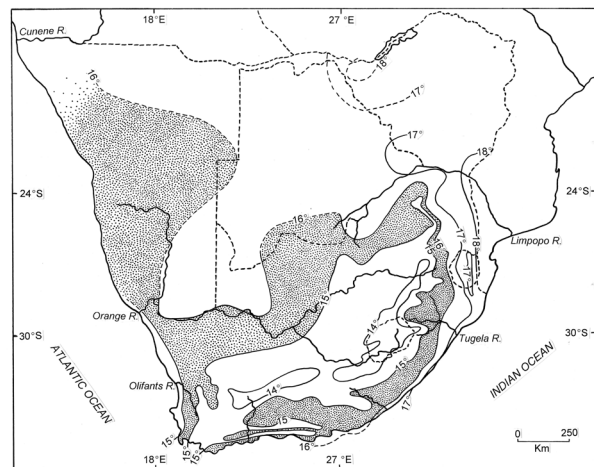


Fig. 3 - Stuckenberg's (1969) effective temperature isotherms for southern Africa. The 15°C to 16°C limits have been emphasized (stippled areas) to help distinguish between the different isotherms.

Two nodels divide South Africa up into hydrobiological regions, based on water chemistry and geology (Harrison, 1959, Nobel and Hemens, 1978). Allanson *et al.* (1990) proposed a classification for South Africa based on catchment characteristics, and divided the country into five limnological regions. Poynton (1964) derived biotic divisions based on the distribution of Amphibia, while Bowmaker *et al.* (1978) divided the southern African sub-region into six zones according to temperature and aridity regimes. Stuckenberg (1969) plotted a model of "effective temperature" isotherms (Fig. 3), using Bailey's (1960) concept of effective temperature, where a simple formula was derived, based on the means of the warmest and coldest months and the mean annual temperature. In essence, effective temperature "measures warmth by defining a sliding scale specifying temperatures at the beginning and end of the warm season, and implicating the duration of that period" (Stuckenberg, 1969). The known Prosopistomatidae distribution (Fig. 1) shows that these tend to be found where the effective temperature isotherms are above 15°C (Fig. 3). An increase in effective temperature implies an increase in the length of summer. Both the Olifants River in the western Cape and the Buffalo River in the eastern Cape fall within this region. It is unlikely that Prosopistomatidae would be found in areas with an effective temperature of much less than 15°C, but they would be expected in warmer regions, like the Limpopo River. Some of

the areas depicted in Fig. 3, although apparently falling into warm enough effective temperature regimes, would not provide suitable conditions for Prosopistomatidae because of other water quality variables and environmental factors. These include pH (the streams of the southern Cape and many of the western Cape are very acidic in nature), and aridity, since some areas have an unpredictable rainfall, and hence the rivers have an unreliable flow.

Conclusions

This paper has briefly examined the world's Prosopistomatidae species, and provided a preliminary examination of the biogeography of some southern African Propistomatidae species. The new species of Prosopistomatidae (species A to D) still need to be formally described. Further collecting of the family in Central, East and West Africa needs to be carried out. Once this has been done, it will be possible to undertake a detailed examination of the phyletic relationships between the all the species. One hopes that this will provide a clearer pattern of the relationships and biogeography of the species in this family.

Acknowledgements

I would like to express my appreciation to the following people: my colleague, Ferdy de Moor, for encouraging me to attend this conference, and providing funding from our research funds; Nancy Bonsor for assisting with the illustrations; Ferdy and Irene de Moor and Nick James, for valuable comments on this manuscript. Thanks also to the Directorate of Museums and Heritage, Eastern Cape Province, for providing research facilities.

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