

A preliminary phylogeny of Prosopistomatidae (Ephemeroptera) based on morphological characters of the larvae, and an assessment of their distribution

Helen M. Barber-James^{a,b*}

^aDepartment of Freshwater Invertebrates, Albany Museum, Grahamstown, South Africa;

^bDepartment of Zoology and Entomology, Rhodes University, Grahamstown, South Africa

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Until recently, only four species of the monogeneric family Prosopistomatidae were described from the Afrotropical realm; one from Madagascar, and three from sub-Saharan Africa. Recent studies have revealed the family to be more diverse, with a further five species from Madagascar, one from the Comores archipelago and seven from sub-Saharan Africa, which are currently in the process of being formally described. This brings the total number of known species globally to 34. Phylogenetic analysis of morphological features of the larvae reveals that the type species, *Prosopistoma variegatum* Latreille, 1883, a Madagascan species, along with two other Madagascan species, belongs to a clade which is different to the majority of other Afrotropical species. It is more closely related to the European species, the species from the Middle East and several of the species from the Oriental and Australasian regions. One possible explanation is diversification of this '*P. variegatum*' clade after Madagascar and India separated from Africa. The precursors of this clade may have been carried northwards on the Indian Plate, and subsequently dispersed to Europe, and to Australia via the Indo-Pacific islands. A concurrent dispersal of the now predominantly mainland African clade may have occurred and, in Madagascar and the Oriental realm, members of this group occur sympatrically with, or in close geographic proximity to, members of the '*P. variegatum*' clade.

Keywords: Ephemeroptera; Prosopistomatidae; phylogeny; Gondwana; distribution; dispersal; vicariance

Introduction

The first known species of the monogeneric ephemeropteran family Prosopistomatidae was discovered in France by Geoffroy (1762), who collected and described a larva from streams near Paris as one of three organisms he thought were Crustacea. It was not until over a century later that it was recognised as a member of the Ephemeroptera, when Joly (1871) managed to rear a larva through to the winged stage. This European species, now known as *Prosopistoma pennigerum* (Müller, 1785), received considerable attention, and due to its confused taxonomic placement, became known by a number of synonymous names, listed in Hubbard (1979). Latreille (1833) separated it from the other Crustacea with which it had been

*Email: h.james@ru.ac.za

classified by Geoffroy, and established the new genus *Prosopistoma*, renaming it *Prosopistoma punctifrons*, and including in this genus a species from Madagascar, which he named *Prosopistoma variegatum*, although these were not yet recognised as mayflies; it was still incorrectly thought that *Prosopistoma* larvae were the adult of an unusual branchiopod crustacean. Latreille did not, however, nominate a type species. Eaton (1883–1888) designated *P. variegatum*, a species from Madagascar, as the type species for the genus. This material is no longer available, and a neotype has been erected (Barber-James, submitted).

A monograph on the detailed morphology of the larva of *Prosopistoma pennigerum* was produced by Vayssi re (1890b), preceded by several shorter works (Vayssi re 1881, 1882, 1890a). This remarkable study included illustrations and descriptions of the external morphology, the gills, the Malpighian tubules, the nervous and tracheal systems, and the musculature of the retractile caudal cerci. Various other authors also contributed to the knowledge of *Prosopistoma*, focusing mostly on *P. pennigerum*, which was the principal species available for study. These include authors such as M ller (1785), Latreille (1833), Dum ril (1816), who all played a role in the development of the nomenclature of the group, and those who purely noted their existence in new localities (e.g. Tr g rdh 1911), or studied morphological and biological aspects (e.g. Lafon 1952). Subsequent species have since been discovered in Africa (Vayssi re 1893; Gillies 1954), the Middle East (Alouf 1977; Dalkiran 2009), the Oriental region (Lieftinck 1932; Peters 1967; Sold n and Braasch 1984; Tong and Dudgeon 2000; Sartori and Gattolliat 2003; Zhou and Zheng 2004), and the Australasian region (Peters 1967; Pearson and Penridge 1979; Campbell and Hubbard 1998). A list of species is given in Table 1.

Prosopistoma deguernei Vayssi re, 1893 is a poorly defined species, being described from an immature larva from the S n gal River (Vayssi re 1839). This was the first record of the family in Africa, but the material is no longer available for study as it could not be found in the collection of the Mus e Nationale d'Histoire Naturelle, Paris, France, and very few characters were available from Vayssi re's description. Thus *P. deguernei* was not included in these analyses. No material from S n gal was available for examination, although one species was found to be relatively widespread in West Africa (Figure 3). Whether this may be *P. deguernei* cannot be determined until fresh material has been collected in S n gal.

Two further undescribed African species are known to exist but no material is available for study at this time. One is reported from north-western Algeria (Gagneur and Thomas 1988; Thomas 1998), with what is probably the same species also recorded from the Atlas Mountains in Morocco (Touabay et al. 2002). The other is from the Olifants River system in the Western Cape, immature stages of which were collected more than once in the 1990s (R. Tharme, personal communication, 1995), but extensive subsequent field sampling has not found it again. It is assumed that the species may have become extinct before it could be described due to major impacts on the river, mostly due to citrus farming, or it may still exist in relict populations in the larger tributaries of this ecologically disturbed mainstream river.

Materials and methods

The initial thrust of the work reported here focussed on Afrotropical *Prosopistoma* species only. Fourteen new species from a number of localities within the

Table 1. World list of named or soon to be named *Prosopistoma* species (in alphabetical order, by region). Abbreviations of species names as in Table 2.

Current species known	Biogeographic region	Distribution	Abbr
<i>P. orhanelicum</i> Dalkiran, 2009	Palaeartic	Turkey	P. orh
<i>P. pennigerum</i> (Müller, 1785)		Europe	P. pen
<i>P. phoenicium</i> Alouf, 1977	Oriental	Israel, Lebanon, Syria	P. pho
<i>P. annamense</i> Soldán & Braasch, 1984		Vietnam, China	P. ann
<i>P. boreus</i> Peters, 1967		Philippines	P. bor
<i>P. funanense</i> Soldán & Braasch, 1984		Vietnam; China (Hong Kong & Guangdong Province)	P. fun
<i>P. indicum</i> Peters, 1967		Kerala, India	P. ind
<i>P. lieftincki</i> Peters, 1967	Australasian	Sri Lanka	P. lief
<i>P. olympus</i> Sartori & Gattolliat, 2003		Borneo	P. oly
<i>P. palawana</i> Peters, 1967		Philippines	P. pala
<i>P. sinense</i> Tong & Dudgeon, 2000	Afrotropical	China (Guangdong Province)	P. sine
<i>P. trispinum</i> Zhou & Zheng, 2004		Southwestern China	P. tri
<i>P. unicolor</i> Zhou & Zheng, 2004	Australasian	Southwestern China	P. uni
<i>P. wouterae</i> Lieftinck, 1932		Thailand, Malaysia, Java, Sumatra	P. wou
<i>P. sedlaceki</i> Peters, 1967	Afrotropical	New Guinea, Solomon Islands	P. sedl
<i>P. pearsonorum</i> Campbell & Hubbard, 1998		Northern Australia	P. pear
<i>P. africanum</i> Gillies, 1954	Afrotropical	Tanzania	P. afr
<i>P. crassi</i> Gillies, 1954		South Africa	P. cras
<i>P. deguernei</i> (Vayssièrè, 1893)		Sénégal	<i>excluded</i>
<i>P. variegatum</i> Latreille, 1883		Madagascar	P. var
African sp 1		KwaZulu-Natal, South Africa	Af. sp1
African sp 2		Namibia	Af. sp2
African sp 3		Democratic Republic of Congo	Af. sp3
African sp 4		Kenya	Af. sp4
African sp 5		Mpumalanga, South Africa	Af. sp5
African sp 6		Democratic Republic of Congo	Af. sp6
African sp 7		West Africa	Af. sp7
African sp 8		Botswana, Zimbabwe	Af. sp8
Madagascar sp 1		Madagascar	Mad. sp1
Madagascar sp 2		Madagascar	Mad. sp2
Madagascar sp 3		Madagascar	Mad. sp3
Madagascar sp 4	Madagascar	Mad. sp4	
Madagascar sp 5	Madagascar	Mad. sp5	
Comores sp 1	Anjouan	Anj	

Afrotropical region (Figures 1 and 3) have been recognised (unpublished data). Although descriptions of most of the new species are almost complete, the prospective names of these taxa cannot be given until these are formally published

elsewhere. For this reason numbers have been allocated to each species. Thirty-three species were used in the phylogenetic analysis (Table 1), excluding *P. deguernei*.

A number of morphological and morphometric characters were found to be useful for studying the phylogeny (Table 2). Several groups were considered for outgroup status, but only *Baetisca rogersi* Berner, 1940 was retained as an outgroup in this analysis, as Baetiscidae and Prosopistomatidae are currently widely believed to be sister taxa (e.g. Wang et al. 1997; Kluge 1998; Ogden and Whiting 2005; Sun et al. 2006). It therefore has more shared characters with *Prosopistoma* than does *Caenis*, *Machadorythus* or *Baetis*, the other outgroups considered. Since they rooted the tree in the same place and made no difference to the grouping between the Prosopistomatidae species, they were excluded.

Analysis of coded characters was done using the program 'Tree analysis using New Technology' (TNT) (Goloboff et al. 2008) which was run using the tree bisection reconnection (TBR) algorithm to search for the most parsimonious trees. Majority Rule consensus was chosen, as the strict Nelsen consensus method was found to collapse the nodes giving too little visual resolution.

As the emphasis of recent research has been on the larvae of the Afrotropical species, over 60 characters have been quantified for these species. However, as many of these characters have not been determined for the remaining world species, only 17 characters were selected for this study (Table 2). For the non-Afrotropical species, most of these characters were extracted from the literature, as material was not at hand for examination for most of the Oriental and Australasian species, or the species from the Middle East. Thus, some potentially useful characters, such as sternal plate ratios, convexity of carapace (length divided by height), posterolateral projection of abdominal segments 7–9, and more detailed mouthpart features, were omitted in this analysis. This study aims to give a global overview of the family and establish the relationship between the Afrotropical species and those found in the Palaearctic, Oriental and Australasia regions.

Material examined for this study was obtained from a number of sources: The Albany Museum, Grahamstown, South Africa (AMGS), The Natural History Museum, London, UK (BMNH), Florida A&M University, Florida, USA (FAMU), the Musée Nationale d'Histoire Naturelle, Paris, France (MNHN), The Musée de Zoologie, Lausanne, Switzerland (MZL), The Royal Museum for Central Africa, Tervuren, Brussels, Belgium (RMCA), The Purdue University Entomological Research Collection, West Lafayette, Indiana, USA (PERC).

The localities plotted on the maps (Figures 2–5) were taken from the AMGS database (Southern and Central African species); from information associated with specimens provided by FAMU, MZL and PERC; collection localities (West Africa and Madagascar) were provided by Jean-Marc Elouard (personal communication, 2005), GBIF records (Global Biodiversity Information Facility 2008) provided some of the European records; Santiago Robles (personal communication, 2001, 2008) and Manuel Toro (personal communication, 2008) provided larvae and some locality information for Spain. Other distribution records were taken from the literature, mostly from papers describing species (Vayssière 1893; Lieftinck 1932; Gillies 1954; Peters 1967; Alouf 1977; Pearson and Penridge 1979; Soldán and Braasch 1984; Campbell and Hubbard 1988; Tong and Dudgeon 2000; Sartori and Gattolliat 2003; Zhou and Zheng 2004; Dalkıran 2009), and grid references were estimated as closely as possible from maps following site descriptions if the sites were not geo-referenced in these papers. Additional information was taken from

publications which indicated range extensions of species already described: Sweden (Trägårdh 1911; Alm 1918); Latvia (Katschalova 1962, 1965); Czech Republic (Ulmer 1927); Russia (Schletterer and Kuzovlev 2007); Hungary (Újhelyi 1966); Austria (Vayssièrè 1890b), Germany (Ulmer 1927); several sites in France (e.g. Joly 1871; Vayssièrè 1882, 1890b; Lafon 1952); Portugal (Terra 1984); Italy (Bellmann 1988). A more detailed account of the European species, including a more comprehensive list of localities, can be seen in Schletterer and Füreder (2009).

Ages in terms of the geological timescale, quoted in the discussion, are from the International Stratigraphic Chart (International Commission on Stratigraphy 2006).

Results

The characters used for estimating the phylogenies are listed in Table 2. The Majority Rule consensus tree produced using TNT indicates two distinct clades (Figure 1). One clade consists of some of the Madagascan and Oriental species, and

Table 2. Selected characters used for determining the phylogeny of the larvae of Prosopistomatidae. Outgroup is *Baetisca rogersi*.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Outgroup	1	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	2
P. orh	0	1	1	1	1	1	1	0	1	0	1	1	2	0	1	1	2
P. pen	0	1	1	1	1	1	0	1	1	0	1	1	2	0	1	1	2
P. pho	0	1	1	1	1	1	1	2	3	0	1	1	2	1	0	1	?
P. ann	0	1	1	1	1	0	1	1	1	1	0	0	1	?	1	0	?
P. bor	0	1	1	1	1	1	0	1	3	0	1	1	1	0	1	1	?
P. fun	0	1	1	1	1	1	1	1	0	1	0	0	1	?	1	0	?
P. ind	0	1	1	1	1	0	1	2	2	1	0	0	1	0	1	0	?
P. lief	0	1	1	1	1	1	1	1	1	0	1	2	2	1	0	1	?
P. oly	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	?
P. pala	0	1	1	1	1	1	0	1	3	1	0	0	1	0	1	0	?
P. sine	0	1	1	1	1	1	1	2	1	0	1	1	1	?	1	1	2
P. tri	0	1	1	1	1	1	1	1	0	0	1	1	2	?	0	1	2
P. uni	0	1	1	1	1	0	1	2	2	1	0	0	1	?	1	0	?
P. wou	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	1
P. sedl	0	1	1	1	1	1	0	1	1	0	1	1	2	0	0	0	?
P. pear	0	1	1	1	1	1	0	1	1	0	1	1	2	0	1	0	2
P. afr	0	1	1	1	1	1	1	1	0	1	0	0	1	0	1	0	0
P. cras	0	1	1	1	1	0	1	1	2	1	0	0	1	0	1	0	0
P. var	0	1	1	1	1	1	1	0	3	0	1	2	2	1	0	1	2
Af sp 1	0	1	1	1	1	0	1	2	2	1	0	0	1	0	1	0	0
Af sp 2	0	1	1	1	1	0	0	2	1	1	0	0	1	0	1	0	0
Af sp 3	0	1	1	1	1	0	1	2	0	1	0	0	1	0	1	0	0
Af sp 4	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0
Af sp 5	0	1	1	1	1	1	1	2	2	1	0	0	1	0	1	0	0
Af sp 6	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	1
Af sp 7	0	1	1	1	1	0	1	2	1	1	0	0	1	0	1	0	2
Af sp 8	0	1	1	1	1	0	1	1	2	1	0	0	1	0	2	0	1
Mad sp 1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0
Mad sp 2	0	1	1	1	1	0	1	1	2	1	0	0	1	0	1	0	1
Mad sp 3	0	1	1	1	1	1	0	0	3	0	1	2	2	1	0	1	2
Mad sp 4	0	1	1	1	1	1	0	1	2	0	0	0	2	1	1	0	0

(continued)

Table 2. (Continued).

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Mad sp 5	0	1	1	1	1	1	1	0	3	0	1	2	2	1	0	1	2
Anj	0	1	1	1	1	0	1	1	1	0	0	0	1	0	1	0	0

Species name abbreviations indicated in Table 1. List of characters and character states. Unknown characters marked by "?". 1: Shape of carapace (0) rounded with entire margin or (1) with spiny extensions. 2: Carapace development (0) gradual as larvae mature or (1) present even in young instar larvae. 3: Type of mandible (0) non-predatory (1) predatory. 4: Glossae and paraglossae (0) partly fused (1) completely fused. 5: Third antennal segment (0) not enlarged; (1) enlarged. 6: Ratio head width: carapace width (0) ≤ 0.5 (1) > 0.5 . 7: Ratio of distance between eyes : maximum head width (0) ≤ 0.6 (1) ≥ 0.61 . 8: Number of antennal segments including scape and pedicel (0) ≥ 7 (1) 6 (2) 5. 9: Antenna (0) longer than or (1) subequal to or (2) shorter than or (3) much shorter than distance from antennal base to anterior margin of head. 10: Length of inner canine of mandible compared to outer canine (0) shorter (1) subequal. 11: Outer canine of mandible (0) of similar width to inner canine or (1) distinctly broader than inner canine. 12: Number of setae beneath canines of mandibles (0) ≤ 3 (1) 4–9 (2) ≥ 10 . 13: Mandible (0) with regular prostheca or (1) with thicker, serrated seta preceding rest of setae below canine or (2) without thicker seta. 14: Position of widest part of postmentum (0) widest near central axis or (1) widest near base. 15: Shape of anterior margin of carapace (0) strongly projecting forward to lie adjacent to lateral margin of head or (1) not projecting forward. 16: When larva viewed dorsally, labrum (0) not prominent or (1) prominent. 17: Number of major filaments branching off gill 1 of mature larva (0) < 10 (1) 10–20 (2) > 20 .

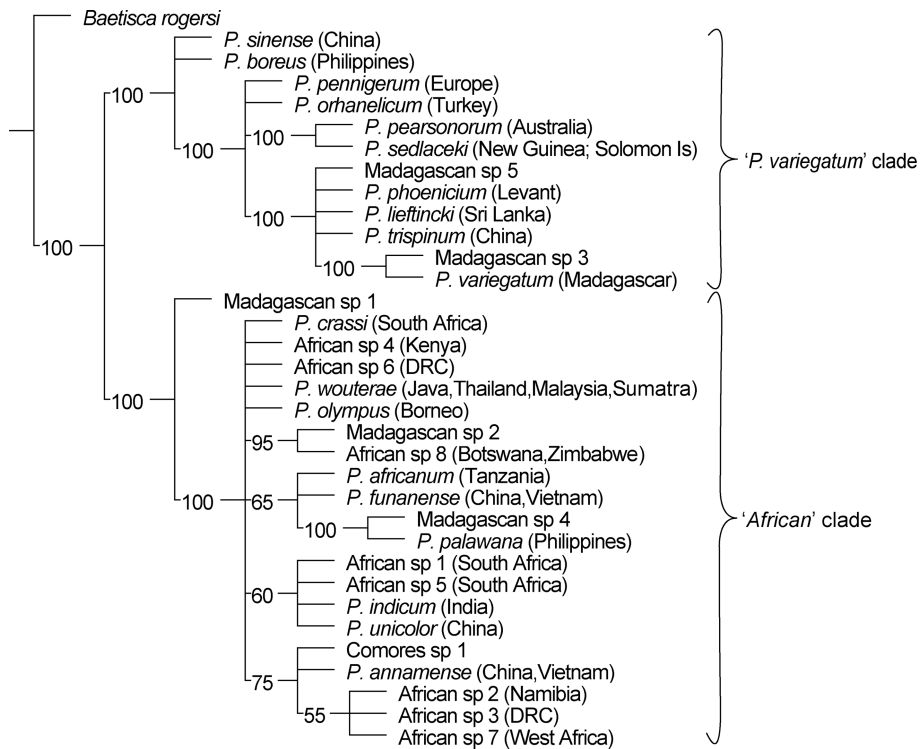


Figure 1. Majority Rule Consensus tree for Afrotropical *Prosopistoma* species calculated from 20 most parsimonious trees derived from characters in Table 2, nodes with over 50% support are indicated. Tree length = 51.

all of the Palearctic and Australasian species, which share many synapomorphies with *P. variegatum*; the other clade links all of the sub-Saharan African species, the Comores species, some Madagascan species and some of the Oriental species. For

the purpose of the biogeographic discussion which is to follow, the species sharing synapomorphies with *P. variegatum* will be referred to as the '*P. variegatum*' clade, while the clade dominated by all of the sub-Saharan African species, and including a few species from Madagascar and Asia, is referred to as the '*African*' clade. It is important to note that, depending on which characters are included in the analysis, the relative position of species within each clade changes, although most species are consistently placed within one or other clade. However, *P. funanense*, an Oriental species, although usually placed within the '*African*' clade, has been placed in the '*P. variegatum*' clade in some combinations (not shown).

The plotted distributions of the known species are shown in Figures 2–5.

Discussion

Distribution and biogeography of Prosopistoma species

Koch (1988), based on mandibular structure of the extant larvae known at that time, proposed a division of the family into a northern and southern group, the result of vicariance because of separation of the two groups by the Tethys Sea during the Upper Cretaceous. While this may indeed have had a role to play in their speciation, his theory does not take certain species in Madagascar into account, namely members of the '*P. variegatum*' clade, as these would fit into his northern group. He postulates a subsequent colonisation of Asia via India by his southern group (which corresponds to the '*African*' clade discussed here).

Edmunds (1972, 1979), considering the relationship between Afrotropical and Oriental mayflies, was the first to postulate a Gondwanan origin of *Prosopistoma*, proposing that India carried the group to Asia. The results of the study presented here appear to support Edmunds' hypothesis, and suggest that both the '*P. variegatum*' and '*African*' clade may have dispersed in this way (Figure 6). However, the plausibility of a Gondwanan origin must be considered – could the ancestors of these animals have existed so far back, or are they likely to be more recent? One needs to turn to the fossil record for evidence. The only fossil reported to date as a member of the Prosopistomatidae (Sinitshenkova 2000a) from Burmese amber, approximately 100 million years old, has subsequently been placed as *Palaeocloeon* (Baetidae) (Kluge 2004). However, other stem group fossils for the Baetiscoidea have been found, covering a surprisingly large geographic range, indicating a Pangaeon origin of the group. The oldest known fossils indicate that the stem group of the Baetiscidae originated at least 200 Ma (Pescador et al. 2009). If modern Prosopistomatidae and Baetiscidae are truly sister lineages, this implies that the ancestral Prosopistomatidae existed as far back as the Triassic, before Pangea had split. Stem line fossils of the Baetiscidae have been reported from the Crato fossil formation in Brazil, dating back to the Upper Aptian stage (125–112 Ma) of the Lower Cretaceous (Staniczek 2007). The Koonwarra fossil beds in Victoria, Australia, have also yielded a prosopistomatoid fossil from the Lower Cretaceous (Late Aptian, some 118–115 Ma). Although provisionally assigned to Siphonuridae (Jell and Duncan 1986), Staniczek (2007) places it as a member of the Baetiscoidea, belonging to the stem group of Baetiscidae, extending the distribution of these precursor taxa considerably. Sinitshenkova (2000b) described a fossil from New Jersey, North America, from the upper Cretaceous (Turonian stage, 93.5–89.3 Ma), which McCafferty (2004) transferred from its original designation, to the Baetiscoidea as a putative Baetiscidae precursor. Other more recent baetiscid fossils have been found in Eocene Baltic Amber, some 45 Ma (Staniczek and Bechly 2002;

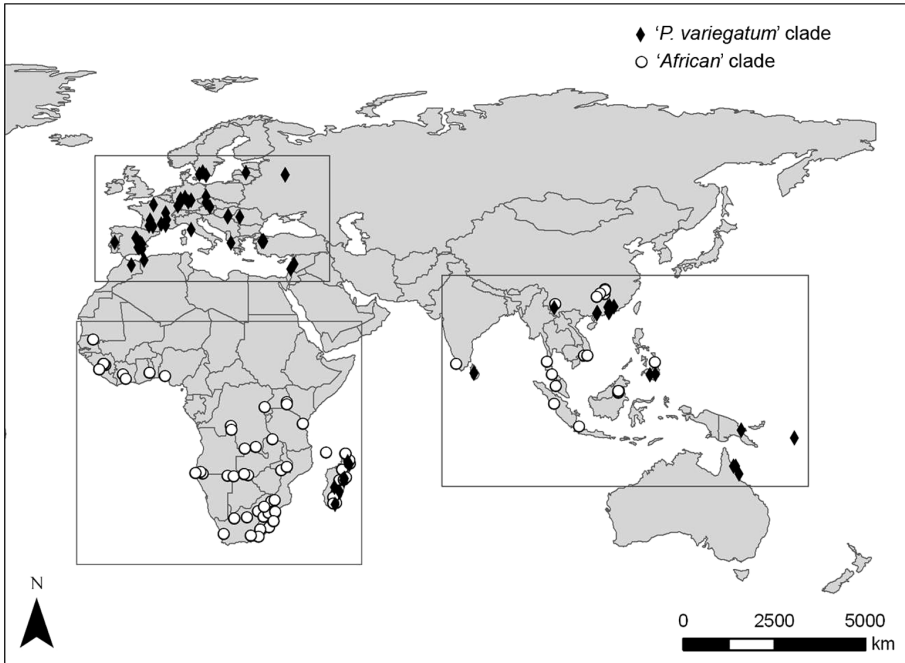


Figure 2. Global perspective of distribution of *Prosopistoma* species, showing the occurrence of the two proposed lineages, which are derived from the clades seen in the phylogenies.

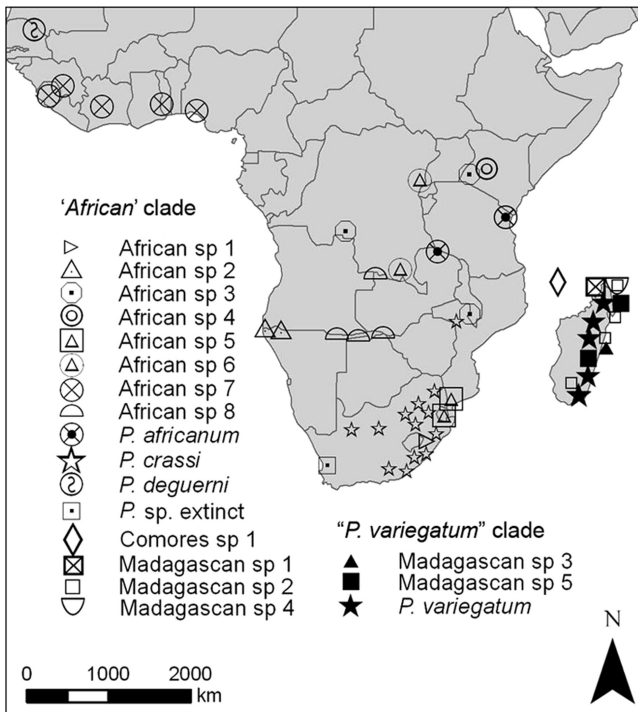


Figure 3. Localities of the species known within the Afrotropical region.

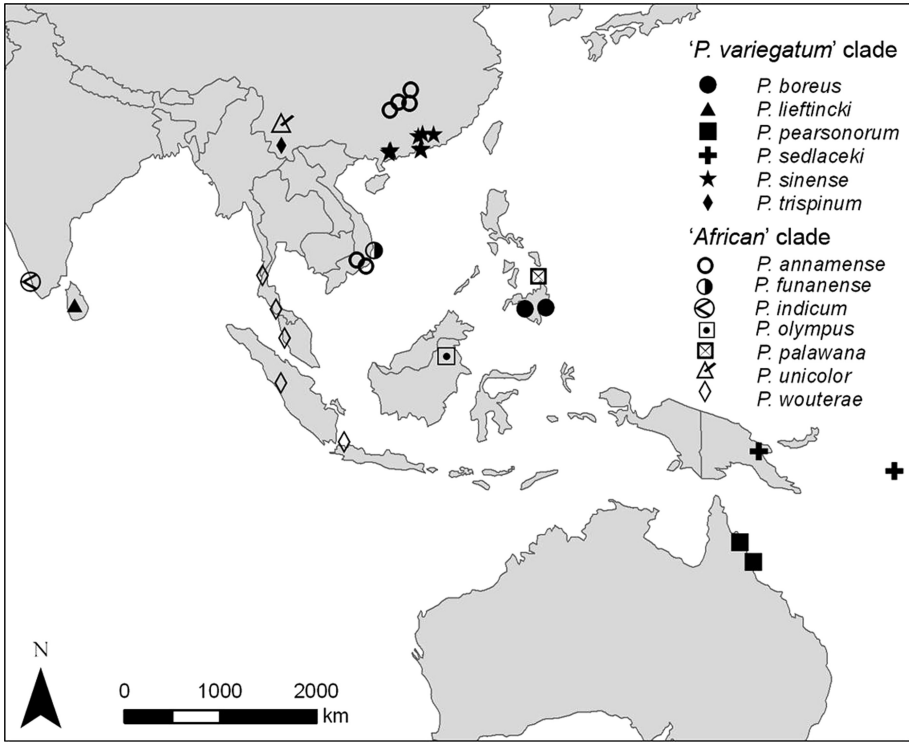


Figure 4. Localities of the species known within the Oriental and Australasian regions.

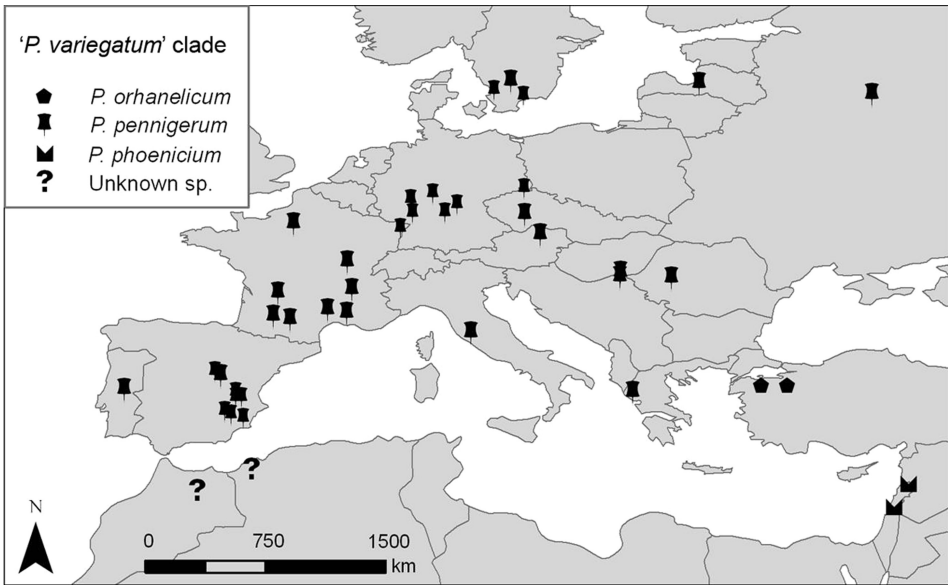


Figure 5. Localities of the species known within the Palearctic region.

Godunko and Krzemiński 2009), indicating a more widespread distribution of this family than it presently occupies. The breakup of Gondwanaland began approximately 165 Ma, considerably after the earlier precursor taxa were established.

The details of the global distribution of the Prosopistomatidae remain biogeographically puzzling. They are absent from the Neotropical and Nearctic regions, but otherwise have a relatively widespread though somewhat disjunct distribution (Figure 2). One must assume that the stem group lineages discussed above did not survive in the Neotropical and Nearctic regions. Another consideration in assessing the absence of the family from South America is the palaeoclimate of the interior of the Gondwanan landmass prior to its splitting. Changes in paleofluvial landscape towards the end of the Permian, into the Triassic (starting some 215 Ma), indicate the onset of a prolonged period of extreme drought in the continental interior (Smith and Botha 2005). Only after the landmasses began to separate would the ocean currents have changed their pattern of circulation, bringing an end to the drought conditions that dominated, producing conditions more suitable for *Prosopistoma* colonisation. It is therefore proposed that the early *Prosopistoma* species on the African mainland migrated westwards across Africa after the split with South America as habitats became more favourable.

The absence of the '*P. variegatum*' clade from mainland Africa may be explained by extinction, or by evolution of precursors to this group on the Madagascan/Deccan landmass after it separated from Africa (vicariance). Considering the age of tectonic events, this would have had to occur after 158–165 Ma (dates given for separation of the African and Madagascan landmasses (Briggs 2003; Yoder and Nowak 2006), but before 84–96 Ma, when the Indian/Seychelles landmass began to separate from Madagascar (Briggs 2003).

Paulian (1961) reported a *Prosopistoma* species from Mohéli Island (also known as Mwali Island) from the Comores. This is currently undescribed and therefore not included here. Starmühlner (1976) reported a *Prosopistoma* species from the island of Anjouan (also known as Nzwani Island), which is in the process of being described (unpublished data). The Comores archipelago forms a chain of volcanic islands in the northern Mozambique Channel, with Anjouan itself being an extinct volcano (Esson et al. 1970; Flower 1972). Schlüter and Trauth (2008) place Anjouan at approximately 3.9 million years old, which gives a minimum age for the Anjouan species; Mohéli Island is 5.0 million years old. Due to the volcanic origin of these islands, the Comores species can only have arrived by dispersal, but this may have taken place a much longer time ago than the ages of the islands imply. As Heads (2005) points out, a species on a volcanic island may be much older than the island itself, as the current fauna may have already existed on a previous, now submerged island within that archipelago chain. The phylogeny shows the Anjouan species to be part of the '*African*' clade (Figures 1–3), although it may equally possibly have dispersed from Madagascar as from Africa. It is interesting to note that the youngest islands of the Comores archipelago are closest to Africa, with the age of the islands increasing eastwards (Schlüter and Trauth 2008); possibly colonisation may have occurred on islands which were formed closer to the African mainland than they are now situated. Dispersal between Africa and Madagascar has been shown to play an important role in accounting for the present day distributions of a number of insect groups. For example, Torres et al. (2001), based on mitochondrial DNA data, postulate dispersal from Madagascar to Africa for a group of Lepidoptera (Saturniidae: Satyrinae:

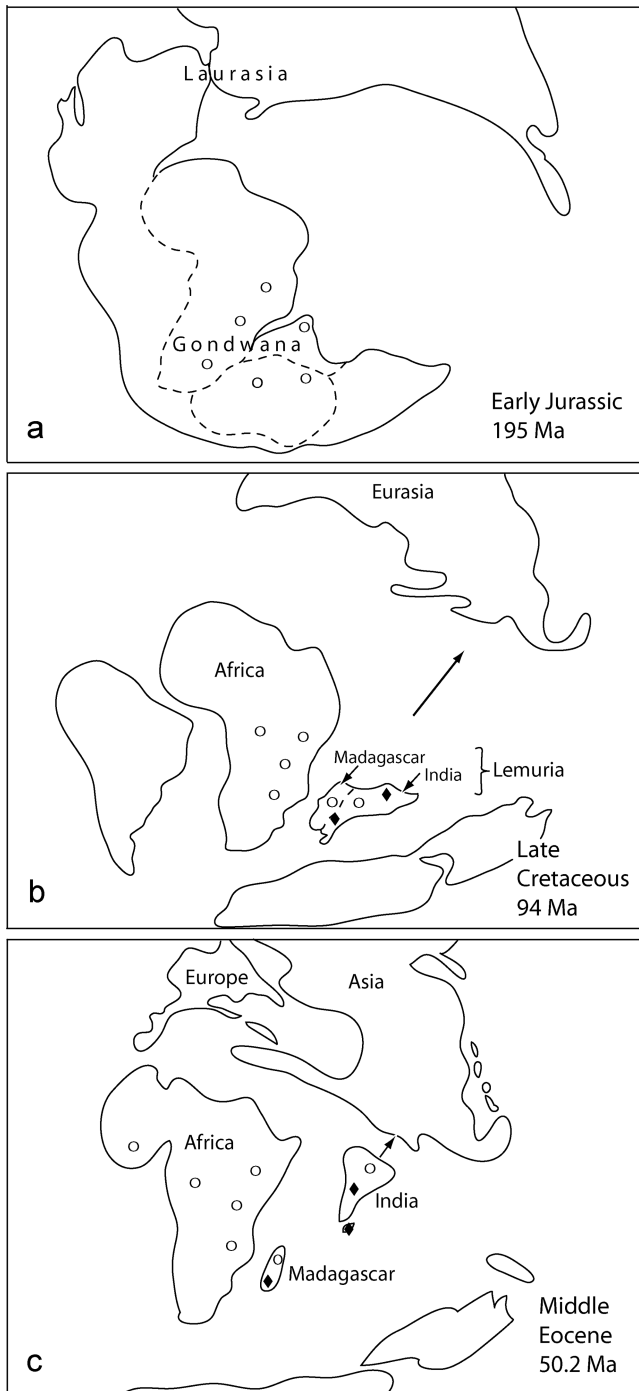


Figure 6. Proposed dispersal of precursor *Prosopistoma* lineages (maps adapted from Scotese 2003).

Mycaltesina). Considering Ephemeroptera, Monaghan et al. (2005) showed that dispersal between Africa and Madagascar plays a larger role than previously thought in Baetidae, and the presence of *Prosopistoma* on the Comores archipelago indicates that this is also true for the Prosopistomatidae. Bearing in mind the short adult life span of *Prosopistoma* species (Gillies 1954), it is perhaps surprising that dispersal over this distance is possible.

Both clades have representatives on Madagascar (Figures 4 and 5). The clade which now dominates Africa, and which presently often co-exists with the '*P. variegatum*' clade in other parts of the world (Figures 2–4), may have evolved first on the Gondwanan landmass before the Lemurian landmass (consisting of Madagascar, Deccan plate and associated fragments – sensu van Steenis 1962) broke off. The absence of the '*P. variegatum*' clade from Africa suggests that it may have had a later Lemurian origin. India collided with Asia some 34 Ma (Aitchison et al. 2007), possibly introducing both clades to what is now the Oriental region. Subsequent colonisation of the Palearctic by the precursors of the '*P. variegatum*' clade, and migration across Southern Asia and the Indo-Pacific islands to Papua New Guinea and Australia by both groups, could provide a possible explanation of the current distribution of this family. This does not, however, account for the absence of members of the '*African*' clade in Europe, and no explanation is apparent at present. It is highly likely that unknown species of *Prosopistoma* will still be found to occur in the largely unexplored rivers of countries between Asia and Europe, such as Kazakhstan, which will fill in some of the gaps currently seen.

The distribution of the known species on a world map (Figure 2) shows that the '*P. variegatum*' clade is widespread across Europe (represented by the questionably single species, *P. pennigerum*), and the species in the Middle East are also of this lineage (*P. orhanelicum* and *P. phoenicium*). It continues to have a rather disjunct distribution, being represented in Sri Lanka (*P. lieftincki*), China (*P. sinense* and *P. trispinum*), the Philippines (*P. boreus*), Papua New Guinea and the Solomon Islands (*P. sedlaceki*), and Australia (*P. pearsonorum*). It is worth noting at this point that Sri Lanka is part of the original Lemurian landmass, breaking off some 109 Ma (Smith and Sandwell 1997; Briggs 2003). Interspersed with these species are members of the '*African*' clade, with *P. indicum* in India, *P. funanense* in China and Vietnam, *P. wouterae* extending through Thailand, Malaysia, Sumatra and Java, *P. olympus* in Borneo and *P. palawana* in the Philippines (Figure 4). Barber-James (2003) suggested that the distribution of *Prosopistoma* species amongst the Indo-Pacific islands follows Huxley's modification of the Wallace line, with Palawan having a different species to the main Philippine Islands. *Prosopistoma boreus* ('*P. variegatum*' clade) is found on Mindanao, while *P. palawana* ('*African*' clade) occurs on Palawan. However, the distribution pattern no longer seems as clear as this as members of both the '*P. variegatum*' and '*African*' clade are found on either side of this hypothetical line. One needs to look at the more recent geological and climatic history of these islands and associated mainland in relation to the distribution pattern seen today to gain greater depth of understanding. To do this in detail would require a much larger database of distribution records than is currently available for the Prosopistomatidae. However, some trends can be extrapolated from what is known. Some parts of the Philippine islands have areas which are over 25 million years old (van der Weerd and Armin 1992), for example Mindanao (where *P. boreus* is found); others

are much younger, from 10 million to 100 000 years only. During the Miocene (24–13 Ma) and again during the Pliocene (5.5–4.5 Ma) (Woodruff 2003), the sea levels in this area were around 100 m higher than present, which would have resulted in much of the land being submerged more than once, thus causing vicariance and speciation in isolated areas that were not submerged, and subsequent secondary dispersal when the sea levels were lower.

The Isthmus of Kra region, a narrow strip of land between Malaysia and Thailand, is a widely recognised biogeographic boundary, representing the transition zone between the Sundaic and Indochinese biotas (sensu Woodruff 2003). The species assemblages of many groups of flora and fauna differ north and south of this region (de Boer and Duffels 1997); e.g. cicadas (Yaakop et al. 2005), butterflies (Corbet 1941), birds (Hughes et al. 2003), frogs and snakes (Inger 1996; Inger and Voris 2001). Such studies have resulted in the postulation that the isthmus was breached during the neogene marine transgressions discussed by Woodruff (2003). Recent phylogeographic analyses of freshwater decapod species (de Bruyn et al. 2005) showed that this biogeographic transition zone between the Sundaic and Indochinese biotas held true for freshwater organisms as well as terrestrial. Examining the distribution of *Prosopistoma* species in this area, *P. wouterae* straddles this region (Figure 4), suggesting a more recent dispersal of this species after the sea level dropped, indicating that it may be a relatively young species.

Considering plate tectonics late in the Neogene, the Australian plate was connected to the eastern side of what is now India. This could imply that *P. pearsonorum*, the Australian species, rather than dispersing from the north, could have been carried on the Australian landmass after its breakup from Gondwana. Subsequent dispersal to Papua New Guinea could have occurred (both *P. pearsonorum* and *P. sedlaceki* are of the '*P. variegatum*' clade). However, the absence of *Prosopistomatidae* across the rest of Australia precludes this hypothesis. It seems more likely that the Australian species arrived by dispersal from the north.

An outlying species that still needs investigating is the one occurring in North Africa (Figure 5), in Algeria (Gagneur and Thomas 1988; Thomas 1998) and the Atlas mountains of Morocco (Touabay et al. 2002). It is likely that it is closely related to the European species. In the western Mediterranean, the Alboran Arc, a small subsea plate, drifted west up against both Spain and North Africa (Duggen et al. 2004). At the same time, deep magmatic upwelling slightly raised the profile of the entire region, resulting in the sealing of the western end of the Mediterranean for about 600,000 years. During this time, the Mediterranean Sea virtually dried up. This would have allowed a greater interchange of fauna between northern Africa and southern Europe, especially at the western end of the Mediterranean basin, where conditions were less harsh and the two adjacent landmasses at their nearest proximity. Thus, the North African species is most likely to have colonised from Europe, and would be expected to be more closely related to *P. pennigerum* than to the nearest African species.

It also would be valuable to examine material from different sites across Europe (Figure 5), to determine whether *P. pennigerum* is really a single widespread species, or whether in fact more than one species is represented here. If one considers the climate difference between a more northerly record such as southern Sweden (Trägårdh 1911), and a southerly record such as Spain (S. Robles, personal communication, 2002, 2008), it would not be surprising to find that there is more than one species here.

Conclusions

Two main lineages within the Prosopistomatidae are evident. A Gondwanan origin is likely for the group as a whole, with a Lemurian origin proposed for the '*P. variegatum*' group, currently clearly represented by three Madagascan species, two Australasian species, three Palaeartic species, and four Oriental species. The other sixteen Afrotropical species and seven Oriental species fall into the '*African*' clade.

Both dispersal and vicariance events evidently played a role in species evolution in this family. Further research is needed to refine the phylogenies presented here, using additional larval morphology with careful analysis of characters, adult morphology and molecular analysis. Although adult material is not available for many of the species, comparison of representatives of each clade is possible. Molecular analysis where fresh material can be obtained will be attempted, again with representatives of both clades, to confirm or refute what has been hypothesised here. A selection of the European species needs to be studied to see whether they are actually represented by more than one species.

Ecological knowledge, such as river size, flow rate, depth, substrate type and season of maturity of the larvae, will also add to the overall understanding of the distribution of this enigmatic group. The validity of the two clades will be tested, and used to decide whether they may represent two separate genera.

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