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Extensive Robertsonian rearrangement: implications for the radiation and biogeography of *Planipapillus* Reid (Onychophora: Peripatopsidae)

D. M. Rowell[1], M. V. Rockman[1]* and N. N. Tait[2]

[1] Division of Botany and Zoology, Australian National University, 0200 Australia
[2] Department of Biological Sciences, Macquarie University, 2109 Australia

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Abstract

The remarkable diversity in chromosome number within *Planipapillus* Reid 1996, the most speciose genus of peripatopsid onychophorans, centred in the alpine region of south-eastern Australia is documented. Robertsonian, whole-arm rearrangements account for the twofold range of diploid numbers in *Planipapillus*. *Ooperipatellus* Ruhberg 1985, another clade of oviparous onychophorans, shows a very different pattern, with no karyotypic diversity among species from Australia and New Zealand. Rate constancy in chromosomal evolution among peripatopsid genera would indicate an ancient radiation in *Planipapillus*, with extant species representing relictual survivors of more recent Pleistocene climatic upheavals. Conversely, if the rearrangements in *Planipapillus* are the result of recent and rapid karyotypic restructuring, the karyotypic and species diversity within the genus may be attributed to recent population fragmentation and isolation resulting from the repeated glaciation and warming cycles of the Pleistocene rather than stemming from a more ancient radiation. Data from other animal groups support a model of accelerated rates of Robertsonian centric fusions concordant with a recent radiation in *Planipapillus*. Karyotype change may be an important factor in the generation and maintenance of *Planipapillus* diversity.

Key words: Centric fusion, Robertsonian rearrangement, chromosomal speciation, Onychophora, peripatus, biogeography, *Planipapillus*

INTRODUCTION

While conservative in most aspects of their anatomy and way of life, members of the phylum Onychophora span the spectrum of reproductive strategies from oviparity with yolky, shelled eggs through ovoviviparity with membrane-enclosed yolky to relatively non-yolky eggs, to yolk-free, placental viviparity (Campiglia & Walker, 1995). The onychophoran faunas of Australia and New Zealand are unique in including oviparous species. The discovery of oviparity and the subsequent identification of oviparous species of onychophorans was accompanied by considerable acrimony and confusion (see Tait, Stutchbury & Briscoe, 1990, for review).

Until recently (Ruhberg, 1985), three species of oviparous onychophorans were recognized:
Ooperipatus oviparus (Dendy 1895) with 15 pairs of legs, widespread along the east coast of the Australian mainland;
Ooperipatellus insignis (Dendy 1890) with 14 pairs of legs from Tasmania and Victoria in southern Australia and the North and South Islands of New Zealand; and
O. nanus Ruhberg, 1985 with 13 pairs of legs from a single locality in the South Island of New Zealand.

Studies of allozymes (Briscoe & Tait, 1995; Tait, Briscoe & Rowell, 1995), chromosomes (Rowell *et al*., 1995), and morphology (Tait & Briscoe, 1990) have revealed that the Australian onychophoran fauna is much more diverse than previously recognized. Furthermore, the degree of variation suggests that the Australian fauna contains a number of very distinct lineages, indicating numerous ancient and more recent radiations. In a major revision of the Australian Peripatopsidae, Reid (1996) recognized 56 species belonging to 30 genera of which 23 species from 12 genera are oviparous. The inferred phylogenetic distribution of these genera within the Peripatopsidae is consistent with multiple independent derivations of oviparity from an ancestral condition of ovoviviparity (Reid, 1996; Gleeson *et al.,* 1998). More recently, Reid (2000) added a further eight species to the four already described from the oviparous genus *Planipapillus* Reid 1996. Considerable allozyme variation among populations

*Present address: Department of Biology, Duke University, Box 90325, Durham, NC 27707-0325 U.S.A.

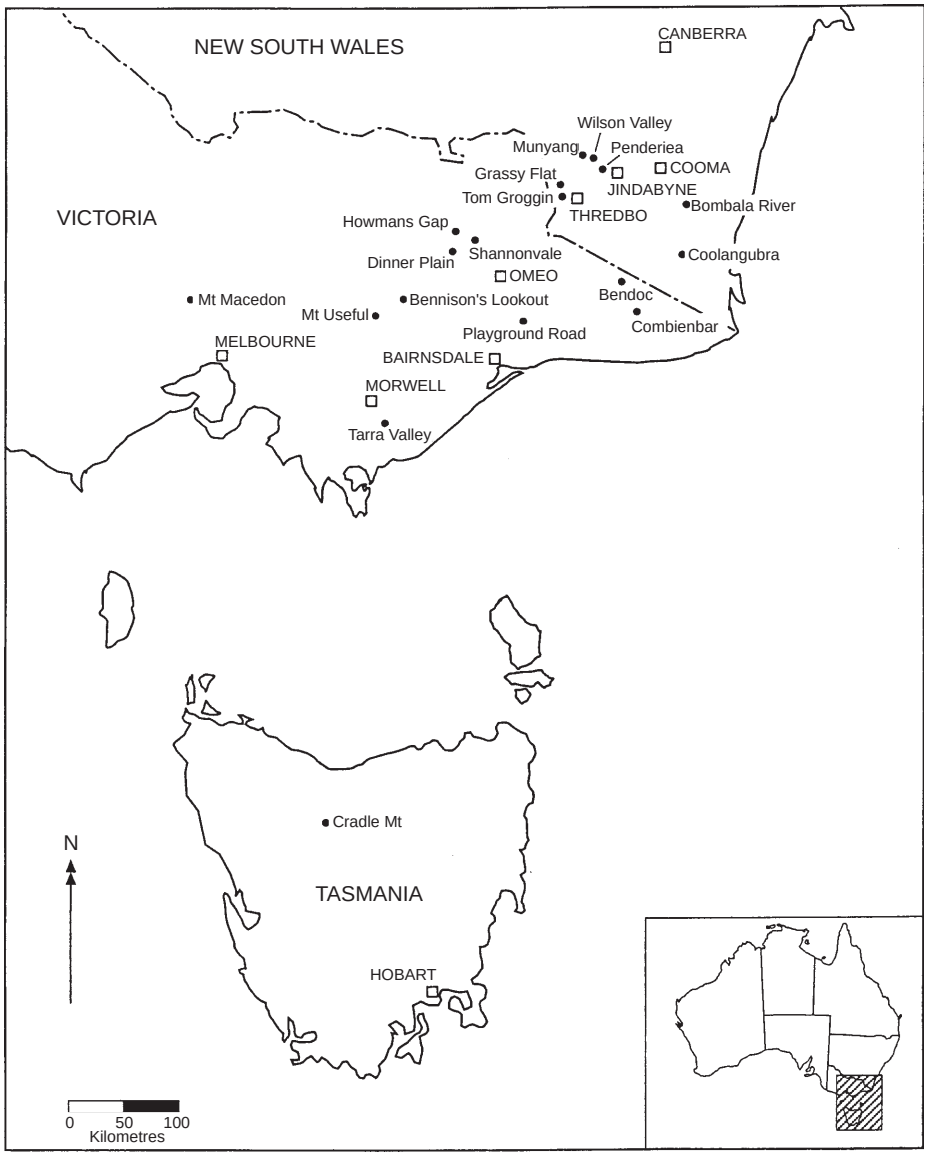

Fig. 1. Collection sites for the species and populations of *Planipapillus* and *Ooperipatellus* listed in Table 1.

referable to *Ooperipatellus insignis* from Tasmania indicate that this is not a full inventory of the Australian oviparous fauna (Briscoe & Tait, 1993). Furthermore, specimens referable to *O. insignis* from New Zealand are genetically distinct from *O. insignis* from its type locality at Mt Macedon, Victoria (Tait & Briscoe, 1995). Reid (1996) also recommends caution in ascribing specimens from other than the type locality to this species.

With 12 described species, *Planipapillus* is the most speciose of all peripatopsid genera and has a geographical distribution covering much of the south-eastern corner of mainland Australia. Although the clade extends to low altitudes in regions of southern Victoria, the majority of species have been identified from the Snowy Mountains of New South Wales and the adjacent Victorian high plains at altitudes over 1000 m (Reid, 2000; Fig. 1). As the range of *Planipapillus* encompasses most of Australia's alpine and subalpine plant communities, biogeographical models describing the history of these communities are also relevant to the evolution and radiation of *Planipapillus*. Climatically the New South Wales and Victorian high country became able to support alpine and subalpine communities sometime between the mid- to late- Miocene and early Pleistocene periods. Subsequent Pleistocene glaciation and warming cycles have resulted in expansions and contractions of this environment associated with repeated fragmentation and fusion of these communities (Smith, 1986). Such cyclical patterns of range expansion followed by contraction and isolation in alpine areas have been implicated in high levels of endemism among plant taxa of apparently relatively recent origin (Morton, 1972). As slow-moving creatures with strict microhabitat requirements, onychophorans would predictably be subject to population fragmentation, isolation and extinction in response to these repeated climatic upheavals. Hence,

Table 1. Collection localities and karyological details for populations and species of *Planipapillus* and *Ooperipatellus*. Numerical designation for undescribed species corresponds with Rockman *et al*. (2001)

Species	Location	Latitude/Longitude	2*n* (male)	Sex chromosomes	No. of specimens
P. biacinaces	Howman Gap, Victoria	36°51′S 147°15′E	40	absent	1
P. bulgensis	Tarra Valley, Victoria	38°29′S 146°31′E	24	absent	1
P. cyclus	Combienbar, Victoria	37°28′S 148°55′E	26	absent	1
P. impacris	Coolangubra, NSW	37°01′S 149°23′E	30	absent	1
P. mundus	Penderlea, NSW	36°26′S 148°30′E	40	absent	6
P. mundus	Wilsons Valley, NSW	36°21′S 148°32′E	40	absent	3
P. mundus	Munyang, NSW	36°19′S 148°25′E	40	absent	3
P. taylori	Bombala R., NSW	36°37′S 149°21′E	38	absent	6
P. sp. 1	Grassy Flat, NSW	36°29′S 148°8′E	22	absent	2
P. sp. 2	Tom Groggin, NSW	36°33′S 148°08′E	20	absent	3
P. sp. 3	Playground Rd, Victoria	37°35′S 147°53′E	32	absent	4
P. sp. 4	Bennison's Lookout, Victoria	37°30′S 146°41′E	32	absent	1
P. sp. 5	Mt Useful, Victoria	37°43′S 146°32′E	36	absent	1
P. sp. 6	Shannonvale, Victoria	36°55′S 147°25′E	38/36[b]	absent	2
P. sp. 7	Bendoc, Victoria	37°9′S 148°53′E	22	absent	2
P. sp. 8	Dinner Plain, NSW	37°01′S 147°15′E	34	absent	5
O, insignis	Mt Macedon, Victoria	37°23′S 144°35′E	42	XY	2
O. sp. 1	Fiordland, NZ	45°03′S 167°55′E	42	[a]	2[b]
O. sp. 2	Cradle Mt, Tasmania	41°38′S 145°57′E	42	[a]	1[b]

[a] Only meiotic preparations were obtained and so sex determination mechanisms could not be identified.
[b] Polymorphic for chromosome number.

the extant *Planipapillus* taxa may represent the surviving fragments of an old radiation persisting from the late Pliocene, or they may be the product of a recent radiation induced by Pleistocene habitat fragmentation with subsequent differentiation leading to speciation, the latter scenario supported by Reid (1996).

In the absence of a robust phylogeny and reliable species descriptions, previous reports on chromosomal variation in the Australian Onychophora have been limited in scope, providing useful qualitative characters for species delineation (Reid *et al.,* 1995: Rowell *et al.,* 1995; Tait, Briscoe *et al.,* 1995), but no insights into the patterns and nature of chromosomal change within individual lineages or clades. However, the taxonomic revision of Reid (1996) identifies monophyletic groupings, with particularly strong support for the *Planipapillus* clade. While the relationships among the 12 species within the genus are unknown, the identification of the group as monophyletic makes it now possible to focus on chromosomal evolution in a single clade within the Australian Peripatopsidae. In this paper, we examine the pattern and process of chromosomal evolution within *Planipapillus* and discuss the significance of the observed chromosomal rearrangements in its radiation and speciation.

MATERIALS AND METHODS

Collection localities

All specimens were hand collected from rotting logs. Specimens were assigned to species on the basis of morphology following Reid (1996, 2000). Specimens whose morphology did not conform to a species diagnosis are designated by numerals. For comparison, specimens from another oviparous genus, *Ooperipatellus* Ruhberg 1985, are included. Species and locality data are given in Fig. 1 and Table 1. Voucher specimens are held by DMR.

Chromosomal preparation

Chromosomes were prepared from testis material using the technique of Rowell *et al.* (1995). As previously reported for onychophorans, the chromosomes were recalcitrant to routine c-banding techniques. These techniques were successful for other taxa analysed simultaneously in the laboratory, indicating that the absence of large c-banding regions is a characteristic of peripatopsid chromosomes. At least 1 karyogram was produced for each specimen and counts verified from a minimum of 5 other cells. Chromosomal size distributions were compared among karyotypes using plots of standardized chromosome lengths as described in Rowell *et al.* (1995).

RESULTS

Karyograms were produced from spermatogonial mitotic cells at metaphase from 19 populations belonging to *Planipapillus* and *Ooperipatellus* (See Table 1 for details). For a number of these, clear meiotic diplotene and metaphase spreads were also obtained, which verified the mitotic counts as every meiosis contained half the number of elements of the mitotic

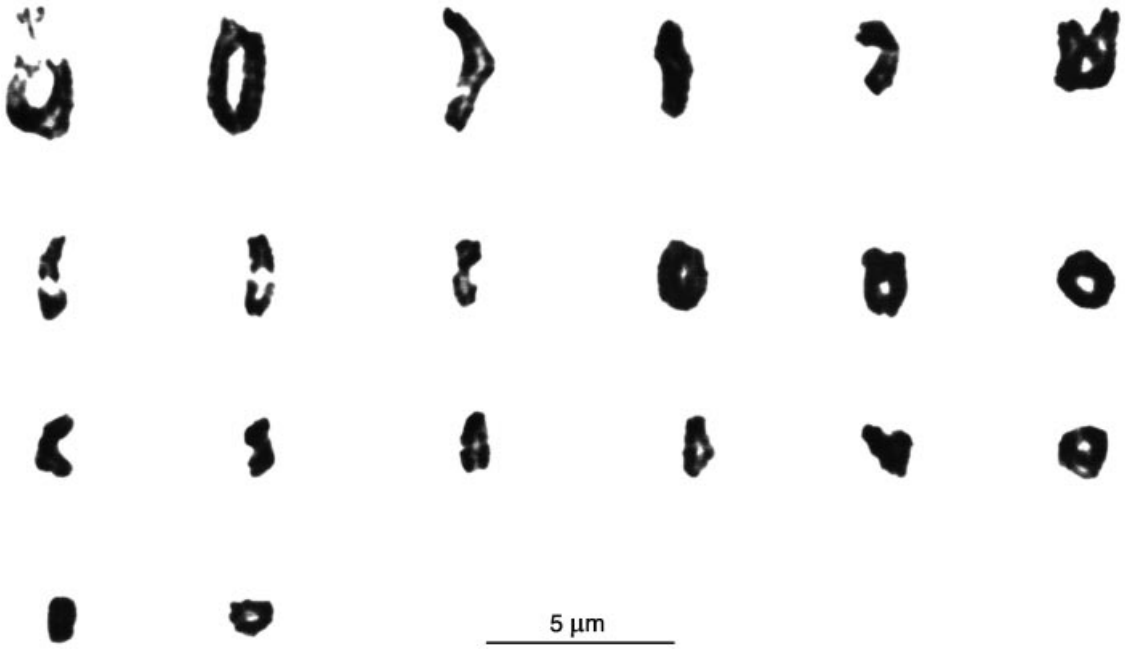

Fig. 2. Meiotic bivalents of *Planipapillus mundus* (see Fig. 4 for mitosis).

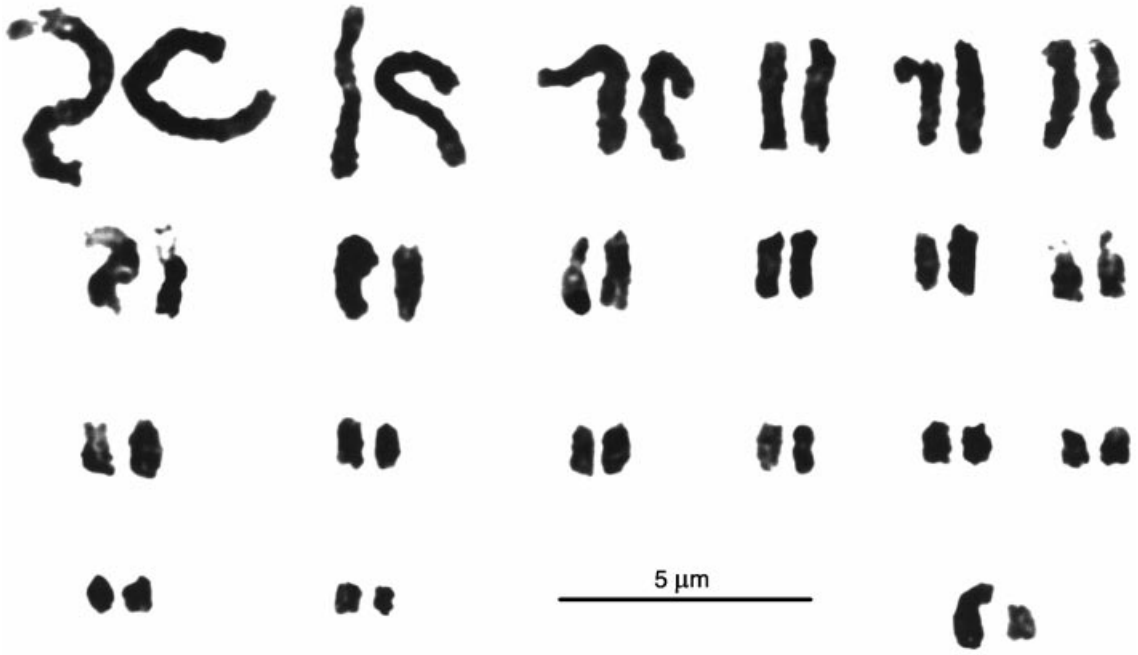

Fig. 3. Karyogram of *Ooperipatellus insignis*. Note presence of heteromorphic sex chromosomes.

spreads (Fig. 2). Chromosome number for *Ooperipatellus* sp. 1 and *Ooperipatellus* sp. 2 was inferred solely from the number of elements visible at meiosis as clear mitotic preparations were not obtained. In these meiotic preparations, the chromosomes were very diffuse making it impossible to establish whether heteromorphic sex chromosomes were present.

A smooth size distribution among some or all of the mitotic chromosomes in each taxon made unequivocal differentiation of each chromosome pair difficult. Nevertheless, karyograms consistent with a normal diploid karyotype were easily constructed in all cases. Moreover, where meiotic preparations were obtained, chiasmate bivalents were clearly visible.

From the appearance of the chromosomes in mitotic and meiotic metaphase and anaphase cells and the fact that they are pulled to the poles by a single point along their length, it is clear that the chromosomes all have localized centromeres. Centromeres were visible in most preparations as gaps or constrictions in the chromosome.

Karyotypes vary markedly between the two genera, but there are distinct similarities among congeners. The diploid chromosome number is the same in all three *Ooperipatellus* populations ($2n = 42$), despite wide geographical separation (Australian mainland, Tasmania and New Zealand). The chromosomes of *Ooperipatellus* include telocentrics, metacentrics and acrocentrics. A heteromorphic pair of chromosomes was visible in mitotic preparations from *O. insignis*, indicative of an XY sex determination system (Fig. 3).

In contrast, *Planipapillus* karyotypes are highly variable in diploid number, with 10 different chromosome numbers ranging from $2n = 20$ to $2n = 40$ observed among the 16 populations analysed. One population (*Planipapillus* sp. 6) was polymorphic, the two individuals examined showing different diploid numbers ($2n = 36$ and 38). Otherwise variation was observed only among species and populations, although this should be verified with larger sample sizes. Nevertheless, the fundamental (arm) number is 40 in all populations. That is, in the $2n = 40$ populations, all chromosomes were telocentric, while in the $2n = 20$ population all possessed an interstitial centromere. The range of karyotypes is consistent with an explosion of Robertsonian rearrangements as illustrated in Figs 4 & 5, where the size distribution of chromosome arms is almost identical between *Planipapillus* sp. 2 ($2n = 20$) and *P. mundus* Reid 1996 ($2n = 40$) (note also that absolute chromosome lengths are comparable between the two). Populations with intermediate diploid numbers showed a mixture of telocentric, metacentric and submetacentric chromosome morphologies consistent with centric rearrangements, and all possible chromosome numbers between 40 (all telocentric) and 20 (all fused) are present, except for $2n = 28$. In the absence of useful markers, such as c-bands, individual chromosomes cannot be reliably identified and hence it is not possible to ascribe homology between chromosomes and chromosome arms among populations.

The similarities among karyotypes within genera are striking, even in *Planipapillus* where, despite differences in chromosome number, the fundamental number and the size distribution of the chromosome arms are conserved. Although the affinities among the karyotypes of the *Planipapillus* are obvious, the relationship between the karyotypes of the two genera is not. The $2n = 42$ of *Ooperipatellus* cannot be reconstructed from the *Planipapillus* karyotypes by simple processes such as Robertsonian rearrangement or polyploidy, nor does the putative XY pair have any parallel in the latter.

DISCUSSION

A striking feature of the karyotypic data is the similarity among the three populations of *Ooperipatellus*, even though they were collected from different land masses. All three show identical chromosome numbers even though the time of separation of New Zealand and Australia is estimated to be 95 MYA (Talent, 1984). While dispersal across oceans has been postulated for some onychophoran species (Hebert *et al.,* 1991), this is considered to be unlikely for Australian and New Zealand taxa given the distances involved and the high degree of allozymic differentiation among *Ooperipatellus* collections from the two land masses: 20 and 21 fixed differences over 21 loci between New Zealand and two Australian populations (Tait & Briscoe, 1995).

Extreme variation in chromosome number has been reported elsewhere for Australian Onychophora although, in the light of the taxonomic revision of Reid (1996), it is clear that this variation occurs among distantly related species only, with more moderate variation among congeners. For example, among the populations analysed in Rowell *et al.* (1995) now referable to *Euperipatoides* Ruhberg, 1985, *E. leuckartii* (Saenger, 1869) and *E. kanangrensis* Reid, 1996 have $2n = 32$, *E. rowelli* Reid 1996 $2n = 33$ and 34, and an undescribed species $2n = 34$. Similarly, in the genus *Cephalofovea* Ruhberg *et al.,* 1998, two diploid numbers occur among species; $2n = 28$ in *C. cameroni* Reid *et al.*, 1995 and *C. clandestina* Reid *et al.*, 1995, and $2n = 34$ in *C. pavimenta* and *C. tomahmontis* (Reid *et al.*, 1995).

In contrast to the karyotypic stability in *Ooperipatellus* and moderate variation in *Cephalofovea* and *Euperipatoides*, *Planipapillus* shows a twofold difference between the lowest and highest diploid numbers. Given the karyotypic similarities among populations of *Ooperipatellus* which have been apparently separated for 95 MY, and if rates of chromosomal change are comparable among genera, the radiation of *Planipapillus* must be very ancient indeed. Under this scenario, the extant species represent the remnants of lineages surviving from an ancient radiation that encompassed the current geographic range. Subsequent climatic upheavals resulted in range fragmentation and the random extinction of chromosomal and morphological intermediates, while gradual chromosomal evolution dating from the time of the original radiation has resulted in the diversity of extant chromosomal forms. A similar sequence of events over a wider geographic and taxonomic range has been put forward to explain the evolution of the Australian Peripatopsidae as a whole, on the basis of extraordinary levels of allozymic and sequence differentiation observed among populations and species (Briscoe & Tait, 1995; Gleeson *et al.,* 1998). However, mitochondrial and nuclear sequence data do not strongly support an ancient origin for *Planipapillus* (Rockman *et al.*, 2001).

The alternative scenario, that the *Planipapillus* radiation is a recent phenomenon, is arguable on the basis of similar patterns of endemism and variability among plant communities in this region attributable to Pleistocene glaciation cycles (Morton, 1972; Smith, 1986). This requires that the rate of chromosomal change has been accelerated in *Planipapillus* in comparison to the other onychophoran genera. The assumption of rate constancy in chromosomal evolution is not robust, and particularly where Robertsonian rearrangements are involved. Robertsonian rearrangements involve fusion of

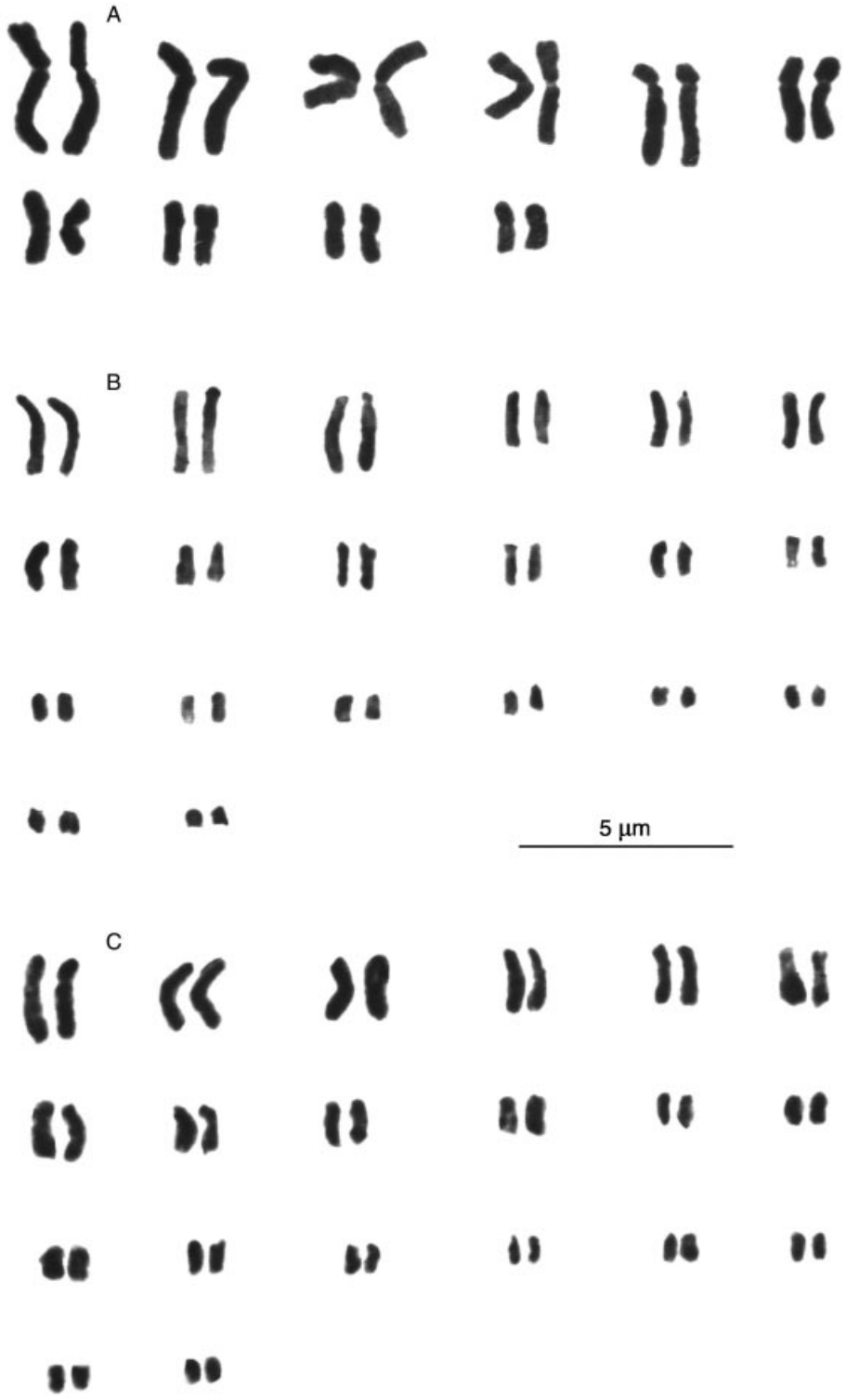

Fig. 4. Karyograms of: (a) *Planipapillus mundus*; (b) *Planipapillus* sp. 2; (c) individual arms for *Planipapillus* sp 2 follow a similar size distribution to *Planipapillus mundus* (see Fig. 5).

telocentric chromosomes at the centromere to form biarmed chromosomes, or fission of biarmed chromosomes to form two telocentric chromosomes. Sporadic chromosomal fusion is well known, for example, human chromosome 2 is a fusion product of two telocentric chromosomes still present in the great apes (Yunis & Prakash, 1982). But there are also many examples from other animal groups where Robertsonian rearrangements have occurred repeatedly and become fixed. Most outgroup and biogeographic analyses favour a scenario of multiple centric fusion, while examples in the literature of multiple, spontaneous fissions are few and equivocal.

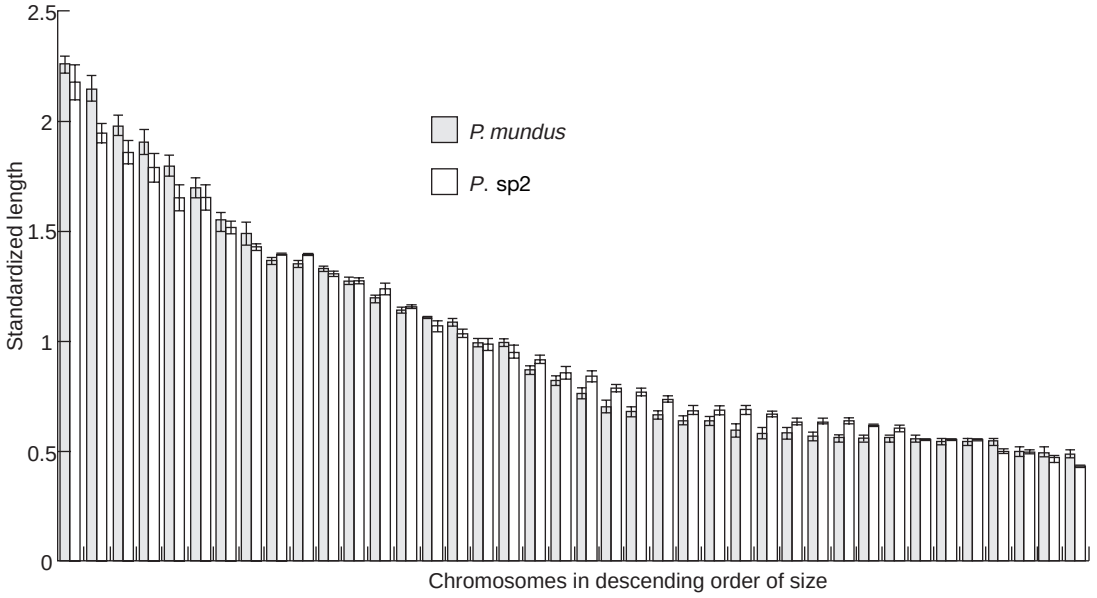

Fig. 5. Comparative plot of chromosome arm lengths for *Planipapillus mundus* (Penderlea, $2n = 40$) and *Planipapillus* sp. 2 ($2n = 20$). All measurements standardized by dividing by total karyotype length. This ratio has been shown to be independent of condensation stage. Measurements averaged for four cells for each species (from three individuals in *P. mundus* and one for *Planipapillus* sp. 2). Bars = standard deviation.

Such repeated Robertsonian rearrangement is not distributed randomly across animal taxa; in some taxa and lineages bursts of rearrangements have occurred on several or many occasions, while others show remarkable karyotypic stability over long periods of time. An excellent example of this has been described in the spiders (Rowell, 1990), where most of species studied (> 330 to date) have entirely telocentric karyotypes while, in a few species that are widely separated taxonomically, the autosomal complement is saturated for Robertsonian fusions (the sex chromosomes may behave independently). Intermediate karyotypes possessing a mixture of telocentric and metacentric autosomes do not occur, except where, of necessity, an odd number of autosome pairs precludes one pair from being involved. This pattern of 'all-or-nothing fusion' can even be seen below the species level in the Australian huntsman spider *Delena cancerides*, where some geographically circumscribed populations have entirely telocentric karyotypes while others exist that are saturated with fusions, of apparently independent derivation (Rowell, 1990). Intermediate forms with a mixture of telocentric and metacentric autosomes are only known from a narrow hybrid zone between a fully telocentric and a fusion-saturated population (Hancock & Rowell, 1995). That these distinct chromosomal races have arisen in the absence of any appreciable morphological or genetic divergence suggests that these bursts of rearrangements are the result of a process that becomes activated in certain lineages, is rapid, and continues to completion.

Similar bursts of Robertsonian rearrangement, in various groups of bats, grasshoppers and rodents, seem to be correlated with accelerated speciation, suggesting that chromosomal fusion may be the driving force behind speciation in certain lineages of these wider taxa (Capanna, Civitelli & Christaldi, 1977; White, 1978; Baverstock Adams & Watts, 1986; Bickham, 1986; Ward *et al.*, 1991; Sage, Atchley & Capanna, 1993). Baker & Bickham (1986) argued that, while heterozygosity for a single fusion may have little impact on fertility, hybrids heterozygous for two or more fusions that share single-arm homology suffer major fitness deficits as a result of segregational failure, leading to speciation through reinforcement of premating isolation mechanisms in hybrid zones ('speciation by monobrachial centric fusions'). Other workers have suggested that changes in chiasma distribution associated with fusions may also play a role in the speciation process through the disruption or construction of coadapted gene complexes (Bidau, 1990; Rowell, 1991; Chatti *et al.,* 1999).

In *Planipapillus*, the relationship between chromosomal change and speciation is unclear. Specific combinations of chromosomal fusion in the European and North American beavers (Ward *et al.,* 1991) and members of the *Rattus villosissimus* species complex, and associated non-disjunction in hybrids of the latter group (Baverstock, Gelder & Jahnke, 1983; Baverstock, Adams *et al.*, 1986) seem to support Baker & Bickham's (1986) model of speciation by monobrachial centric fusions. While there are clear differences among many of the *Planipapillus* populations analysed here, our inability to distinguish individual chromosomes and arms makes the identification of homologous fusions in different populations difficult. An alternative approach would be to establish whether sister taxa in *Planipapillus* are karyotypically distinct, as predicted by the chromo-

somal speciation models. Many of the taxa analysed here are newly described species, and, while their monophyly is well supported (Reid, 1996), a robust phylogeny is not yet available. Moreover, it is not clear whether the two specimens of *Planipapillus* sp. 6, which differed in chromosome number, represent polymorphism within a species, or are cryptic species. A more detailed examination of specimens from this site is warranted.

If *Planipapillus* is undergoing 'all or none fusion', as has occurred among the spiders, the existence of intermediate forms carrying a mixture of telocentric and metacentric chromosomes may be construed as evidence for a recent radiation that is in transition between fully telocentric (for example *P. mundus*) and fully metacentric karyotypes (as in *Planipapillus* sp. 2). Unfortunately, this possibility cannot be addressed without a robust phylogeny for the species and populations within the genus. A phylogeny may show a single, clear and easily followed succession in chromosome number, from an ancestral $2n = 40$ to a derived $2n = 20$ (i.e. 10 fusions having been fixed progressively through the evolution of the group), or it may reveal a much larger number of fusions, with independent reductions in diploid number in many lineages. If rearrangements are concentrated in some lineages and absent in others, we may be able to identify features associated with accelerated karyotype evolution. An assessment of the distributions of karyotype change in the context of a phylogeny will clarify the pattern of karyotype evolution and the processes underlying it.

Clearly there is a need for a phylogenetic analysis of this genus in order for the pattern and process of fusion accumulation to be characterized. Nuclear and mitochondrial sequence data in combination with morphological data are currently being used to address this issue.

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