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TAXON TURNOVER IN ODONATA ACROSS A 3000 m ALTITUDINAL GRADIENT IN SOUTHERN AFRICA

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In Natal, South Africa (30°E, 29°S), the land elevation ranges from 0m a.s.l. to 3000 m a.s.l. along an E-W 200 km transect. The area is in Zonobiome II. It is strongly modified by a montane climate at the higher elevations, and has a subtropical/tropical climate at sea level. A total of 117 spp. was recorded across this transect. The narrow coastal plain (< 200 m a.s.l.) supported 86 spp. From 200-1400 m elevation there was fairly constant species richness of about 43 spp. dropping to 4 spp. between 2400-3000 m. The Libellulidae accounted for 44% of all spp., and declined from 50% in the 0-200 m belt to 25% at 2800-3000 m. The Coenagrionidae accounted for 24% and remained at this level across the whole 3000 m range. The Aeshnidae accounted for 9% and remained fairly constant at about that level up to 1600 m, thereafter increasing to reach 35% at 3000 m. The Gomphidae accounted for 8%, remaining at that level from 0-1400 m, declining to zero at 1600 m. The Lestidae remained fairly constant at about 5% from 0-1600 m, above which they disappeared. The Chlorolestidae ranged from 1% at 0 m increasing steadily to 25% above 2400 m. The Chlorocyphidae, Calopterygidae, Protoneuridae and the Corduliidae are consistently rare, low-altitude families, while the Platycnemididae is a rare middle-altitude family. The Lestidae, Libellulidae, Corduliidae and Gomphidae are moderate-climate families, while the Coenagrionidae is equally tolerant of all climatic conditions. The Aeshnidae tolerate the harsher climate of the high altitudes, and the Gondwana relic family Chlorolestidae is a conspicuous feature of the very high altitudes.

INTRODUCTION

From a biogeographical viewpoint, the Province of Natal in South Africa is particularly interesting (Fig. 1). The coastal plain is warmed by the southward-moving Agulhas current. The warm sea and moderately low latitude (about 29°S) gives a subtropical climate (SCHULZE, 1982) with moderately high summer precipitation. The hinterland climbs steadily, reaching over 3000 m a.s.l. within 200 km (Figs 2 & 3). These altitudes have a severe climate with only a short moderate summer period (PEARSE, 1982).

This geographical setting, within the larger continent of Africa to the North, and a long period of isolation, deposition, uplifting and erosion since the breakup of Gondwana in the late Jurassic/early Cretaceous, about 130 million years ago (PARTRIDGE & MAUD, 1987), provides an ideal natural laboratory for ecological and biogeographical studies. Additionally, the altitudinal gradient lies along one East-West latitudinal transect, thus avoiding interpretive problems associated with changes in latitude.

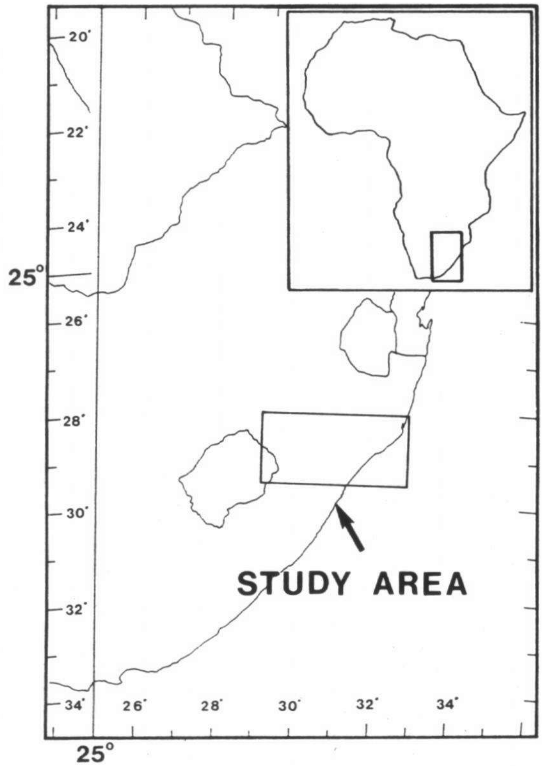

Fig. 1. Location of the study area.

The dragonfly fauna in South Africa, including the Natal altitudinal gradient, has been checklisted by PINHEY (1951, 1984a, 1985). This background provides a valuable taxonomic foundation on which to carry out a biogeographical study. This paper focuses on the taxon turnover of Odonata across the Natal altitudinal gradient up through fifteen 200 m elevation belts. The aim is to determine overall trends at the level of order,

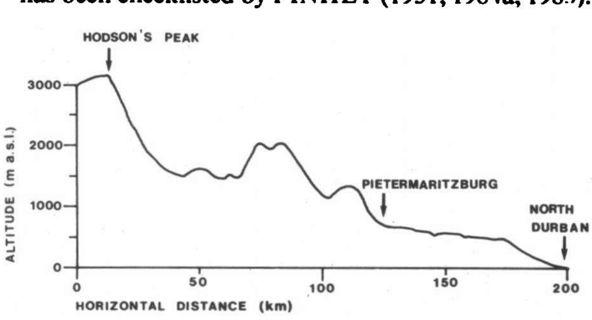

Fig. 2. Topographic West-East profile across the centre of the study area.

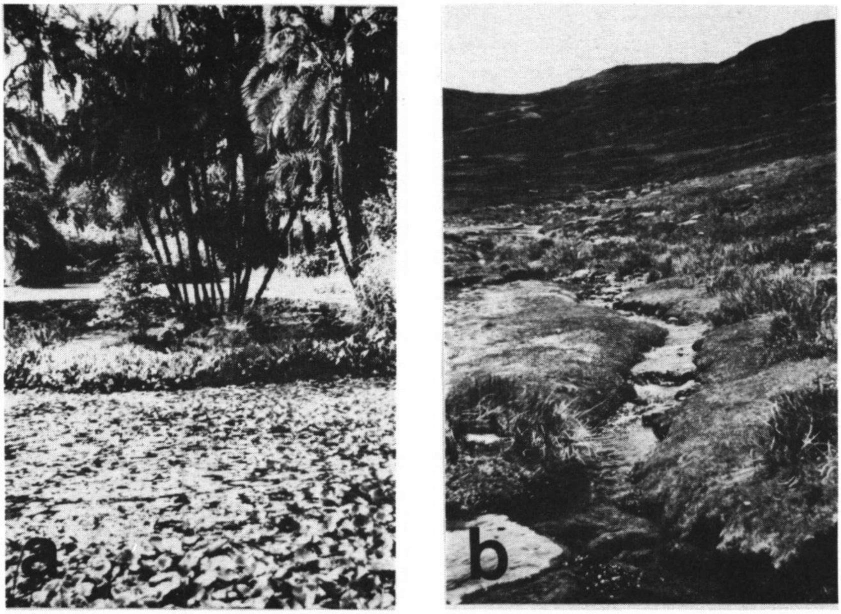

Fig. 3. Range of habitats across the Natal altitudinal gradient: (a) A pond in a subtropical setting at 600 m a.s.l.; (b) Contrast with the bleak setting of a mountain stream at 2900 m a.s.l.

suborder and family, and to relate these trends to general climatic severity.

GEOLOGY AND CLIMATE OF THE STUDY AREA

The geology and topography of the area has been described by KING (1982), although the interpretation of historical events is in dispute (PARTRIDGE & MAUD, 1987). The highest elevations (> 1700 m) comprise a thick succession of volcanic lava beds. These overlie sandstones and mudstones, which in turn overlie basement granites and gneisses. Only the narrow costal strip comprises Cenozoic and Recent deposition.

The southern African climate has been discussed by TYSON (1986), that of Natal by SCHULZE (1982) and that of the Drakensberg by TYSON et al. (1976). Mean January temperatures range from 12° C at 3000 m a.s.l. to 25° C at sea level. Mean July temperatures range from 2° C at the highest altitudes to 17° C at the lowest. Mean annual precipitation is about 1000 mm at the coast reaching 2000 mm on the high Drakensberg. In terms of WALTER & LEITH's (1960-67) climate diagrams, at sea level the Zonobiome is type II (I) a while above 1500 m a.s.l., it is type II 3a.

METHODS

The area under study was 29°0'E to 32°30'E and 28°30'S to 30°30'S. The 200 km east-west transect increased from 0 m a.s.l. in the east to approximately 3000 m a.s.l. in the west. The high elevations are a tableland [Lesotho Plateau and High Drakensberg Escarpment physiographic region (SCHULZE, 1982)] supporting an extensive network of rivers, streams, ponds and bogs.

Between 1 January 1987 and 31 January 1989 over 10,000 km were covered by road to sample as many habitats as possible at all elevations. The altitudes of all sample sites were determined to the nearest 50 m a.s.l. Adults were captured by net, and occasionally taken at electric lights and spiders' webs. Identification was from PINHEY (1951), and the classification followed was that of PINHEY (1984a, 1985). There is insufficient knowledge at this stage to attempt a parallel study with larvae. The conspicuousness of adults and relatively easy identification meant a fairly accurate and comprehensive study could be made. The disadvantage of an adult study is that it is not always clear whether a species is truly resident. This is especially the case for *Pantala flavescens* and *Hemianax ephippiger*. Even oviposition is not necessarily conclusive as evidence that a species can complete its whole life-cycle in the area. However, from teneral adults and from repeated localised observations the residency status of most species could be ascertained.

On completion of the survey, supplementary records from BALINSKY (1961) and PINHEY (1984a, 1985) on a few rare, lowland species was also included to make this survey as realistically complete as possible.

SPECIES RICHNESS

A total of 117 species were recorded, all except one *Enallagma* sp. are described species, viz.

Chlorolestidae

Chlorolestes draconica Bal.
C. fasciata (Burm.)
C. tessellata (Burm.)

Lestidae

Lestes ictericus Gerst.
L. pallidus Ramb.
L. plagiatus Burm.
L. tridens McLach.
L. uncifer Karsch
L. virgatus (Burm.)

Protoneuridae

Elattoneura glauca (Sel.)

Platycnemididae

Allocnemis leucosticta Sel.

Çoenagrionidae

Ceriagrion glabrum (Burm.)
Pseudagrion acaciae Först.
P. caffrum Burm.)
P. citricola Barn.
P. commoniae (Först.)
P. gamblesi Pinh.
P. hageni Karsch
P. inopinatum Bal.
P. kersteni (Gerst.)
P. massaicum Sjöst.
P. newtoni Pinh.
P. salisburyense Ris.
P. spernatum Karsch.
P. sublacteum (Karsch)
P. umsingaziense Bal.
Ischnura senegalensis (Ramb.)
Enallagma elongatum (Martin)
E. glaucum (Burm.)
E. nigridorsum Sel.
E. rotundipenne Ris
E. sinuatum Ris
E. sapphirinum Pinh.
Enallagma sp. ("two-spot frons")
Agriocnemis exilis Sel.
A. falcifera Pinh.
A. gratiosa Gerst.
A. pinheyi Bal.
A.R. ruberrima Bal.

Calopterygidae

Phaon iridipennis (Burm.)

Chlorocyphidae

Chlorocypha consueta (Karsch)
Platycypha caligata (Sel.) *P. fitzsimonsi* (Pinh.)

Gomphidae

Ictinogomphus ferox Ramb.
Lestinogomphus angustus Martin
Notogomphus praetorius (Sel.)
Paragomphus cognatus (Ramb.) *P. elpidius* (Ris)
P. genei (Sel.)
Onychogomphus supinus Hag.
Crenigomphus hartmanni (Först.)
Ceratogomphus pictus Hag.

Aeshnidae

Aeshna minuscula McLach. *A. subpupillata* McLach.
A. triangulifera McLach.
Anax imperator mauricianus Ramb. *A. speratus* Hag.
Anax tristis Hag.
Hemianax ephippiger (Burm.)
Gynacantha manderica Grünb. *G. villosa* Grünb.
G. zuluensis Bal.

Corduliidae

Syncordulia gracilis (Burm.)
Macromia bifasciata (Martin) *M. picta* Hag.
Hemicordulia asiatica Sel.

Libellulidae

Tetrathemis polleni (Sel.)
Notiothemis jonesi Ris
Orthetrum abbotti Calv. *O. brachiale* (Beauv.)
O. caffrum (Burm.) *O. guineense* Ris
O. hintzi Schmidt *O. icteromelas* Ris
O. julia falsum Longfield *O. machadoi* Longfield
O. robustum Balin. *O. trinacria* Sel.
Nesciothemis farinosa (Först.)
Palpopleura jucunda Ramb. *P. lucia* (Dru.)
Chalcostephia flavifrons Kirby
Hemistigma albipuncta (Ramb.)
Acisoma panorpoides ascalaphoides Ramb.
Diplacodes deminuta Lieft. *D. lefebrvrei* (Ramb.)
Crocothemis erythraea (Brullé) *C. sanguinolenta* (Burm.)

Bradinopyga cornuta Ris
Brachythemis leucosticta (Burm.)
Philonomon luminans (Karsch)
Sympetrum fonscolombei (Sel.)
Trithemis aconita Lieft.
T. arteriosa (Burm.)
T. dorsalis (Ramb.)
T. hecate Ris
T. pluvialis Först.
Zygonyx natalensis (Martin)
Olpogastra fuelleborni Grün.
Rhyothemis semihyalina Desj.
Zyxomma atlanticum Sel.
Parazyxomma flavicans (Martin)
Tholymis tillarga (Fab.)
Pantala flavescens (Fab.)
Tramea burmeisteri Kirby
Urothemis assignata (Sel.)
U. luciana Bal.
Macrodiplax cora Brauer

T. annulata (Beauv.)
T. donaldsoni (Calv.)
T. furva Karsch
T. kirbyi ardens Gerst.
T. stictica (Burm.)
Z. torrida (Kirby)

T. continentalis Sel.
U. edwardsi (Sel.)
Aethriamanta rezia Kirby

Figure 4 shows that 11 families were recorded, with their relative percentage abundance following an exponential decrease.

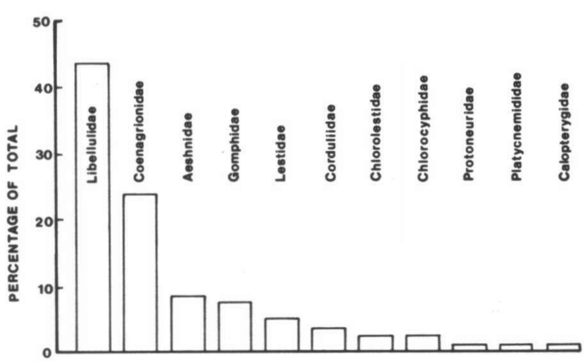

Fig. 4. Proportionate species richness of the odonate families across the Natal altitudinal gradient.

Species richness across the altitudinal gradient showed a sigmoid decrease (Fig. 5). The narrow coastal plain was rich with 86 species. From 200 m a.s.l. to 1400 m a.s.l., species richness was fairly constant at about 43 species. Above 1400 m a.s.l., species richness dropped exponentially, with only 4 species being found above 2400 a.s.l.

BETWEEN-FAMILY COMPARISONS

In terms of number of species per family as a percentage of the total, the Chlorocyphidae, Calopterygidae and Protoneuridae were consistently rare lowland families (Fig. 6). In contrast, the Platycnemididae was a rare middle-altitude family reaching a peak at 1800-2000 m a.s.l. (Fig. 6). The Coenagrionidae

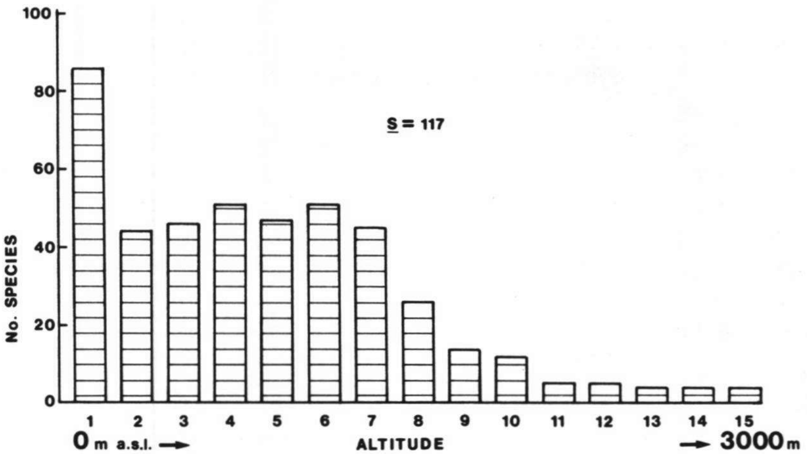

Fig. 5. Decreasing species richness with increasing altitude (a.s.l.) across the Natal altitudinal gradient: 1=0-199 m; — 2=200-399 m; — 3 =400-599 m; — 4=600-799 m; — 5=800-999 m; — 6=1000-1199 m; — 7=1200-1399 m; — 8=1400-1599 m; — 9=1600-1799 m; 10=1800-1999 m; — 11=2000-2199 m; — 12=2200-2399 m; — 13=2400-2599 m; — 14=2600-2799 m; — 15=2800-3000 m.

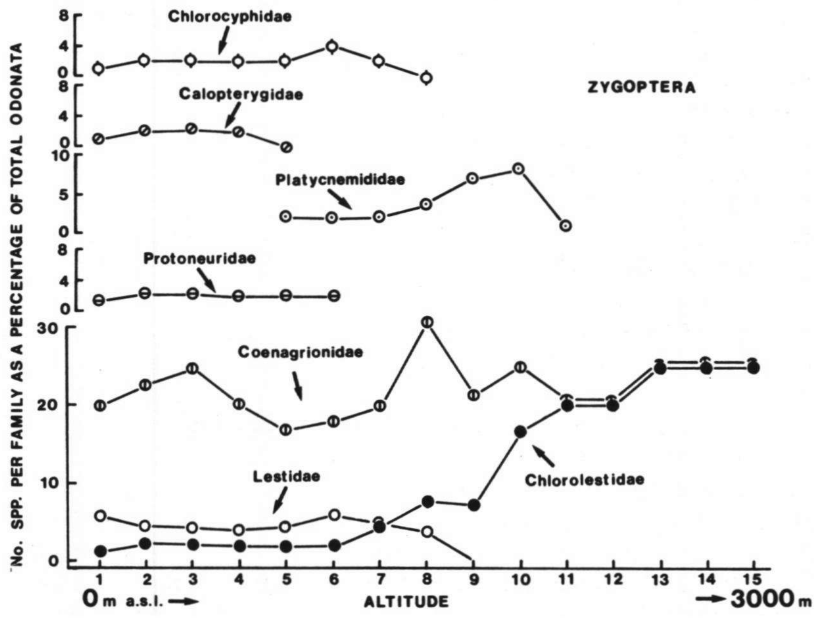

Fig. 6. Proportionate species richness of each zygopteran family as a percentage of total Odonata for each 200 m belt across the Natal altitudinal gradient. — [Altitudinal belts 1-15 as in Fig. 5].

was fairly abundant at about 20% of the total throughout the whole 3000 m altitudinal range. The Lestidae was a moderately rare lowland family, being replaced by the ecologically similar Chlorolestidae at the high altitudes.

By far the most dominant family was the Libellulidae, which accounted for 50% of the total at sea level (Fig. 7). With increasing altitude the percentage dominance decreased erratically, but it was still the most species-rich family up to 2400 m a.s.l., when it became equal with the Coenagrionidae, Chlorolestidae and Aeshnidae. Indeed, the Aeshnidae was the only anisopteran family that steadily increased in species dominance with increasing altitude. The remaining two families, the Gomphidae and the Corduliidae, were consistently rare low-and middle-altitude families.

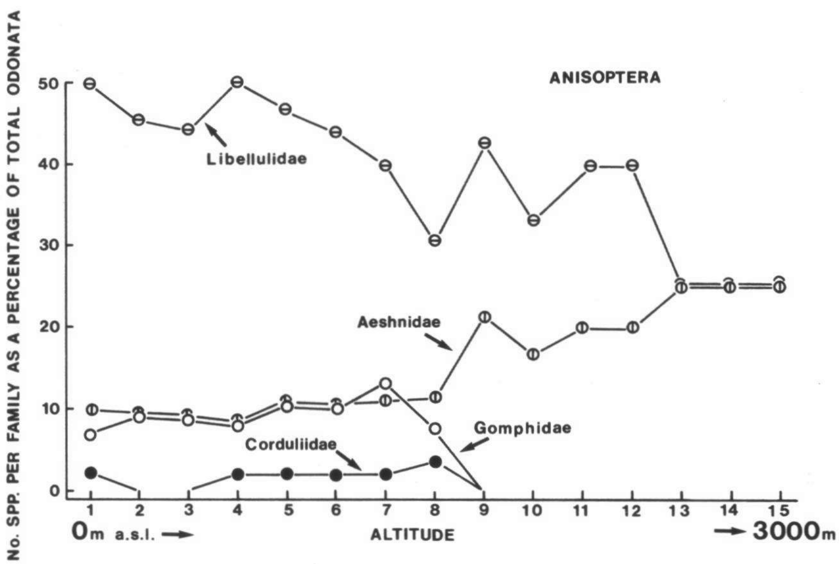

Fig. 7. Proportionate species richness of each anisopteran family as a percentage of total Odonata for each 200 m belt across the Natal altitudinal gradient. — [Altitudinal belts 1-15 as in Fig. 5].

WITHIN-FAMILY COMPARISONS

For each altitudinal belt the percentage number of species at that altitude was calculated as a percentage of the total recorded for that family (Figs 8 & 9). Over 80% of species within the Lestidae and 60% with the Coenagrionidae occurred in the 0-200 m a.s.l. altitudinal band (Fig. 8). For both families, the decline with increasing altitude was at first rapid. This pattern contrasted with that of the Chlorocyphidae, which was richest at 1000-1200 m a.s.l., but dropped sharply thereafter. The Chlorolestidae appeared above 200 m a.s.l. but peaked at 1200-

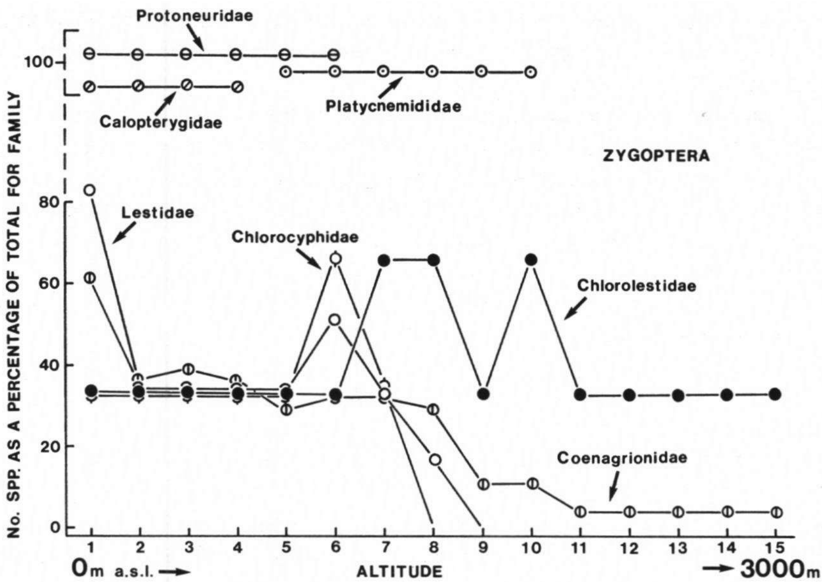

Fig. 8. Proportionate species richness as a percentage of the total for each zygopteran family for each 200 m belt across the Natal altitudinal gradient. — [Altitudinal belts 1-15 as in Fig. 5].

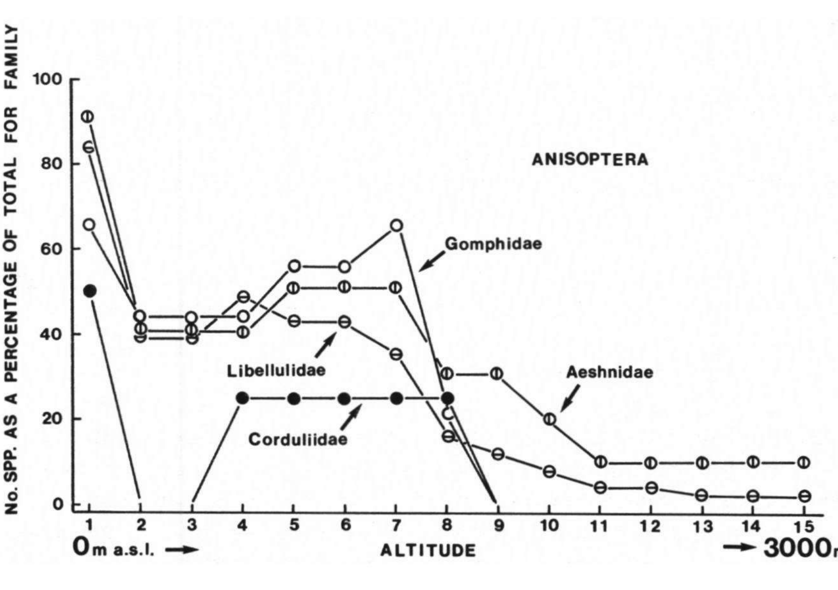

Fig. 9. Proportionate species richness as a percentage of the total for each anisopteran family for each 200 m belt across the Natal altitudinal gradient. — [Altitudinal belts 1-15 as in Fig. 5].

-2000 m a.s.l. The small families (Protoneuridae, Platycnemididae and Calopterygidae), owing to their small number of species, did not show any significant trends (Fig. 9).

Interestingly, the Aeshnidae, Gomphidae and Libellulidae showed very similar trends (Fig. 9), with by far the majority of their species occurring at 0-200 m a.s.l. They troughed between 200 and 600 m a.s.l., but peaked at just over 1000 m a.s.l., before the general decline above 1400 m a.s.l. The same general trend was shown by the Corduliidae, only at a much lower general level (Fig. 9).

DISCUSSION

This survey is fairly exhaustive, but in due course further species are likely to be discovered in the region. Similarly, the altitudinal range of some species is likely to be found to be wider than reported here. However, the general trends at family level will remain very much the same. The study area was relatively species-rich with 117 species, which is a large proportion of the 162 definitely recorded as resident in the South African region (PINHEY, 1984a). One of the reasons for this high number of Natal species is the great variety of biotopes across the altitudinal gradient, and fairly high rainfall (BRINCK, 1955). Additionally, the tropical coastal conditions, which have been so influential on other animal and plant groups (BRUTON & COOPER, 1980) have allowed tropical species to spread far south on the eastern seaboard (BRINCK, 1955; PINHEY, 1978).

The dominant family by far is the Libellulidae, accounting for almost half of all the recorded species. It is always well represented at dams, ponds, marshes and bogs, but generally less common at streams and rivers. Because of the relatively steep altitudinal gradient, the waterways tend to be fast running and generally unsuitable for the usually weed- or mud-inhabiting libellulid larvae.

A quarter of the species were in the Coenagrionidae, which was characteristically tolerant of a wide range of habitats. The same applied to the next most abundant family, the Aeshnidae. It was only these eurytopic families, Libellulidae, Coenagrionidae and Aeshnidae, and the indigenous montane family Chlorolestidae, that were found at the very high altitudes (2800-3000 m a.s.l.). Of the remaining families, none accounted for more than 8% of the total, with the Chlorolestidae, Platycnemididae, Calopterygidae, Chlorocyphidae and Gomphidae generally being associated with running water, and the Lestidae, Corduliidae and Protoneuridae usually associated with still or sluggish water.

Fairly constant species richness (about 43 species) occurred across the middle altitudinal belts from 200 m a.s.l. to 1400 m a.s.l. However, below this, on the coastal plain, richness almost doubled. Besides the advantages of a warm climate promoting larval development, there was a wide range of habitat types. Additionally, there are no mountain chains that might otherwise prevent either temporary or permanent movement south from the species-rich northern areas

(PINHEY, 1962, 1984b). The Lebombo mountains, which run roughly north--south, may possibly channel species into the coastal area.

Above 1400 m a.s.l., species richness declines dramatically. Here, trees on exposed hillsides become infrequent (Fig. 3b), and frosts are a regular feature. The species decline becomes particularly acute above 2000 m a.s.l. This is the sub--alpine zone (1800-2800 m a.s.l.), and begins to encompass the Lesotho Plateau and High Drakensberg Escarpment physiographic region (SCHULZE, 1982) which is well known for its harsh alpine climate (> 2800 a.s.l.) (HILLIARD & BURTT, 1987).

The only two families that become an increasingly greater percentage of the total odonatan fauna with increasing altitude are the Chlorolestidae (Fig. 6) and the Aeshnidae (Fig. 7). The Chlorolestidae is a prominent representative of the montane streams and pools, and constitutes a relic family confined to isolated areas of southern Africa, and of Australia and the Far East (DAVIES & TOBIN, 1984). The Aeshnidae are visually conspicuous at all altitudes and certain species are clearly able to fly up into the alpine zone (e.g. *Hemianax ephippiger*). Others are resident, such as the indigenous *Aeshna minuscula* which is an abundant species in the frost-prone 1800-2000 m a.s.l. belt. The Aeshnidae and Chlorolestidae however, differ considerably in that many species of the Aeshnidae are represented near sea level (Fig. 8), whereas the Chlorolestidae is absent (Fig. 9).

The only family that remains a fairly constant percentage feature at all altitudes is the Coenagrionidae. This is because certain species, particularly *Pseudagrion caffrum* and *Enallagma glaucum* are particularly tolerant of the high altitude climate. Most species however, occur predominantly on the coastal belt. Similarly, the Lestidae is characteristically species-rich at the lowest altitudes, but unlike the Coenagrionidae, it has no representatives that can tolerate the sub--alpine and alpine climates. Ecologically, the Chlorolestidae replaced the Lestidae at the higher altitudes.

The trends in percentage within-family species richness for the Lestidae, Coenagrionidae and all the Anisoptera was remarkably similar (Figs 8 & 9). At the lowest altitudes, over half the species in each family were represented. This immediately dropped to less than half between about 200 m and 900 m a.s.l. For the Lestidae, Coenagrionidae, Gomphidae and Aeshnidae there was a second peak at just over 1000 m a.s.l. The first peak indicates that these families flourish in a warm moist climate, and decline with an increasingly cool climate. The second peak appears to arise from the presence of patchily distributed rare and/or indigenous species e.g. *Agriocnemis falcifera, Aeshna minuscula, Crenigomphus hartmanni* combined with the tendency for overlap between lowland and upland species (e.g. *Pseudagrion salisburyense* and *P. spernatum natalense*). The patchiness and variety of species in the midland plateau region (see Fig. 2) is also due to a wide range of habitats, including marshes (BEGG, 1986) in the area.

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