PHYLOGENETIC RELATIONSHIPS AMONG BEETLES WITHIN THE GENUS ONYMACRIS (COLEOPTERA : TENEBRIONIDAE): A PHENETIC VERSUS CLADISTIC APPROACH

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To Lundi

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DECLARATION

I hereby certify that this thesis is the result of my own original investigation, except where acknowledged herein, and has not been submitted for a degree at any other university.

Signed by candidate

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ABSTRACT

Phylogenetic relationships among species within the beetle genus *Onymacris* (Coleoptera : Tenebrionidae) are identified using phenetic and cladistic approaches. Phylogenetic results from cladistic analyses proved to be more robust than those derived with phenetic approaches. However, phenetic analyses proved to be useful in identifying possible interspecific hybridization. Two monophyletic subgenera are recognized. The subgenus *Melanonymacris* comprises *O. lobicollis*, *O. rugatipennis*, *O. paiva*, *O. boschimana*, *O. multistriata*, *O. hottentota* and *O. plana*, all of which have black elytra. The subgenus *Onymacris* comprises *O. langi*, *O. marginipennis*, *O. brainei*, *O. candidipennis* and *O. bicolor*, all of which have pale-coloured elytra, and two species with black, 'bullet-shaped' ~~eytra~~ elytra, *O. laeviceps* and *O. unguicularis*. The resulting cladogram and the characters and synapomorphies underpinning it are compared with those from an independently conducted study (Penrith 1984). The implications of the cladogram are discussed in the light of the tenets of vicariance biogeography and the constraints of adaptation to the extreme desert environment.

1. PREFACE

The human mind has long been preoccupied with ordering phenomena. Similar objects have been grouped together, and descriptive and collective nouns have proliferated within our vocabularies. These groupings or classifications have facilitated succinctness of expression by providing a means of summarizing information.

Living organisms have not escaped this trend, with Aristotle presenting the earliest formal biological classifications. The success of any classification is directly related to its intelligibility, usefulness and the criteria used in its establishment. Thus, the Aristotelean school attempted to discover 'natural' groupings by "defining the essence of each taxonomic group" (Sneath & Sokal 1973). The practice of assigning individuals to groups or classes using single, readily observed traits has been pursued from Aristotle's time until the present. Although Aristotle perceived an underlying order in nature, the causal basis for the observed similarity patterns was not apparent. As a result of this lack of understanding of underlying process, Aristotle's classifications, and others based on his guidelines, have proved to be inadequate. The publication of Darwin's <u>The Origin of Species</u> (1859) provided a biological watershed. With Darwin's theories on the processes of evolution, the reason for the existence of 'natural' (i.e. genealogically based) groupings became apparent. It was realized that 'natural' taxa were monophyletic groups <u>sensu</u> Hennig (1966). The construction and interpretation of classifications now revolved around the concept of descent from a common ancestor. While earlier systematic works often fortuitously identified natural groupings, this intention could now be pursued explicitly and cognitively. Darwin (1859) himself expressed the wish that "classifications will come to be, as far as they can be so made, genealogies".

While a shift in emphasis had been mooted, the practice and philosophy of systematics changed little for many years after the publication of The Origin (Sneath & Sokal 1973). Wiley (1981) suggests that evolutionary theory marched ahead of systematics, since theorists working toward the Synthetic Theory of evolution concentrated on the processes as opposed to the patterns of evolution. By the time The New Systematics (Huxley 1940) was published, many systematists had expressed dissatisfaction with the state of systematics from both methodological and philosophical perspectives.

Hennig (1966) summarized the views of Paramonow (1935) and Martini (1938), who realized the fundamental inadequacies within systematics, agreeing that the time was ripe for a discussion of the foundations and methods of biological systematics. Similarly, Bather (1927) and Gilmour (1937) addressed the definition of 'natural' taxa. Gilmour (1937), in particular, emphasized that groups should be formed through the comparison of several characteristics, rather than the single defining 'essence' which had been proposed by Aristotle. Gilmour (1937) and Ziehen (1939) raised the question of homoplasy, elaborating upon the drawbacks of the methods of Aristotle.

Homoplasy encompasses the concepts of parallelism and convergence. Parallelism refers to the independent development of similar characters in heterospecific taxa derived from a common origin, whereas convergence reflects the evolution of similar characters in distantly related taxa (Wiley 1981). Any classification based on a single, homoplastic characteristic alone, would be highly artificial and misleading. Similarly, two closely related taxa might not be recognized as such if the 'essential' trait was masked in one group. Gilmour (1937) and Ziehen (1939) suggested that, since natural organisms are in fact multi-dimensional entities, many different characteristics should be considered when constructing a classification. Through analysis of many features, classifications would not only become more robust, but also would have some predictive value. These arguments had also been voiced as early as 1763 by the botanist Adanson.

Three major independent systematic schools arose from the ferment surrounding these philosophical and methodological problems: Evolutionary Systematics, Phenetics and Cladistics. While adherents of each school accepted the theoretical principle of descent with modification as being responsible for the existence and structure of the observed natural system, different approaches were proposed to derive the 'best, natural' classifications.

1.1 Evolutionary Systematics

Mayr (1969) regards the primary goal of Evolutionary Systematics as a maximal representation of the genetic similarity as judged by the phenotype. In other words, the evolutionary systematist wishes to incorporate into a classification as much information about the evolutionary process as possible. Ashlock (1979) claims that "The goal of Evolutionary Systematics (is) to provide classifications of maximum utility through maximum use of evolutionary theory" or, as Bock (1977) states, to include "all laws, mechanisms of change and subfactors thereof".

Hull (1979) has implicitly levelled the criticism that evolutionary systematists attempt to portray too much information in their classifications. Similar reservations were expressed by Sneath & Sokal (1973), who doubt whether rates of evolution could be portrayed accurately, even if they could be measured accurately. Another point of contention is that objectivity is sacrificed by evolutionary systematists when certain features, which best explain preconceived evolutionary processes, are given a priori weighting. Pheneticists and cladists strongly criticize any system of character weighting. Cladists go one step further, and maintain that evolutionary novelties are not even recognized at the correct level by evolutionary systematists, since they do not distinguish between characters which have been retained for a long period and those which represent recent evolution (Eldredge & Cracraft 1980).

Thus, while evolutionary systematists attempted to co-ordinate and maintain the mainstream of systematic thought, the two other 'schools' gained in popularity.

1.2 Phenetics

Phenetics was formalized by the appearance of Sokal and Sneath's (1963) "Principles of Numerical Taxonomy". These authors claim a long intellectual pedigree, tracing similar methodologies as far back as the work of Adanson in 1763. Adanson's lack of success using numerical techniques is attributed to the limited amount of data available in his time, as well as to the absence of the computational aids necessary for handling large data matrices. With improvements in computing and the presence of comprehensive collections, a reapplication of this numerical approach to systematics was possible by the middle of the twentieth century.

The aims of phenetics are stated in Sneath & Sokal (1973) as "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities". Pheneticists aim to "reformulate the process of delineating life's orderliness in a more standardized, repeatable, rigorous and objective fashion" (Sneath & Sokal 1973). The tenet of objectivity is the foundation of the scientific approach adopted by pheneticists. The system retains its integrity through objective data collection, and the unbiased statistical manipulation of these data. Moreover, an almost infinite number of characters can, in theory, be investigated. The more characters used, the better each organism will be described and the resultant classification will be rendered as 'natural' or 'true' as possible.

Pheneticists analyze a broad array of quantifiable morphological, physiological, behavioural and ecological traits of organisms (Sneath & Sokal 1973). No trait, or character, is given any a priori weighting, and, through the process of multivariate analysis, groupings and relationships are identified objectively.

1.3 Cladistics

The other school which rose in response to deficiencies of Evolutionary Systematics was Cladistics. Cladists, who are also known as phylogenetic systematists, follow principles established by Hennig in 1950, who questioned "the tenacious persistence of the idea that biological systematics should deal primarily with creating an inventory catalogue of all plant and animal species" (Hennig 1966). Hennig argued cogently that all classifications should have a phylogenetic component. The primary aim of a phylogenetic or cladistic classification is to act as a general reference system for all biological entities since, ultimately, all taxa are related through descent.

The philosophical basis of cladistics rests with the realization that there are three alternative explanations for the occurrence of shared characters (Hennig 1966). Similar traits may arise as a consequence of homoplasy, or they may have a recent or ancient origin. Taxa which share recently derived homologous characters (apomorphs) share a recent common ancestor, and are therefore closely related. The presence of shared plesiomorphs (primitive characters) provides no evidence of phylogenetic relationship. The identification of these primitive and derived characteristics is the essence of cladistics. The more derived features common to different taxa (i.e. synapomorphies), the more closely they are related. The state of each character, whether primitive or derived, is most often determined through ontogenetic study or comparison with an outgroup, but other methods may be used (Eldredge & Cracraft 1980). A suitable outgroup is one which shares many plesiomorphs and, ideally at least, one apomorph with the group under study. Shared derived features are identified through comparison with the outgroup. Synapomorphs indicate not only the degree of relatedness between taxa, but also identify evolutionary novelties important in defining the taxa. Once synapomorphs have been identified, classifications are constructed by cladists in much the same way as by pheneticists.

Cladistics and phenetics are, superficially, very similar approaches, in that characters are selected, and numerical techniques are used to display similarity patterns inherent in the data. Why then, is there such disagreement between cladists and pheneticists? The most important difference is surely the information content of the classifications.

Phenograms reflect patterns of overall similarity, whereas cladograms include an explicit phylogenetic component. It is around this point that the rhetoric, polemic and spirited debate of recent years has raged (Scoble 1983).

The problem of recognizing and minimizing the effects of homoplasy has also been approached differently by cladists and pheneticists due to the different way in which they view similarity between organisms. Pheneticists attempt to overcome the problem of homoplasy by examining a large number of characters. They argue that the number of convergent and parallel features which are included in a set of characters will be relatively few, and thus any distortion to the classification will be minimal.

Cladists offer an alternative solution, believing that only one cladogram can represent the true phylogenetic relationship between organisms, and that the derivation of this phylogenetic tree is unambiguous. Any homoplasous features included in the analysis will cause ambiguities in the expression of phylogenetic relationship. This implies that many different tree diagrams could be constructed from the same set of characters. The rule of parsimony, described as "economy or simplicity" by Wiley (1981), is thus invoked by cladists. The simplest or most parsimonious cladogram, which is the one least distorted by homoplasy, is selected as the best approximation to the true pattern of evolutionary genealogical relationship. A corollary of this is that the best tree requires the least number of steps to explain any homoplasies included in the data.

Both pheneticists and cladists argue that their methods allow homoplasies to be identified and eliminated, but the similarities do not end there. Both pheneticists and cladists hope that 'true' characters greatly outnumber the homoplasies, and that their respective classifications will thus reflect natural relationship. This hope has been questioned by Gosliner & Ghiselin (1984), who claim that "rampant ~~Rampant~~ parallelism, far from being a peculiarity of certain taxa, may be a general rule". They propose an alternative phylogenetic method which involves character weighting.

In addition to problems dealing with homoplasies, the philosophies of the two schools have suffered other criticism, which is chronicled in the journals Systematic Zoology and Cladistics. Hennig (1966) and Hull (1979) agree that taking extremist positions on scientific issues is wrong. Hull (1979) argues that, during debate, scientists "tend to be suspiciously self-serving". Methodological principles are "designed to put one's opponent at a disadvantage while shoring up one's own position". Thus, while defending their objective and scientific approach to systematics, Sneath & Sokal (1973) claim, "We cannot make use of a phylogeny for classification since in the vast majority of cases phylogenies are unknown". Similarly, pheneticists have been criticized for not proposing hypotheses for testing in the hypothetico-deductive, scientific fashion (Kitts 1978).

If we can accept that the aim of both phenetics and cladistics is to produce the most natural classifications, we must ask whether or not the two systems are reconcilable. Pheneticists claim that cladists sacrifice objectivity in their selection of characters and assignment of apomorphic or plesiomorphic character states (Sneath & Sokal 1973). Cladists argue that it is better to represent something about phylogeny in a classification than nothing at all (Hull 1979), and maintain that a cladogram is, in any event, the most succinct way of summarizing character information (Farris 1979).

A trade-off thus exists between retaining 'objectivity' and obtaining the greatest information content in a classification. Until such time as a compromise is reached by these two schools or one is eliminated, it is useful to consider both approaches in systematics research.

2. INTRODUCTION

2.1 Aims

The aims of this thesis are: 1) to identify phylogenetic relationships between species of the genus *Onymacris* (Coleoptera : Tenebrionidae) through comparative use of phenetics and cladistics; 2) to discuss the resulting phylogeny in the light of vicariance biogeography; and 3) to assess the importance of adaptation in the evolution of these beetles. The use of phenetics and cladistics allows for critical evaluation of the stability of any resultant classification, and highlights the strengths and weaknesses of the two approaches.

2.2 Previous systematic research on *Onymacris*

The genus *Onymacris* is a member of the tribe Adesmiini, and is endemic to the more arid regions of western southern Africa (Penrith 1975). Specifically, *Onymacris* is confined to northern Namaqualand, Namibia and southern Angola (Figure 1). Particular interest in the systematics of this genus has been fostered by the considerable body of comparative work in the fields of ecology, physiology, biochemistry and behaviour of *Onymacris* species (Penrith 1975, 1984). Penrith (1975) identified three species groups within the genus. In the present study, I refer to these as the White, Black and Bullet-shaped groups (Table 1). The White group comprises *O. bicolor*, *O. candidipennis*, *O. langi* and *O. marginipennis*, and is so named because all members have pale-coloured elytra. The Black group includes: *O. boschimana*, *O. hottentota*, *O. lobicollis*, *O. multistriata*, *O. paiva*, *O. plana* and *O. rugatipennis*. These seven species have uniformly black elytra. The Bullet-shaped group comprises two species *O. unguicularis* and *O. laeviceps*. They have black, relatively narrow, bullet-shaped elytra.

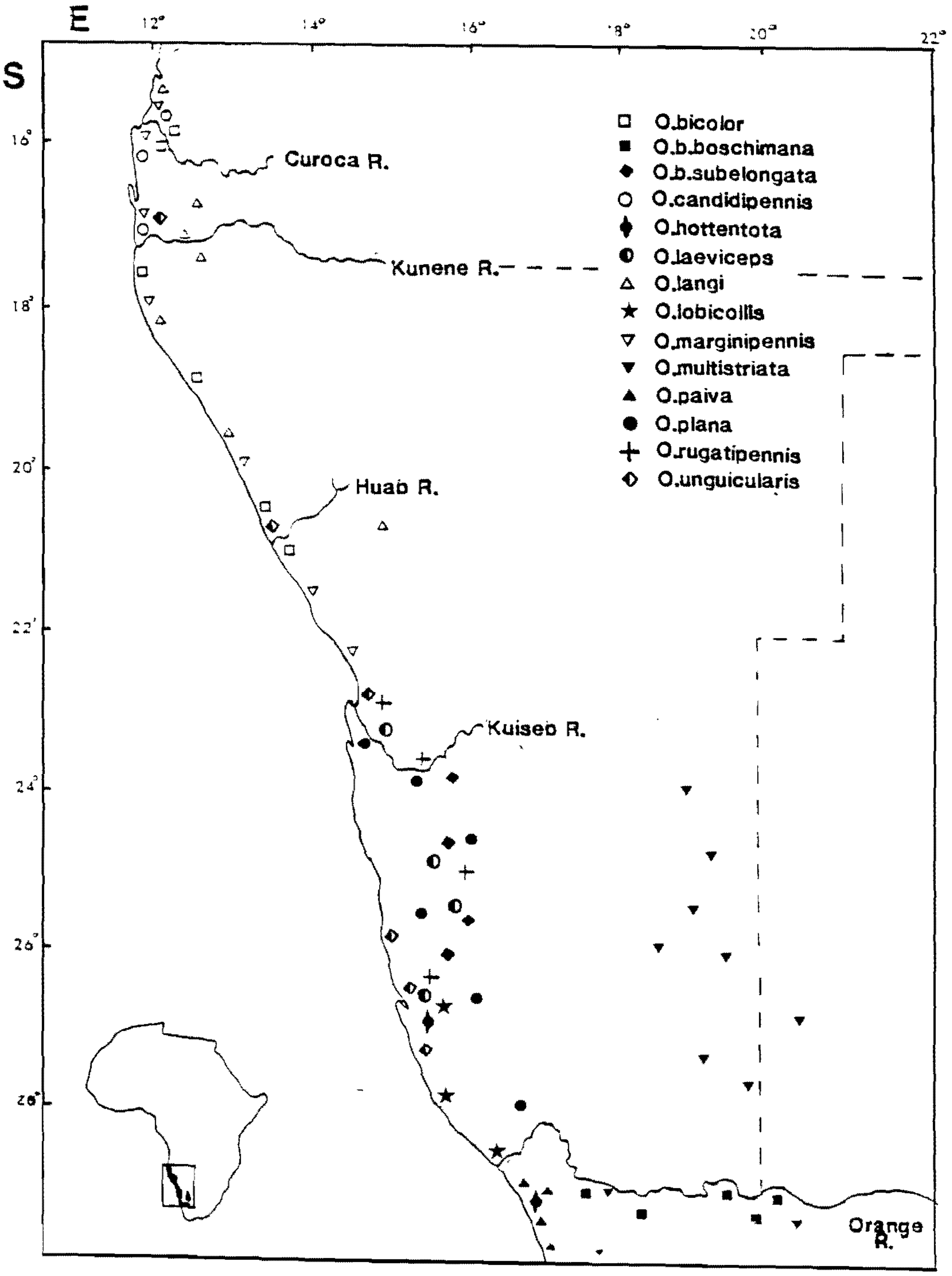

Figure 1 ~~Distributions~~ Distribution of Onymacris spp. Inset shows range of the genus within Africa.

Table 1 Species, subspecies and species groups of the genus _Onymacris_ recognized by Penrith (1975, 1979, 1984). Taxa marked with an asterisk were not available for study.

Species	Group
Onymacris _rugatipennis_ _rugatipennis_ (Haag)	Black
rugatipennis _albotessellata_ Schulze	
Onymacris _lobicollis_ (Fairmaire)	Black
Onymacris _boschimana_ _boschimana_ (Péringuey)	Black
boschimana _subelongata_ Gebien	
Onymacris _paiva_ _paiva_ (Haag)	Black
paiva _conjuncta_ (Haag)	
Onymacris _multistriata_ (Haag)	Black
Onymacris _hottentota_ (Péringuey)	Black
Onymacris _plana_ _plana_ (Péringuey)	Black
plana _debilis_ Koch	
Onymacris _laeviceps_ Gebien	Bullet-shaped
Onymacris _unguicularis_ _unguicularis_ (Haag)	Bullet-shaped
* _unguicularis_ _schulzeae_ Penrith	
Onymacris _langi_ _langi_ (Guérin)	White
langi _cornelli_ Penrith	
langi _meridionalis_ Penrith	
langi _visseri_ Koch	
Onymacris _marginipennis_ (Brême)	White
* _Onymacris_ _brainei_ Penrith	White
Onymacris _candidipennis_ (Brême)	White
Onymacris _bicolor_ (Haag)	White

Prior to Penrith (1984), no phylogenetic study of the genus had been attempted. The research underpinning this thesis overlapped temporally with that of Penrith (1984) and was conducted independently.

2.3 Hybridization

Despite the extensive systematic work on the genus *Onymacris*, identification of species is complicated by the natural occurrence of morphologically determinate ~~identifiable~~, putative hybrids. Penrith (1975) reported a swarm of *O. candidipennis* X *O. marginipennis* hybrids and Hamilton and Penrith (1977) described an inter-generic hybrid between *Physosterna globosa* (now *Physadesmia globosa* (Penrith 1979)) and the sympatric *Onymacris rugatipennis*. A further possible hybrid swarm of *O. candidipennis* x *O. l. cornelli* has also been reported (Penrith 1984). The occurrence of hybridization within *Onymacris* raises some important questions, particularly the problem of the definition of 'species'. Wiley (1981: 25) defines an evolutionary species as a "single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate". It is unlikely that any "definition" of species would adequately accommodate the phenomenon of the naturally occurring hybrids. Indeed, Nelson and Platnick (1981) go as far as to caution against criticising terms such as "species" because "all definitions utilize other words that are themselves in need of definition". Scoble (1983) states that species have a fundamental status in nature irrespective of how they are defined, and used 'morphological criteria' to define species. These intuitive groupings were checked by means of phenetic analysis. This system of phenetic checking of species is also applied in the present study.

Ghiselin (1974) suggested that, since species are the units of evolution, they should be treated as individuals, and Cracraft (1983), like Nelson & Platnick (1981), argues that phylogenetic systematists should not ignore geographically discrete, taxonomically identifiable groups of populations simply because there is a limited amount of 'hybridization' between them and other such taxa. Therefore, the *Onymacris* species described in Penrith's (1975) monograph are adopted as the operational taxonomic units (OTUs) for this study and no individuals from any obvious hybrid swarm are included in the analysis.

2.4 Monophyly

Farris (1974) describes a monophyletic group as "a group of species that includes an ancestral species and all its descendent species". Phylogenetic relationships within the group can therefore be represented unambiguously in the form of a tree diagram. Penrith (1975) questioned the monophyly of *Onymacris*, but linked its constituent species through similar ratios of hind tarsal segment length, extent of tarsal claw hypertrophy and the degree of elytral inflatedness. Morever, she noted the discrete, relatively ~~small~~ unlike geographical distribution of the genus, and the considerable morphological uniformity among the larvae of *Onymacris* species (Penrith 1975). Having examined specimen material of all putative *Onymacris* species recognized by Penrith (1975), I accept the generic synapomorphies identified by Penrith (1975, 1984) and treat the genus as a monophyletic assemblage for the purposes of this thesis.

3. METHODS AND MATERIALS

3.1 Collection of data

Specimens of *Onymacris* were obtained from the Desert Ecological Research Unit at Gobabeb, Namibia, the Windhoek State Museum, the Transvaal Museum and the South African Museum. Localities of individuals and sample sizes for each species studied are shown in Appendix 1. I had no access to the material of a newly described species *Onymacris brainei* (Penrith 1984), a close relative of *O. marginipennis* one of the White species. Since live representatives of all species could not be obtained, characters used in phenetic and cladistic studies were restricted to hard exoskeletal, ~~genetalic~~ genitalic and ovipositional features which are not distorted by pinning and drying. In cases in which the adeagus or ovipositor was not visible, extrusion was induced after immersion of the specimen in hot water for five minutes. Schulze's (1964) key provides some useful character information relating to the larvae of some *Onymacris* species. However, not all species ~~attributed to~~ included in the genus are covered, and visualization of larval characters is difficult, since the specimens are usually wet-preserved and soft-bodied. Therefore, characters from larvae were not included in this present research.

3.2 Sexual dimorphism and subspecies

Penrith (1975) states that adults of all *Onymacris* species are sexually dimorphic in leg length, elytral width and pronotal dimensions. Preliminary statistical analyses of mensural data (Table 2) showed that elytra length and the length of the third

Table 2 Sexual dimorphism in elytra length (ELL) and length of abdominal sternite 3 (ABST3L) in *Onymacris* spp. In every comparison females are significantly (*P* < 0,001; *t* test) larger than males.

Species	N	Sex	ELL (mm)	S.D.	Max	Min	ABST3L (mm)	S.D.	Max	Min
O. bicolor	35	Male	12,74	0,67	14,10	11,62	0,98	0,06	11,0	8,4
	19	Female	15,06	1,13	18,36	13,64	1,66	0,13	19,2	14,6
O.b. boschimana	30	Male	11,95	0,90	13,84	9,30	0,91	0,10	11,4	5,6
	30	Female	14,65	1,40	17,04	12,08	1,72	0,19	20,8	14,6
O.b. subelongata	31	Male	10,69	0,58	12,00	9,08	0,80	0,05	9,2	7,0
	21	Female	13,41	0,96	15,32	12,10	1,63	0,11	18,6	14,6
O. candidipennis	29	Male	14,14	1,06	16,64	12,80	1,22	0,13	14,6	9,8
	31	Female	17,53	1,20	19,78	14,06	1,95	0,16	22,8	15,0
O. hottentota	30	Male	10,37	0,93	12,46	8,30	0,93	0,08	11,4	7,8
	30	Female	12,01	0,95	14,00	9,94	1,43	0,10	15,8	12,2
O. laeviceps	28	Male	11,61	0,84	13,86	10,14	0,78	0,10	10,2	5,6
	30	Female	13,56	0,98	15,46	11,68	1,40	0,11	16,2	12,2
O. langi	34	Male	12,66	1,36	15,88	10,52	0,95	0,12	11,8	7,2
	26	Female	13,96	1,45	17,78	10,72	1,51	0,15	18,4	13,0
O. lobicollis	28	Male	11,59	0,86	13,64	10,20	1,11	0,11	13,0	9,0
	31	Female	14,11	1,16	16,44	11,90	1,59	0,13	20,0	13,8
O. marginipennis	28	Male	12,26	0,97	14,00	10,02	0,84	0,11	10,8	6,4
	31	Female	13,67	1,20	16,68	11,12	1,57	0,14	18,8	13,2
O. multistriata	30	Male	10,75	0,86	12,30	9,10	0,89	0,08	10,6	7,6
	30	Female	12,87	1,11	14,92	10,60	1,51	0,15	19,2	13,0
O. paiva	31	Male	10,84	0,63	12,00	9,44	0,99	0,07	11,2	8,6
	29	Female	13,54	0,76	14,80	11,98	1,71	0,10	20,0	15,6
O. plana	30	Male	13,75	1,28	16,00	10,88	0,90	0,09	11,2	7,4
	26	Female	15,15	1,31	17,24	11,76	1,52	0,16	18,4	10,6
O. rugatipennis	30	Male	12,43	1,21	15,62	10,62	0,95	0,11	12,0	7,8
	29	Female	15,46	0,83	17,86	13,44	1,61	0,11	19,0	14,0
O. unguicularis	24	Male	11,76	1,19	14,80	9,40	0,84	0,09	10,4	6,6
	29	Female	13,28	1,32	15,72	10,76	1,32	0,14	15,8	9,6

abdominal sternite are also sexually dimorphic. Therefore, the sexes are treated separately throughout in all analyses of mensural data.

Not all subspecies ascribed to *Onymacris* spp. were analyzed. Both subspecies of *Onymacris boschimana* were analyzed, but for *O. rugatipennis*, data for the two subspecies were pooled as no statistically significant mensural difference was evident in preliminary analyses. *O. paiva* and *O. plana* were accorded the same treatment. Owing to small sample sizes, of the four *O. langi* subspecies, mensural data only for *O. langi langi* are presented.

3.3 Phenetic analysis - mensural characters

22 characters (Table 3; Figure 2) were measured to 0,05 mm accuracy, 13 using specially ground vernier calipers, and nine using a microscope graticule. The untransformed character data were analyzed using uni- and multivariate statistical programs from the BMDP series (Dixon 1981). Specifically, BMDP-7D was used to obtain univariate statistics, and patterns of multivariate phenetic similarity were obtained using factor analysis (BMDP-4M) and cluster analysis (BMDP-2M).

In factor analysis, principal components analysis was used to extract initial factors, which were subsequently subjected to a varimax rotation. Since the number of specimens was too large for a cluster analysis of the entire data set, only mean values of each character for each species (obtained from the BMDP-7D run) were used. In these analyses, euclidean distance and a centroid clustering algorithm were used to construct phenograms.

3.4 Size

In multivariate analyses, mensural character data were also $\log_{10}$ transformed in an attempt to de-emphasize the effects of

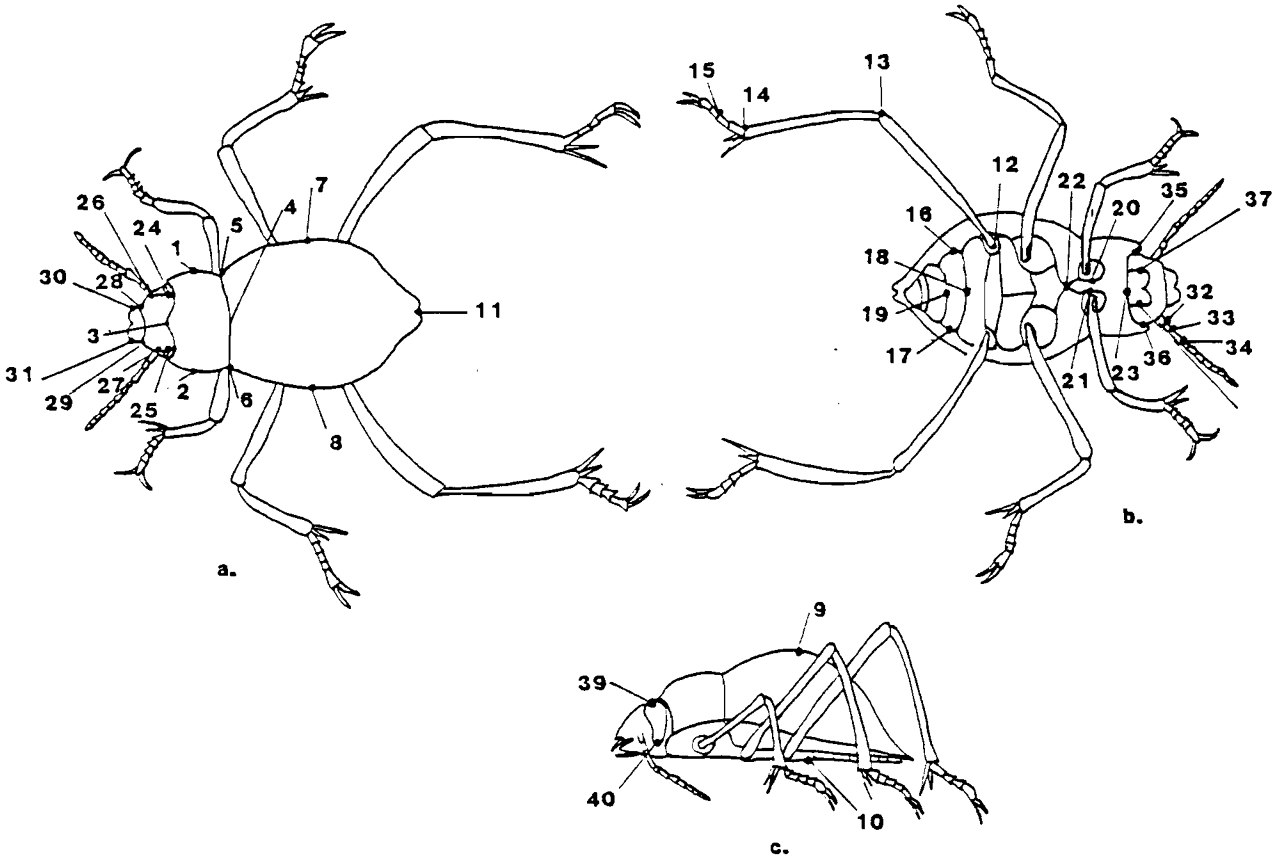

Figure 2 Dorsal (a), ventral (b) and lateral (c) views of a typical Onymacris beetle indicating reference points for mensural characters. See Table 3 for descriptions of mensural characters.

Table 3 Description of mensural characters from the exoskeleton of the Onymacris species and subspecies. Characters 1 to 13 were measured with vernier calipers and 14 to 22 with a microscope graticule.

Character number	Character abbreviation	Reference points in Figure 2		Description of character
1	THW	a	1-2	thoracic width at widest point
2	THL	a	3-4	thoracic length (mid-dorsal)
3	WAIST	a	5-6	width at junction of pronotum and elytra
4	ABW	a	7-8	width of abdomen (at widest point)
5	ABD	c	9-10	maximum abdominal depth
6	ELL	a	4-11	mid-dorsal elytral length
7	FEM3	b	12-13	length of femur (leg 3)
8	TIB3	b	13-14	length of tibia (leg 3)
9	TARL	b	14-15	combined length of tarsal segments 1 and 2 (leg 3)
10	ABST3W	b	16-17	width of abdominal sternite 3
11	ABST3L	b	18-19	mid-ventral length of abdominal sternite 3
12	PTLS	b	20-21	minimum distance between prothoracic legs
13	PAL	b	22-23	length of prosternal apophysis from anterior edge of pronotum
14	INTOC	a	24-25	distance between eyes (dorsal)
15	INTANT	a	26-27	distance between antennae (dorsal)
16	CLYP	a	28-29	clypeal width
17	LABRW	a	30-31	width of labrum
18	ANT2	b	32-33	length of 2nd antennal segment
19	ANT3	b	33-34	length of 3rd antennal segment
20	GENA	b	35-36	genal width
21	LABIW	b	37-38	width of labium
22	EYE	c	39-40	length of eye

intraspecific size variation, as well as to detect their possible effects on the results of cluster analysis. The transformation of data to reduce the effect of size has been criticized by Wood (1983), who questions the assumption that interspecific variation in size is unimportant from an evolutionary point of view.

3.5 Cladistic and phenetic analysis - qualitative characters

32 qualitative characters (Table 4) were analyzed using the WAG-78 cladistic analysis program (Farris 1970), and an all-plesiomophic species was selected as the hypothetical ancestor. Character state polarity was determined by means of the outgroup method (Wiley 1981; Watrous and Wheeler 1981), with the outgroup comprising *Physosterna cribipes*, *Physadesmia globosa*, *Stenocara gracilipes*, *Cauricara phalangium rufofemorata* and *Epiphysa arenicola* - all species from other adesmiine genera. For comparative purposes, this same character matrix was analyzed phenetically using cluster analysis (BMDP-2M).

Table 4 Descriptions and states of qualitative characters used in cladistic analyses

Character no. and description	Character states
1. adeagus shape:	0 mitre shaped, 2 tapering
2. width of ovipositor sclerites:	0 thin, 1 wide
3. shape of femur at trochanter:	0 rounded, 1 + 2 intermediate states, 3 pointed
4. foreleg comb in male:	0 absent, 1 present
5. tarsal claw size:	0 small, 1 medium, 2 large and expanded
6. projections on mesothoracic femur:	0 absent, 1 present
7. elytral convexity:	0 globose, 1 intermediate, 2 flattened
8. elytral carina:	0 sharply defined, 1 faint
9. roughness of elytra:	0 sculptured, 1 smooth
10. pseudo-pleural crest:	0 present, 1 ill-defined, 2 absent
11. nature of elytral indentations:	0 absent, 1 ill-defined, 2 obvious
12. form of elytral sculpture:	0 rugose, 1 parallel venation, 2 smooth, 3 smooth with bumps
13. pattern of elytral costae:	0 few elytral costae, 1 many elytral costae
14. thoracic rugosity:	0 smooth, 1 intermediate, 2 pitted
15. thoracic indentations:	0 absent, 1 two indentations
16. thorax length to width ratio:	0 < 1:3, 1 > 1:3
17. prosternal apophysis shape:	0 angular, 1 intermediate, 2 mitre-shaped and rounded
18. sternite configuration above mesothoracic leg:	0 overlapping, 1 touching, 2 adjacent
19. lateral pronotal carina:	0 present, 1 absent
20. sternite flatness:	0 flat, 1 indented
21. antennal tip shape:	0 rounded, 1 pointed
22. meriston to pedicel ratio:	0 > 2,5, 1 < 2,0
23. clypeus shape:	0 straight at sulcas, 1 angled
24. degree of clypeal identation:	0 little, 1 marked
25. supra-orbital ridge:	0 present, 1 well defined
26. antennal thickness	0 slender, 1 thick
27. elytral side verticality:	0 subvertical, 1 vertical
28. elytral hardness:	0 hard, 1 soft
29. metathoracic femur to elytra ratio (male):	0 << 1, 1 = 1, 2 >> 1
30. colour of elytra:	0 black, 1 pale
31. colour of appendages:	0 black, 1 reddish
32. tarsi 1 and 2 to tibia ratio:	0 > 5,2, 1 < 4,8

4. RESULTS

4.1 Phenetic analyses

Factor analysis of untransformed mensural data explained more of the variance than did analysis of log-transformed data (Table 5), and produced very similar factor score plots. Therefore, only factor analysis results for untransformed mensural data are presented below. However, the cluster analyses of transformed data yielded markedly different phenograms from those of untransformed data and are therefore presented separately.

4.1.1 Factor analysis

Plots of the factor 1 vs 2 scores for the female and male *Onymacris* data are given as Figures 3 and 4. Results for each species and subspecies are displayed as one standard deviation 'envelopes' around the group mean factor scores. Table 6 lists characters which were heavily weighted in the two factors. For *Onymacris* females, differences in thorax length (a measure of overall size) and abdomen and head-related characters account for much of the variance along factor 1, whereas eye and abdomen-related characters dominate in factor 2. In factor analysis of data for males, thorax length and head and abdomen-related characters separate the species along factor 1, and measures of antenna length and leg length account for the vertical displacement in factor 2.

The factor analysis species plots for *Onymacris* are similar for both females (Figure 3) and males (Figure 4), despite differences in factor weightings between sexes. Members of the Black group tend to fall above the Y = X axis, and members of the White and Bullet-shaped groups below. Black males, plus one of the Bullet-shaped species (*O. laeviceps*), have longer legs (factor 2) and smaller heads and abdomens (factor 1).

Table 5 Cumulative variances explained by factors 1 and 2 for untransformed and log-transformed data in factor analysis

Sex of individuals	Nature of data analysed	Variance explained % Factor 1	 Factors 1+2
Female	Untransformed	65,12	78,12
Female	Log-transformed	63,62	76,28
Male	Untransformed	59,15	75,80
Male	Log-transformed	58,73	72,64

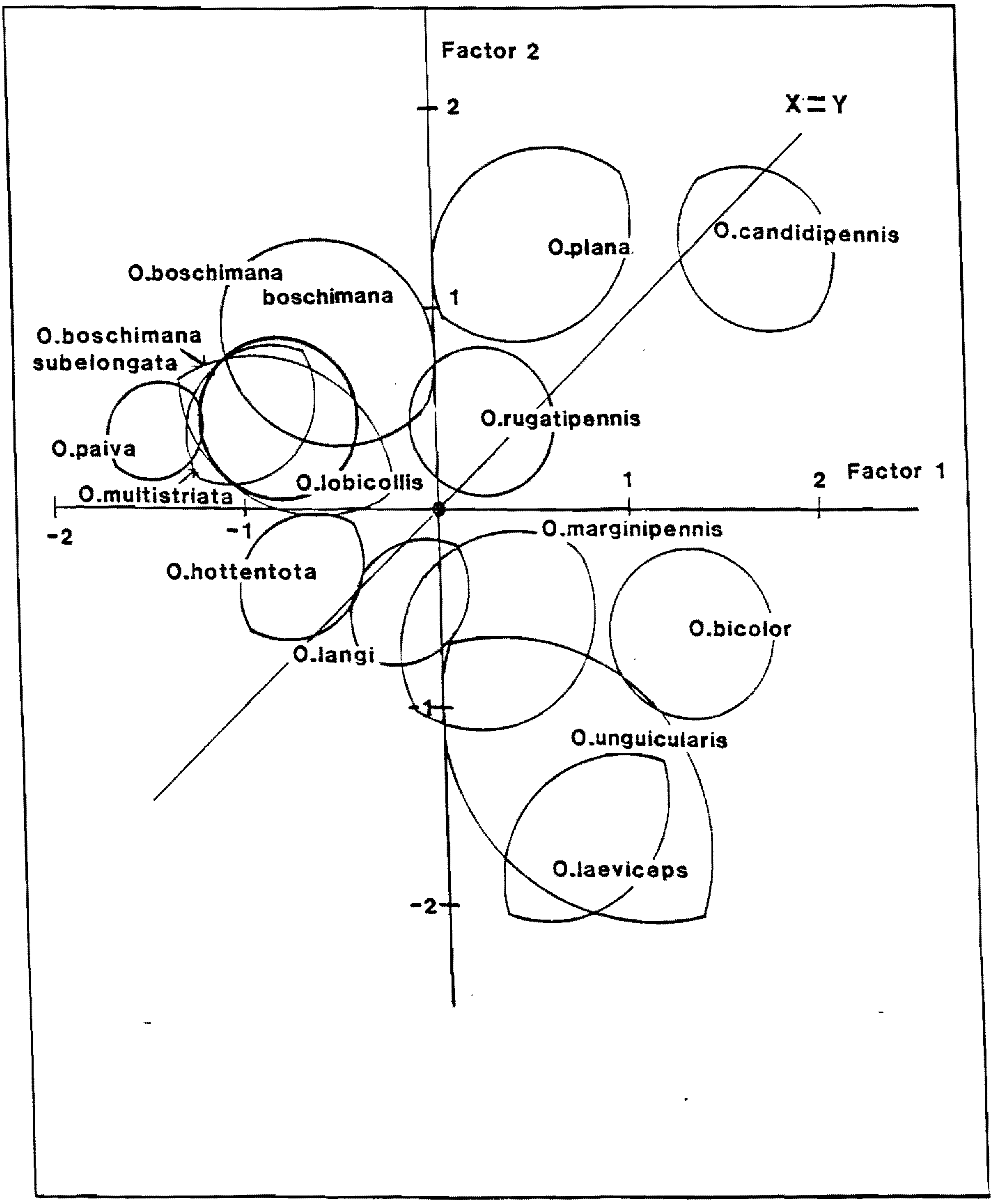

Figure 3 Plots of factor analysis scores for Onymacris spp. females from analysis of mensural characters.

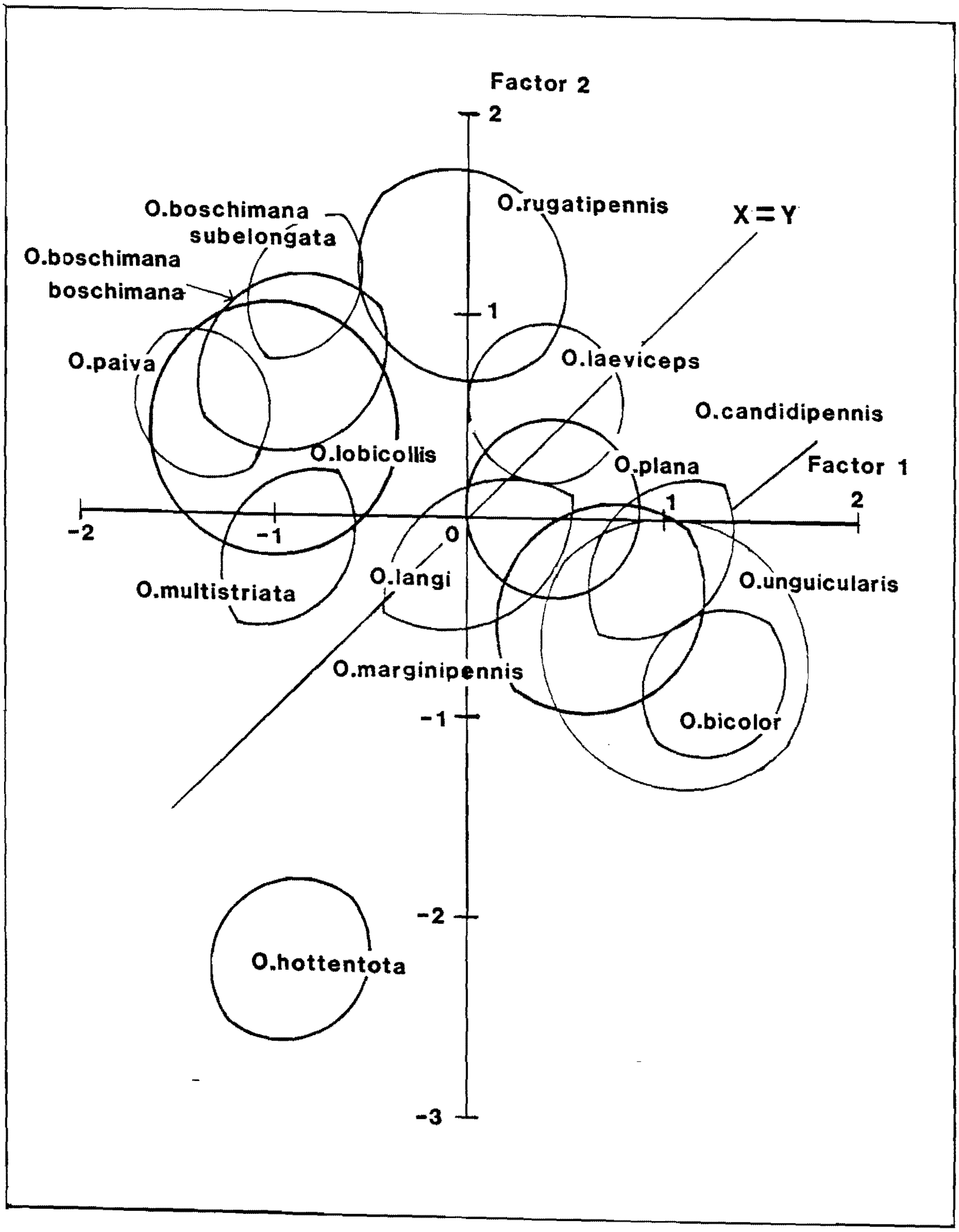

Figure 4 Plots of factor analysis scores for <u>Onymacris</u> spp. males from analysis of mensural characters.

Table 6 Sorted factor loadings of the 22 mensural characters of the Onymacris species and subspecies. See Table 3 for a key to character abbreviations.

Females			Males		
Character no. and abbreviation	Factor 1	Factor 2	Character no. and abbreviation	Factor 1	Factor 2
2 THL	0,949	0,000	15 INTANT	0,954	0,000
15 INTANT	0,946	0,000	2 THL	0,936	0,000
14 INTOC	0,919	0,000	14 INTOC	0,911	0,000
20 GENA	0,811	0,334	18 ANT2	0,877	0,000
16 CLYP	0,807	0,320	10 ABST3W	0,819	0,000
10 ABST3W	0,800	0,473	6 ELL	0,788	0,297
1 THW	0,785	0,523	16 CLYP	0,780	0,000
21 LABIW	0,783	0,365	20 GENA	0,770	0,251
18 ANT2	0,773	0,000	21 LABIW	0,761	0,316
3 WAIST	0,772	0,531	19 ANT3	0,000	0,875
5 ABD	0,702	0,499	8 TIB3	0,000	0,868
6 ELL	0,702	0,628	9 TARL	0,000	0,861
22 EYE	0,394	0,833	7 FEM3	0,000	0,760
4 ABW	0,321	0,819	Cumulative variance explained	0,59	0,76
11 ABST3L	0,000	0,752			
8 TIB3	0,000	0,718			
Cumulative variance explained	0,65	0,78			

4.1.2 Cluster analysis

Phenograms constructed from the group means of untransformed and log-transformed mensural data are presented in Figures 5 (females) and 6 (males). The amalgamation distances for the log-transformed plots were converted to the same scale used in the untransformed phenograms. Broad groupings, similar to those obtained by factor analysis (Figures 3 and 4), are also apparent in these phenograms. The two phenetic nearest neighbours of each species are listed in Table 7.

In these phenograms and Table 7, the Black beetles (group 3) cluster together, whereas members of the White group (group 1) usually cluster with the two Bullet-shaped species (group 2). O. plana, due to its atypical physiognomy (large females; broad, flat males), and the tiny O. hottentota and large O. candidipennis are usually 'outliers' in these phenograms.

Cluster analysis of the qualitative character data in Table 8 shows two major groupings (Figure 7): the White and Bullet-shaped species join a distance of 3,38 and the Black species and hypothetical ancestor at 3,21. There are no outliers in this phenogram, but, once again, there is evidence of 'hybridization', with O. langi cornelli linking with O. marginipennis and O. candidipennis and not with other O. langi subspecies.

4.2 Cladistic analysis

The cladogram generated by the WAG-78 program (Figure 8) from the data presented in Table 8 shows that Onymacris species also separate into two major groups. The Black species link closely with the hypothetical ancestor, whereas the White species share

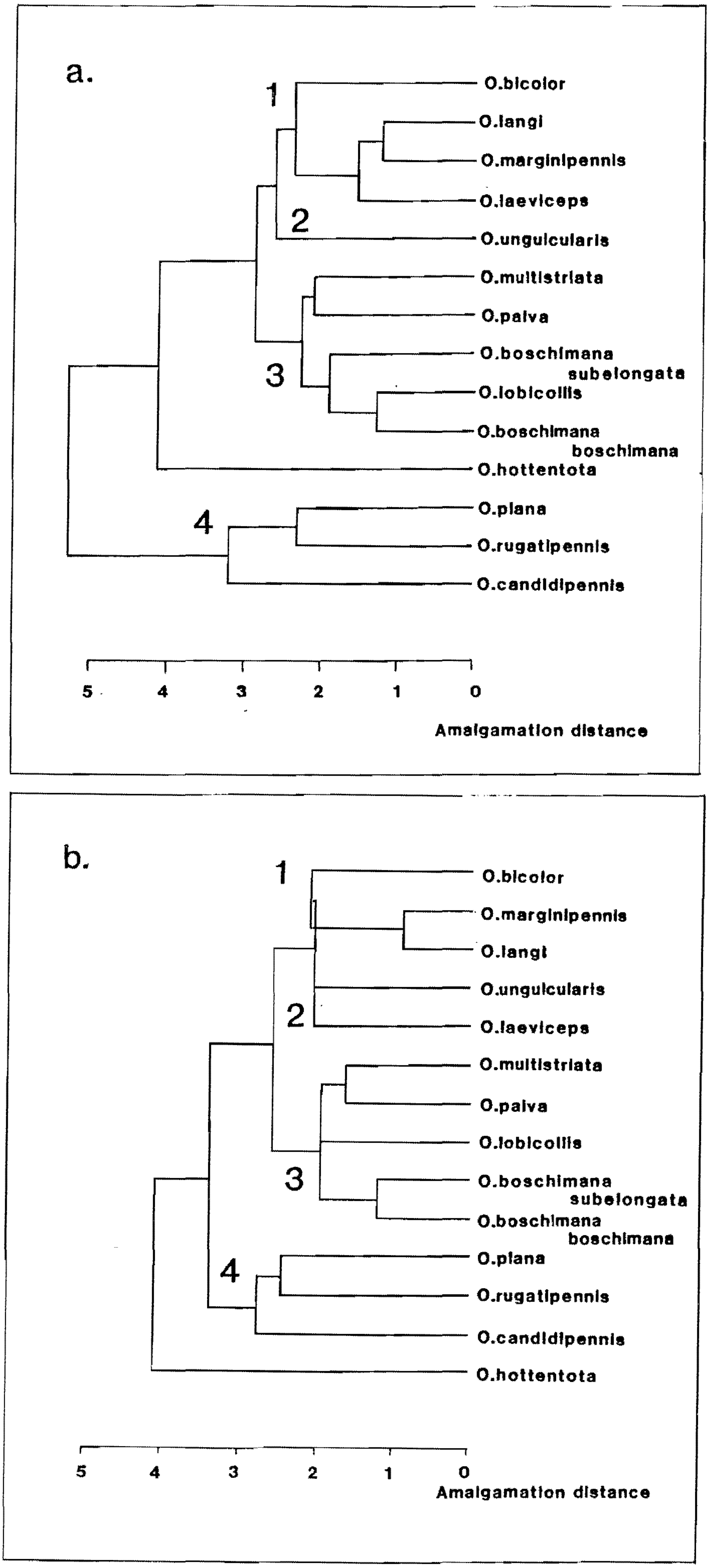

Figure 5 Phenograms from analyses of mensural character data from female Onymacris spp.: a) untransformed data; b) log-transformed data. See text for information on cluster numbers (1-4).

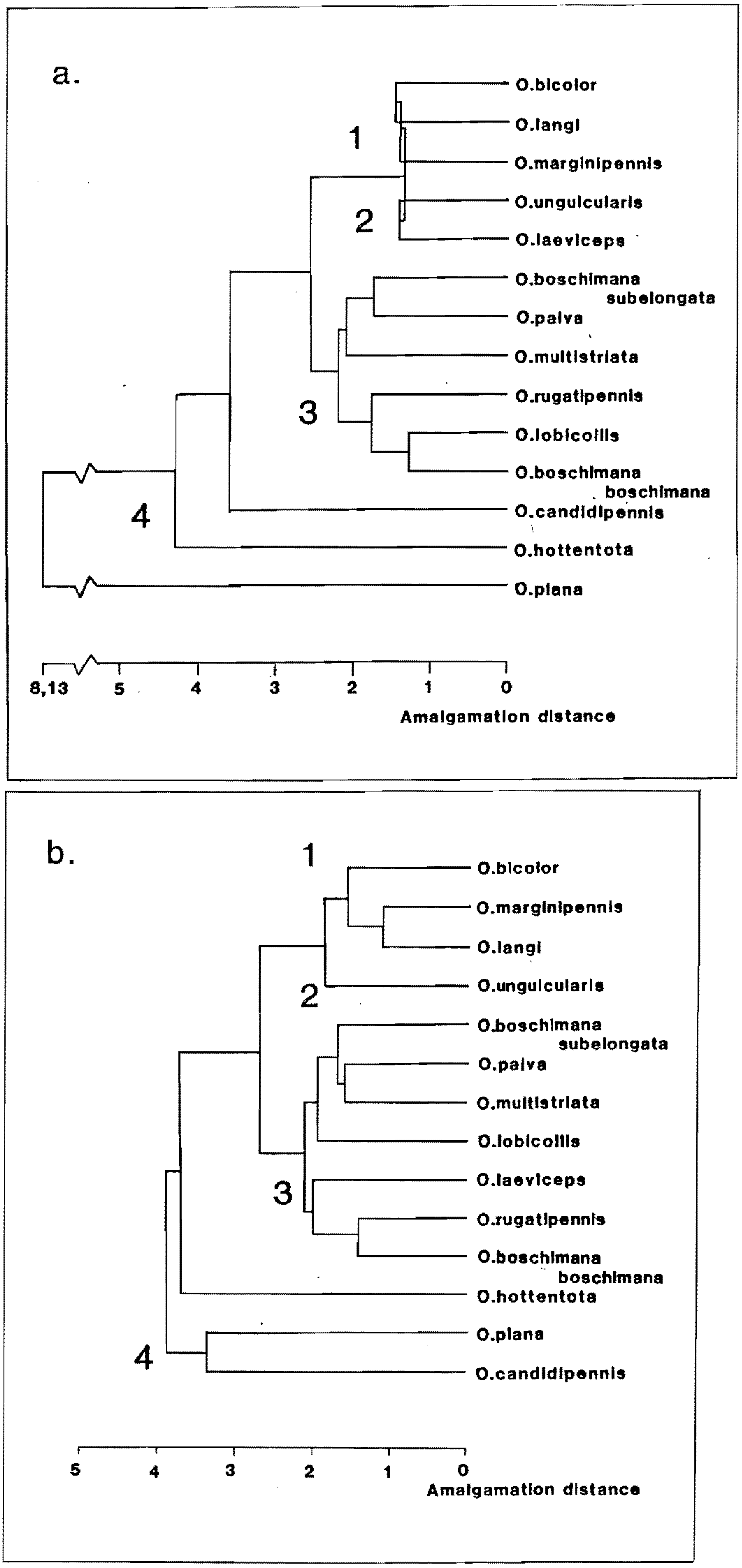

Figure 6 Phenograms from analyses of mensural character data from male *Onymacris* spp.: a) untransformed data; b) log-transformed data. See text for information on cluster numbers (1-4).

Table 7 Phenetic nearest two neighbours of Onymacris species according to analysis of mensural characters

Species	Group	Nearest neighbour species			
		Females		Males	
		Untransformed	Transformed	Untransformed	Transformed
O. bicolor	White (W)	laeviceps (B-S)	marginipennis (W)	langi (W)	langi (W)
		marginipennis (W)	langi (W)	marginipennis (W)	marginipennis (W)
O. candidipennis	White	rugatipennis (B)	plana (B)	rugatipennis (B)	bicolor (W)
		plana (B)	bicolor (W)	bicolor (W)	langi (W)
O. langi	White	marginipennis (W)	bicolor (W)	bicolor (W)	marginipennis (W)
		laeviceps (B-S)	unguicularis (B-S)	marginipennis (W)	langi (W)
O. marginipennis	White	langi (W)	bicolor (W)	langi (W)	langi (W)
		laeviceps (B-S)	unguicularis (B-S)	laeviceps (B-S)	bicolor (W)
O. laeviceps	Bullet-shaped (B-S)	langi (W)	unguicularis (B-S)	unguicularis (B-S)	marginipennis (W)
		marginipennis (W)	marginipennis (W)	marginipennis (W)	b. boschimana (B)
O. unguicularis	Bullet-shaped	laeviceps (B-S)	laeviceps (B-S)	laeviceps (B-S)	bicolor (W)
		langi (W)	marginipennis (W)	bicolor (W)	marginipennis (W)
O.b. boschimana	Black (B)	lobicollis (B)	b. subelongata (B)	lobicollis (B)	rugatipennis (B)
		b. subelongata (B)	lobicollis (B)	rugatipennis (B)	b. subelongata (B)
O.b. subelongata	Black	b. boschimana (B)	b. boschimana (B)	plana (B)	multistriata (B)
		lobicollis (B)	lobicollis (B)	b. boschimana (B)	b. boschimana (B)
O. hottentota	Black	multistriata (B)	multistriata (B)	multistriata (B)	multistriata (B)
		marginipennis (W)	langi (W)	marginipennis (W)	plana (B)
O. lobicollis	Black	b. boschimana (B)	b. subelongata (B)	b. boschimana (B)	b. boschimana (B)
		b. subelongata (B)	paiva (B)	multistriata (B)	multistriata (B)
O. multistriata	Black	paiva (B)	paiva (B)	lobicollis (B)	plana (B)
		langi (W)	lobicollis (B)	plana (B)	b. subelongata (B)
O. paiva	Black	b. boschimana (B)	multistriata (B)	b. boschimana (B)	multistriata (B)
		multistriata (B)	b. subelongata (B)	multistriata (B)	b. subelongata (B)
O. plana	Black	rugatipennis (B)	rugatipennis (B)	rugatipennis (B)	candidipennis (W)
		b. boschimana (B)	candidipennis (W)	candidipennis (W)	rugatipennis (B)
O. rugatipennis	Black	plana (B)	b. boschimana (B)	b. boschimana (B)	b. boschimana (B)
		candidipennis (W)	plana (B)	lobicollis (B)	lobicollis (B)

Table 8 Cladistic character states assigned to the hypothetical ancestor (outgroup) and extant *Onymacris* species and subspecies. See Table 4 for description of characters.

	Character No.																															
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. rugatipennis	1	0	1	0	2	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0
O. lobicollis	0	0	1	0	1	0	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
O. boschimana boschimana	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0
O. boschimana subelongata	0	0	1	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	1	0
O. paiva paiva	0	0	1	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	0	0
O. paiva conjuncta	0	0	1	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
O. multistriata	0	0	1	0	1	1	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
O. hottentota	0	0	1	0	1	1	2	0	0	0	2	0	1	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0
O. plana plana	0	0	1	0	2	0	2	0	0	0	2	0	0	2	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
O. plana debilis	0	0	1	0	2	0	2	0	0	0	2	0	0	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
O. laeviceps	1	0	2	0	2	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	1
O. unguicularis	1	0	2	1	2	0	0	1	1	0	0	1	0	0	0	1	1	2	0	1	1	1	1	0	0	1	1	1	0	0	0	0
O. langi langi	2	1	3	0	1	0	1	0	1	0	0	2	0	0	0	1	2	2	0	1	0	1	1	0	0	1	0	1	0	1	0	0
O. langi meridionalis	2	1	3	0	1	0	1	0	1	0	0	2	0	0	0	1	2	2	0	1	1	1	1	0	0	1	0	1	0	1	0	0
O. langi cornelli	2	1	3	0	1	0	0	1	1	1	0	2	0	0	0	1	2	2	0	1	1	1	1	0	0	1	0	1	0	1	0	0
O. langi visseri	2	1	3	0	1	0	1	0	1	0	0	2	0	0	0	1	2	1	0	1	0	1	1	0	0	1	0	1	0	1	0	0
O. marginipennis	2	1	3	0	1	0	1	1	1	1	0	2	0	0	0	1	2	1	0	1	1	1	1	1	0	1	0	1	0	1	0	0
O. candidipennis	2	1	3	0	2	0	1	1	1	1	0	2	0	0	0	1	2	1	0	1	1	1	1	0	0	1	0	1	0	1	0	0
O. bicolor	2	0	3	0	2	0	1	1	1	2	0	3	0	0	0	1	2	2	1	1	1	1	1	1	0	1	0	1	0	1	0	0

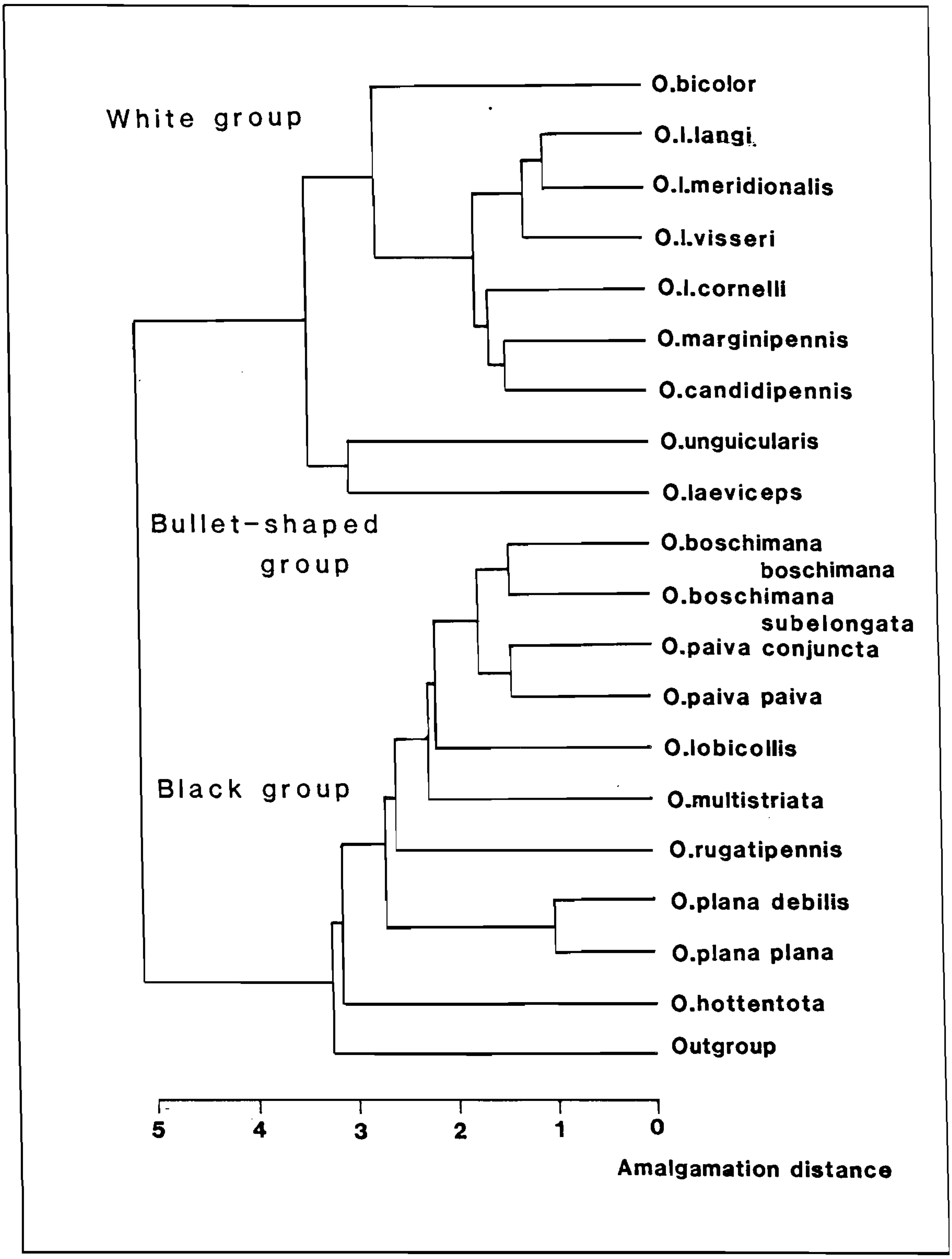

Figure 7 Phenogram from analysis of qualitative character data from male and female *Onymacris* species and subspecies.

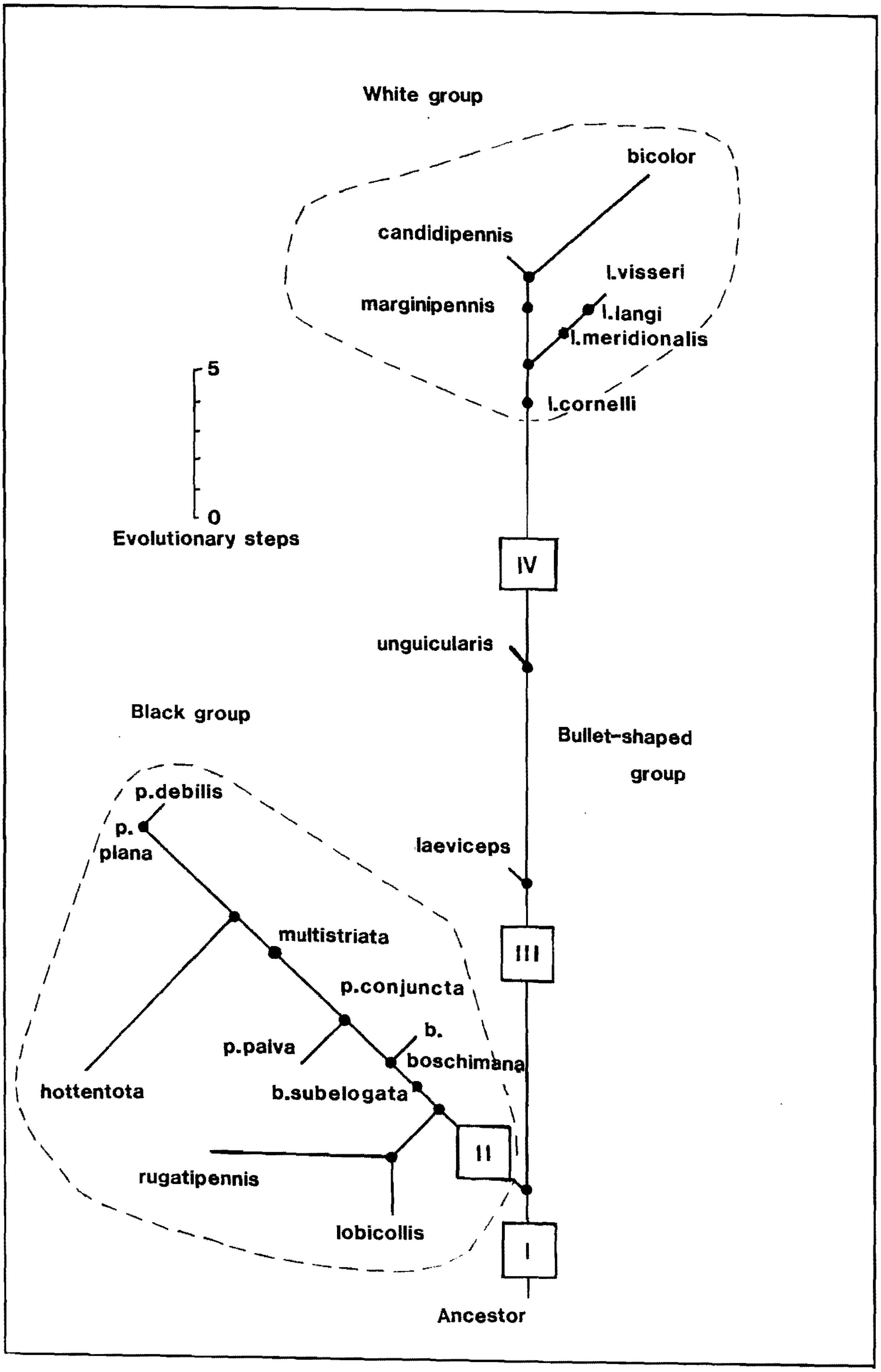

Figure 8 Cladogram for <u>Onymacris</u> spp. Roman numerals refer to synapomorphies listed in Table 3.

many highly derived features. The two Bullet-shaped species form an intermediate paraphyletic group with *O. unguicularis* as the sister species to the White group.

Synapomorphies which define monophyletic groups (depicted by the numerals in Figure 8) are listed in Table 9. The extant species in the Black group have no entirely unique synapomorphies. However, most species have flat elytra (character no. 7), relatively long hind femora (29) and sharply defined supra-orbital ridges (25). The White/Bullet-shaped lineage is defined by broad range of characters relating to the thorax (16), elytra (9, 12, 28), adeagus (1), and femur (3). The White group is distinguishable from the Bullet-shaped species through characters relating to reproductive organs [sharply tapering adeagus (1) and wide ovipositor sclerites (2)], the prosternum (17), and, of course elytral colour (30) and smoothness (12).

O. unguicularis shares several derived features with the White species, in particular, modifications to antennal morphology. Shape of the terminal antennal segment, relative thickness of the antennae and ratio of the second to third antennal segment distinguish the White species and *O. unguicularis* from *O. laeviceps* and the Black species.

A phenogram and a WAG-78 cladogram from a re-analysis of character data presented in Figure 8 of Penrith (1984) are ~~presented~~ shown here as Figures 9 and 10. Synapomorphies defining monophyletic groups in the cladogram are listed in Table 10 and phenetic nearest neighbours are listed in Table 11. Penrith (1984) used 23 characters to construct her cladogram for 14 species. Character polarity was determined through comparison with *Physadesmia*, *Eustolopus*, *Renatiella* and *Adesmia*. Two

Table 9 Synapomorphies for monophyletic groups within the genus *Onymacris* as shown in Figure 8.

Group name and numeral in Figure 8	Character	State	Description
Genus *Onymacris*	3	1	femur not rounded
(I)	5	1	tarsal claws expanded
Black group	7	2	elytra flattened (reversal to state 1 in *rugatipennis*)
(II)	25	1	supra-orbital ridge well defined (reversal to state 0 in *lobicollis* and *hottentota*)
	29	1	metathoracic femur : elytra ratio > 1 (reversal to state 0 in *hottentota*)
Bullet-shaped and White group	1	1	adeagus shape tapering
	3	2	femur shape intermediate
(III)	9	1	elytra lacking rugose indentations
	12	1	elytra not rugose
	16	1	thoracic length : width > 1 : 3
	18	1	sternites above mesothoracic leg adjacent
	23	1	clypeus angled at genal ~~sulcas~~ sulcus
	28	1	elytra soft
White Group	3	3	femur pointed
(IV)	12	2	elytra smooth or smooth with bumps
	17	2	prosternal apophysis mitre-shaped and rounded
	30	1	elytra pale

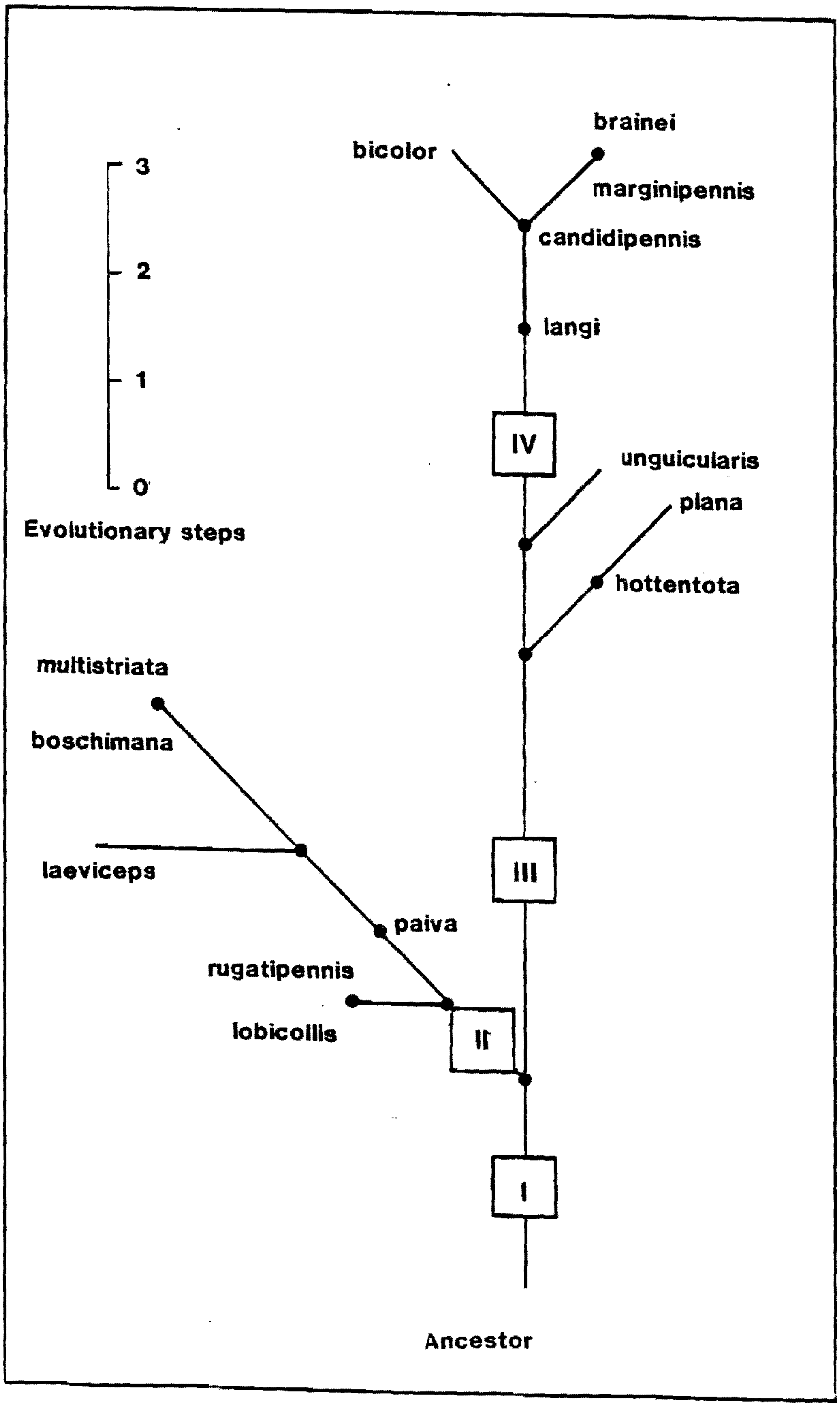

Figure 9 Cladogram for Onymacris spp. after Penrith (1984). Roman numerals refer to synapomorphies listed in Table 10.

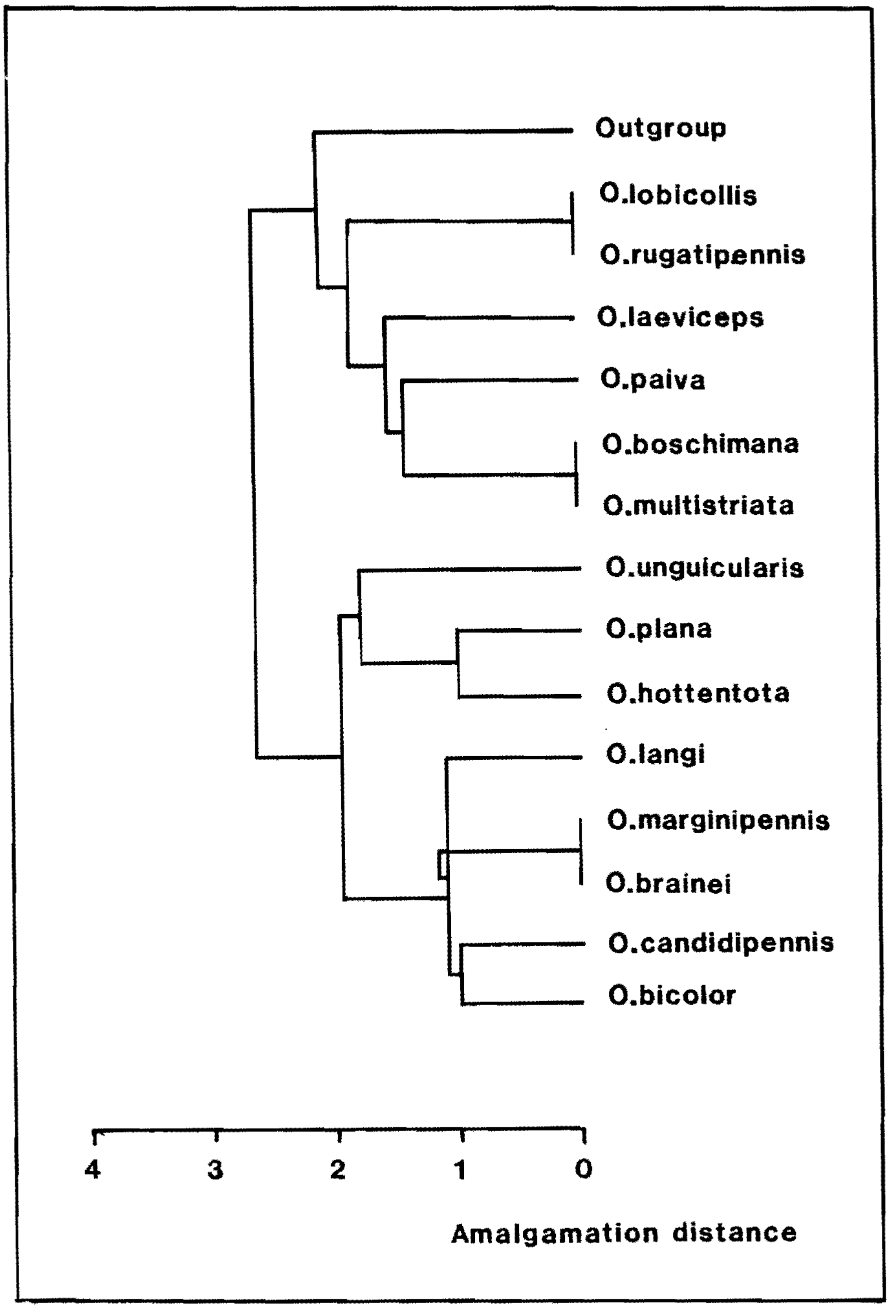

Figure 10 Phenogram from analysis of qualitative data from <u>Onymacris</u> species after Penrith (1984).

Table 10 Synapomorphies for monophyletic groups within the genus *Onymacris* in Figure 9 (after Penrith 1984).

Group name and numeral in Figure 9	Character	State	Description
Genus *Onymacris* (I)	22	1	metatarsal segment 1 shorter than segment 2 + 3
	23	1	tarsal claws and spurs long
Lineage I (II)	21	1	metatarsi compressed
Lineage II (III)	10	1	broad mesosternum
	11	1	metatarsal segment 1 scarcely longer than segment 2
	12	1	elytra lacking microgranulation
	13	1	clypeus angled at genal ~~sulcas~~ sulcus
White species (IV)	4	1	pale elytra
	5	1	adeagus heavily sclerotised

Table 11 Nearest two neighbours of *Onymacris* spp. according to analysis of qualitative characters

Species	Group	Nearest neighbour species This study	 Penrith (1984)
O.b. boschimana	Black (B)	*b. subelongata* (B)	*multistriata* (B)
		paiva (B)	*paiva* (B)
O.b. subelongata	Black	*b. boschimana* (B)	-
		p. conjuncta (B)	-
O. hottentota	Black	*multistriata* (B)	*plana* (B)
		p. plana (B)	*unguicularis* (B-S)
O. lobicollis	Black	*b. boschimana* (B)	*rugatipennis* (B)
		p. paiva (B)	*paiva* (B)
O. multistriata	Black	*p. conjuncta* (B)	*boschimana* (B)
		b. boschimana (B)	*paiva* (B)
O.p. paiva	Black	*p. conjuncta* (B)	*multistriata* (B)
		b. boschimana (B)	*laeviceps* (B-S)
O.p. conjuncta	Black	*p. paiva* (B)	-
		b. boschimana (B)	-
O.p. plana	Black	*p. debilis* (B)	*hottentota* (B)
		multistriata (B)	*unguicularis* (B-S)
O.p. debilis	Black	*p. plana* (B)	-
		multistriata (B)	-
O. rugatipennis	Black	*lobicollis* (B)	*lobicollis* (B)
		p. paiva (B)	*paiva* (B)
O. laeviceps	Bullet-shaped (B-S)	*unguicularis* (B-S)	*paiva* (B)
		rugatipennis (B)	*multistriata* (B)
O. unguicularis	Bullet-shaped	*laeviceps* (B-S)	*hottentota* (B)
		l. cornelli (W)	*langi* (W)
O. bicolor	White (W)	*candidipennis* (W)	*candidipennis* (W)
		marginipennis (W)	*brainei* (W)
O. candidipennis	White	*marginipennis* (W)	*bicolor* (W)
		l. cornelli (W)	*marginipennis* (W)
O.l. langi	White	*l. meridionalis* (W)	*bicolor* (W)
		l. visseri (W)	*candidipennis* (W)
O.l. cornelli	White	*marginipennis* (W)	-
		candidipennis (W)	-
O.l. meridionalis	White	*l. langi* (W)	-
		l. visseri (W)	-
O.l. visseri	White	*l. langi* (W)	-
		l. meridionalis (W)	-
O. marginipennis	White	*candidipennis* (W)	*brainei* (W)
		l. cornelli (W)	*candidipennis* (W)
O. brainei	White	-	*marginipennis* (W)
		-	*candidipennis* (W)

characters establish the monophyly of the genus. The remaining 21 characters are used to describe the 14 species, but *O. brainei* is not separated from *O. marginipennis* and, similarly, *O. rugatipennis* is not differentiated from *O. lobicollis* by any autapomorphy.

5. DISCUSSION

5.1 Phenetic analyses

5.1.1 Species

Scoble (1983) used phenetic analysis successfully to check intuitive estimates of morphological resemblance of the Nepticulidae (Lepidoptera). However, in the present study, it can be seen that there is considerable overlap between the envelopes describing factor score standard deviations for certain species (Figures 3 and 4). Michener & Sokal (1957) suggest that at least 60 characters need to be visualized for optimal separation of taxa. However, with the extensive size overlap and the inherent continuous nature of the mensural characters, it is questionable whether an increase in the number of characters would make a substantive difference (Mickevich 1978). Some overlap between the species may be expected, since the mensural characters analyzed did not necessarily reflect all characters important in defining the species. The two-dimensional factor analysis plots (Figures 3 and 4) may also display more overlap than would be evident in a multi-dimensional plot. However, extensive overlap between O. b. boschimana and O. lobicollis, and between certain members of the White group (e.g. O. langi, marginipennis and candidipennis) is consistent with a hypothesis of 'interspecific' hybridization (Hamilton & Penrith 1977; Penrith 1975, 1984).

5.1.2 Phenetic grouping patterns

In cluster and factor analyses (Figures 3-6) there are two robust species groupings. Four Black species, O. boschimana, O. paiva, O. lobicollis and O. multistriata cluster consistently, as do three White species, O. bicolor, O. marginipennis and O. langi. The two Bullet-shaped species also generally cluster with the White group. Two Black species, *O. plana* and *O. hottentota*, and *O. candidipennis*, a White species, are consistent outliers in the phenograms, and a third Black species, *O. rugatipennis*, is an outlier in the phenogram for females.

O. unguicularis occupies a similar position in phenograms and factor score plots close to the White species. Moreover, this species is characterized by relatively large factor score standard deviations (0,53 and 0,90) for factors 1 and 2 in females and males (0,63 and 0,76) (Figure 4). Overall mean standard deviation for factors 1 and 2 are 0,41 and 0,43 for females, and 0,46 and 0,54 for males. Figure 1 shows the wide, patchy distribution of *O. unguicularis* (see also Penrith (1975: Figure 9). This distributional pattern prompted Gebien (1938) to erect a subspecies for the small individuals of the southern populations of the species. Penrith (1975) rejected subspecific separation, suggesting that any differences within the species are clinal. However, in the present study, a substantial reduction in the high factor score standard deviation for this species was achieved by dividing it into two subgroups around an arbitrary geographical division (the 24th parallel). These results suggested that, with more data, the northern and southern populations of *O. unguicularis* might warrant subspecific status. In fact, Penrith (1984) provides *a posteriori* support for this suggestion, since she now recognizes two subspecies, *O. u. unguicularis* and *O. u. schulzeae*, the geographical division of these occurring between the Unjab river (20° 12'S) and Swakopmund (22° 40'S).

In the phenograms based on analyses of mensural data, some taxa are shown to be more closely related to the 'average' of two other taxa than to either of the 'averaged' taxa themselves. Such anomalous results in cluster analysis are known as 'reversals', and are a result of the clustering algorithm employed, not anomalies in the data (Sneath & Sokal 1973). In Figure 6a, for example, *O. marginipennis* links with *O. bicolor* and *O. langi* at a distance of 1,42, although these two species link to one another only at a level of 1,46. This phenomenon can be explained by the fact that continuous morphometric data were used in construction of the phenograms. It is indeed possible for any taxon to have dimensions most similar to those of the average of two (or more) other taxa. To mimimize false impressions created by this deficiency in the clustering algorithm, nearest neighbour species, obtained from the original distance matrix generated by cluster analysis, are also presented (Table 7). Crowe and Crowe (1985) employed a similar strategy in his research on congeneric birds.

5.1.3 Nearest neighbour analysis

The phenograms derived from the untransformed and log-transformed cluster analysis of mensural data for both sexes (Figures 5 and 6) are not congruent, and, in some instances, are beset with reversals. However, Table 7 shows that the White species, with the exception of *O. candidipennis*, are all phenetically most similar to one another and, to a lesser degree, to the Bullet-shaped species pair. *O. candidipennis*, a species reputed to be involved in hybridization, has an equal number of nearest neighbours from both the White and Black groups. *O. laeviceps* and *O. unguicularis* are phenetically closest to one another and to White species.

Of the Black species, O. boschimana, O. lobicollis, O. multistriata, O. paiva and O. rugatipennis all have Black species as their nearest neighbours (Table 7). Around this central cluster of Black species, O. hottentota always has O. multistriata as its nearest neighbour, but its second-nearest neighbours are generally White species (Table 7). This is also the case for O. plana, whose nearest neighbour is most often O. rugatipennis, with O. candidipennis, a White species, a near neighbour in three out of eight instances (Table 7).

Nearest neighbour analysis also draws attention to the possible hybridization between the two O. boschimana subspecies and other members of the Black group.

In summary then, the phylogenies derived from mensural characters generally show a close association between the White species, except O. candidipennis. The Bullet-shaped group, O. unguicularis and O. laeviceps, is usually the sister group of the White group. Four Black species, O. paiva, O. multistriata, O. boschimana and O. lobicollis also consistently group together. The affinities of three Black species, O. plana, O. hottentota and O. rugatipennis, and one White species, O. candidipennis, are uncertain.

5.2 Cladistic analysis

5.2.1 Phylogenetic concordance and discordance

Of the 23 characters analyzed by Penrith (1984) only 12 are common to this study. Relationships within Onymacris presented in the two studies differ in several instances, but there are also areas of accord. The White species form a discrete grouping in both studies, and, of the Black group, O. multistriata, O. boschimana, O. paiva, O. rugatipennis and O. lobicollis are closely related. A close relationship between O.

unguicularis and the White group is also evident in both cladograms (Figures 8 and 9).

The major difference between the two cladograms concerns the relationships of O. laeviceps and the O. plana-O. hottentota species pair, since they occur within different lineages in the two studies. O. laeviceps moves from its position amongst Black species in Penrith (1984) to a close but paraphyletic association with O. unguicularis in the cladogram presented in this thesis. Similarly, the O. plana - O. hottentota subgroup appears with the unguicularis-White group lineage in Penrith (1984) as opposed to the Black group here. These relationships are mirrored in the nearest neighbour analysis of qualitative data (Table 11).

Penrith (1984: Figure 8) uses three synapomorphies (common to at least three species) to define lineage II in Figure 9. In the present study, synapomorphies common to at least three species within the Black group are: character 6, the presence of bumps on the mesothoracic femur; character 7, flattening of the elytra; character 11, presence of deep elytral indentations; character 13, many elytral costae; and character 25, a well defined supraorbital ridge.

Character 13 which describes reduction in the number of elytral costae is homologous with character 20 of Penrith (1984). The synapomorphy is shared by O. rugatipennis and O. lobicollis in both studies, but is also attributed to O. paiva paiva and O. hottentota in the present study (Table 8).

Sexual dimorphism in eye size is also a character used by Penrith (1984) to define her first lineage. Mensural character 22 (Table 3) in the present study can be used to determine sexual dimorphism in eye size. Results of univariate analysis of this character (Table 12) conflict with those presented by Penrith (1984), who linked *O. laeviceps*, *O. multistriata*, *O. paiva* and *O. boschimana* with this apomorphy. In Table 12, *O. laeviceps*, *O. multistriata*, *O. candidipennis*, *O. hottentota* and *O. marginipennis* show a significant difference in eye length ($P < 0,01$; *t* test) between sexes.

Compression of metatarsi, character 21 of Penrith (1984), was not investigated in this study. However, in her detailed species descriptions (Penrith 1975), metatarsi are described as being as wide as long in all species except *O. paiva* and *O. lobicollis*. *O. hottentota* is reported as having metatarsi wider than long. These data do not accord with the data presented by Penrith (1984) in which *O. multistriata*, *O. boschimana*, *O. laeviceps*, *O. paiva*, *O. rugatipennis* and *O. lobicollis* are grouped by this synapomorphy.

The second lineage described by Penrith (1984) comprises the White species, *O. unguicularis*, and the *O. plana*-*O. hottentota* species pair. Penrith (1984) cites four synapomorphies which link this second lineage (III in Table 10). In the present study, characters 9 and 23, roughness of elytra and shape of clypeus (Table 4), are comparable with Penrith's (1984) characters 12 and 13. However, I interpret distribution of these characters differently, resulting in the assignment of *O. plana*, *O. hottentota* and *O. laeviceps* to different lineages.

This discrepancy may have resulted from a study of different features, despite the similarity in description of the characters. The presence of distinct microgranulation of the elytra has been linked to production of a waxy bloom in the genus (Penrith 1984). Lack of elytral microgranulation links the White species with *O. unguicularis* and *O. hottentota* and *O. plana* (Penrith 1984) and yet, *O. plana* is known to bloom

Table 12 Sexual dimorphism in eyelength of *Onymacris* spp.

Species	Eyelength males (mm)	N	S.D.	Eyelength females (mm)	N	S.D.	*t*	*P*	Dimorphism present	Dimorphism reported in Penrith (1984)
O. candidipennis	1,95	29	0,09	2,02	31	0,09	-3,10	0,003	Yes	No
O. hottentota	1,54	30	0,14	1,45	30	0,11	2,70	0,009	Yes	No
O. laeviceps	2,19	28	0,14	1,48	30	0,11	20,90	<0,001	Yes	Yes
O. marginipennis	0,81	28	0,17	1,69	31	0,15	2,94	0,005	Yes	No
O. multistriata	1,94	30	0,15	1,83	30	0,09	3,26	0,002	Yes	Yes
O. bicolor	1,59	35	0,10	1,61	19	0,11	-0,52	0,354	No	No
O. b. boschimana	2,23	30	0,17	2,13	30	0,19	2,06	0,044	No	Yes
O. b. subelongata	2,17	31	0,09	2,16	21	0,13	0,15	0,88	No	Yes
O. langi	1,75	14	0,15	1,69	14	0,13	1,50	0,137	No	No
O. lobicollis	1,69	28	0,11	1,76	31	0,13	-2,25	0,028	No	No
O. paiva	1,81	31	0,13	1,76	29	0,08	1,77	0,081	No	Yes
O. plana	2,45	30	0,15	2,45	26	0,22	-0,05	0,954	No	No
O. rugatipennis	1,96	30	0,12	2,00	29	0,09	-1,65	0,104	No	No
O. unguicularis	1,47	24	0,15	1,46	29	0,14	0,15	0,881	No	No

(McClain, et al ~~Seely, Hadley and Gray~~ 1985). Similarly, *O. laeviceps* was coded as having no microgranulation in this study and it is known to bloom. The validity of this character, particularly when correlated with the occurrence of a waxy bloom, is questioned both here and by Penrith (1984). Interpretation of the other common character pair, which describe the angle of the clypeal/genal junction, is similar in both studies except that *O. plana* is included with the White lineage in Penrith (1984), and *O. rugatipennis* with the Black lineage in this study.

Mesosternal broadness, character 10 in Penrith (1984), was not considered in this study. However, a similar character, intercoxal separation of the prothoracic legs was measured (Table 3: character 12). This character did not contribute significantly in the factor analyses weight (< 0.70) in either factor 1 or 2 in Figures 3 and 4 (Table 5). Nevertheless, the mensural character data for mean leg separation were considered in all species for both females and males (Table 13). *O. hottentota* and *O. plana* grouped with the White species in both males and females, but *O. unguicularis* is more similar to the Black species. These data should be viewed in conjunction with the mesosternal data of Penrith (1984) for which the synapomorphy is common to the lineage of White species, *O. unguicularis* and *O. hottentota* and *O. plana*.

Similar specimen material was studied in this thesis and in Penrith (1984). While in some cases, the synapomorphies claimed by Penrith (1984) have been questioned, further discrepancies between the classifications need explanation. Differences in the topology of the cladograms obtained in the two studies may be explained through a comparison of the methods used to obtain the classifications. Phenograms and cladograms were constructed

Table 13 Mean prothoracic leg separation in _Onymacris_ spp.

Species	N	Males (mm)	S.D.	N	Females (mm)	S.D.	Separation observed (Penrith 1984)
O. candidipennis	29	1,25	0,10	31	1,56	0,19	Yes
O. plana	30	1,22	0,13	26	1,24	0,10	Yes
O. bicolor	35	1,01	0,05	19	1,08	0,08	Yes
O. hottentota	30	1,00	0,10	30	1,06	0,09	Yes
O. marginipennis	28	0,91	0,11	31	0,95	0,11	Yes
O. lobicollis	28	0,90	0,09	31	0,98	0,10	No
O. langi	14	0,87	0,06	14	1,02	0,09	Yes
O. laeviceps	28	0,87	0,08	30	0,89	0,08	No
O. b. boschimana	30	0,82	0,09	30	0,79	0,08	No
O. rugatipennis	30	0,80	0,08	29	0,89	0,07	No
O. unguicularis	24	0,80	0,08	29	0,80	0,06	No
O. multistriata	30	0,73	0,06	30	0,77	0,08	No
O. paiva	31	0,70	0,05	29	0,72	0,05	No
O. b. subelongata	31	0,64	0,04	21	0,71	0,07	No

from different data sets, different numbers of OTUs, and using different algorithms. Penrith's (1984) cladogram was constructed manually. No scale for patristic distance is included in her cladogram and, in one instance, the stem defined by four synapomorphies is much shorter than a stem defined by only one character.

Three species, O. plana, O. hottentota and O. laeviceps fall into different lineages depending on the approach to character analysis. In both phenograms (Figures 7 and 10) the euclidean amalgamation distance of these species with the remaining species within each lineage is relatively high. The position of these species is therefore tenuous and each could be displaced from one lineage to the next with little change in the character data.

Groupings which are common to results of phenetic and phylogenetic analyses (including that of Penrith 1984), are regarded as robust. In all cases the White species O. langi, O. marginipennis and O. bicolor are closely associated and found with O. unguicularis. O. candidipennis is also linked with the other White species, except in the phenograms for mensural characters in which it is an outlier due to its size. The Black group, comprising O. multistriata, O. boschimana, O. paiva, O. lobicollis and usually O. rugatipennis, is always closely related to the hypothesized ancestor.

While some characters proposed by Penrith (1984) have been questioned, the use of 32 characters in the cladistic study here and the close relationship of subspecies analyzed, lead me to prefer the cladogram presented in Figure 8 above Figure 9. The close relationship of O. laeviceps with O. unguicularis in phenetic as well as cladistic analyses also suggest that this interpretation of relationship is preferable. The discovery of further synapomorphies, perhaps through more complete study of the anatomy of *Onymacris* larvae and of biochemical characters, may help to resolve this problem.

5.3 Adaptation - constraints and correlations

Biological adaptations resulting from selection imposed by environmental constraints ~~are~~ may be manifested as phenotypic characters (Bock 1967). Therefore, it follows that all phenotypic characters are prone to homoplasy. Many twentieth century systematists (e.g. Bock 1980; Gosliner & Ghiselin 1984) have emphasized the importance of the confounding effects of parallelism due to adaptation, on phylogenetic analyses. Gosliner & Ghiselin (1984) go much further, and assert that the frequency of parallelism increases dramatically with propinquity of phylogenetic relationship.

The harsh Namib environment has imposed considerable evolutionary constraints on its tenebrionid fauna. Therefore it seems reasonable to expect that 'Parallelists' would predict rampant homoplasy among closely related taxa which have radiated into the dune environment, such as many of the ultra-psammophilous *Onymacris* species investigated here. The generally hot, arid environment in the Namib also requires morphological adaptations for water conservation and thermoregulation. Effective thermoregulation, for example, is complicated by the need for a trade-off between achieving maxithermy (relatively high body temperatures for long periods each day) and avoiding overheating (Henwood 1975).

Namib tenebrionids have apparently adapted to their abiotic environment through evolutionary changes in size and colour. Small beetles heat much faster than larger beetles, and lighter coloured beetles heat more slowly than do black species (Hamilton 1975). Large beetles also lose relatively less water than do smaller individuals of the same species (Edney 1971), and geographical variation in leg length increases clinally with aridity (Broza ~~Pener and Borut~~ et al 1983). Since cooling may depend on transpiration, resulting in increased water loss (Edney 1971), thermoregulation and water conservation are thus closely linked processes.

If parallelism were rampant in *Onymacris*, species from the two areas of similar precipitation, e.g. the northern and southern sectors of the distribution of the genus, should have similar morphologies. However, beetles in the northernmost areas have white elytra, and those in the south have black eytra. Moreover, there is considerable variation in body size and leg-length of species within each area. Species which inhabit the central Namib (*O. plana*, *O. b. subelongata*, *O. rugatipennis*, *O. unguicularis* and *O. laeviceps*) are exposed to the most arid conditions and would thus be expected to have relatively large bodies and/or long legs (Broza *et al*. 1983). The results of factor analysis (Figures 3 and 4, Table 6), show that *O. plana* is relatively large and that *O. b. subelongata* and *O. rugatipennis* have long legs. However, the two Bullet-shaped species *O. unguicularis* and *O. laeviceps* are neither large nor particularly long-legged. How then, have these two species 'solved' this adaptive problem?

Thermoregulation and water conservation may also be effected by behavioural adaptations, e.g. burrowing in sand to escape hot surface temperatures, stilt-walking to avoid contact with the hot surface of the sand, and fog-basking to accumulate water (Medvedev 1965; Henwood 1975; Broza *et al*. 1983; Seely 1979). *O. unguicularis* and *O. laeviceps* both have behavioural adaptations which enable their survival in the harsh arid reaches of the central Namib. *O. unguicularis* employs fog-basking behaviour (Hamilton & Seely 1976; Seely 1979), whereas *O. laeviceps* is most active during the cooler twilight hours (Edney 1971). The morphological constraints imposed by thermoregulation on leg length and body size, are therefore not directly applicable in these two species.

Onymacris species have therefore adaptated to a hot and arid environment via a myriad of alternative pathways, which include morphological and behavioural changes. If there are alternative avenues open to organisms for survival in specific environments, as there are to these beetles, it is unlikely that, where several adaptive characters are shared, they can all be explained by parallelism.

The constraints of adaptation elucidated above are most evident in quantitative, mensural characters. Morphometric data are one dimensional, and mensural variation may simply reflect allometric growth and not be important from an evolutionary point of view. In this study, abdominal size and shape (defined by five mensural characters) and leg-length (three mensural characters) are obviously adaptive, and thus the potential for parallelism is high. And yet, as shown above, it is very difficult, if not impossible to predict beetle morphology from knowledge of the environment.

Another obvious source of homoplasy would be found amongst those characters relating to an ultra-psammophilous lifestyle. In both the present study and Penrith (1984) the two major *Onymacris* lineages include representatives of ultra-psammophilous species. The high patristic distances between these highly adapted species in each clade (Figures 8 and 9) suggest that parallelism is adequately catered for in the cladograms through application of the parsimony approach (Brady 1983, Farris 1983). If homoplasy were "rampant", all ultra-psammophilous species would group together in one clade.

Alternatives to parsimony include rejection of putative homoplasous characters, character weighting and re-appraisal of character homology (Gosliner & Ghiselin 1984; Watrous & Wheeler 1981). The identification of homoplasous characters is, however, impossible if the phylogeny of the group is unknown. Moreover, any approach which allows character exclusion or weighting, is clearly biased toward some preferred cladogram or evolutionary process (e.g. parallelism). The phylogenetic truth can only be identified by means of consensus among characters not among systematists.

Lastly I suggest that the understanding of the adaptive morphology of Namib tenebrionids is still in its infancy. Correlation between anatomy and environment is by no means sufficient evidence of adaptation. Therefore, before patterns of morphological similarity observed in the present study of Onymacris can be attributed to parallelism due to adaptations to common selective pressures, functional anatomists, behaviourists, physiologists and systematists need to have much better information about the causal basis behind correlations between beetle behaviour and anatomy and variation in the environment.

5.4 Deficiencies of phenetics

I encountered three obstacles in applying phenetics in a phylogenetic analysis of the genus Onymacris. First, complementary sets of mensural character data for males and females did not yield congruent results. Second, analyses of untransformed mensural character data yielded different results from those of log-transformed mensural data and those of qualitative data. Mickevich (1978) found similar differences between phenograms of quantitative and qualitative data, and also found incongruities in the phenetic classifications of the same taxa produced from different character sets. Rohlf & Sokal (1981) claim that phenograms are stable (robust) when new characters, or even additional OTUs, are added to the data matrix. Farris (1971), however, has shown that phenograms are not robust, since the same data analyzed using different algorithms, and data from different characters analyzed using the same algorithms, can yield markedly different results, as is the case in the present study.

The third obstacle is illustrated by a comparison of the phenogram and cladogram (Figures 7 and 8) based on analyses of qualitative character data. On a gross scale, the major difference is that the phenogram suggests that the Bullet-shaped group is monophyletic, whereas the cladogram suggests a paraphyletic relationship. Within the Black and White species groups, sister species relationships are also markedly different. For example, O. bicolor is the sister species to the remaining White species in the phenogram, but perhaps the most derived species in the cladogram. I attribute this to the inherent inability of phenetics to cope with symplesiomorphy and autapomorphy. Thus, phenetics seems, at best, suitable for the determination of broad trends in morphological similarity (e.g. in hybridization studies) only, and has no place in phylogenetic analysis.

5.5 Classification

The mensural characters described above are prone to homoplasies which may have resulted from morphological adaptations to the arid desert environment. Mickevich (1978) has shown that homoplasies have a more pronounced effect on phenetic classifications than on phylogenetic classifications. She has also demonstrated that classifications constructed phenetically (even those which draw phylogenetic conclusions) are less stable than Wagner tree classifications. Because pheneticists regard their groupings as abstract classifications, not necessarily indicative of kinship (Farris 1982), any number of phenograms may be constructed. Cladists, however, recognize only one correct classification which reflects kinship of the group, since there is only one true genealogy (Farris 1982). Congruence between trees which attempt to display phylogenetic relationships occurs because characters are analyzed at their appropriate hierarchical levels (Mickevich 1978). Cladograms also have a greater information content than phenograms because phylogenetic relationships are displayed. For these reasons the cladogram (Figure 8) presented here is regarded as the best reflection of relationships within the genus *Onymacris*.

5.5.1 Taxonomy

As a result of all the evidence presented above, I propose to erect subgenera to accomodate the two monophyletic groups of beetles comprising the genus *Onymacris*. The nominate subgenus comprises *O. laeviceps*, *O. unguicularis*, *O. langi*, *O. marginipennis*, *O. candidipennis*, and *O. bicolor*. The newly described species *O. brainei* (Penrith 1984) would also fall into this subgenus. I now propose *Melanonymacris subgen. nov.* for the non-Bullet-shaped species with black elytra *viz.*, *O.*

lobicollis, *O. boschimana*, *O. hottentota*, *O. paiva*, *O. plana* and *O. rugatipennis*, with type species *Adesmia lobicollis* Fairmaire 1888. The first part of the name *Melanonymacris* is derived from the Greek adjective *melas* meaning black and refers to the uniformly black elytra common to this group. This adjective is not intended to describe the colour of the beetles' claws as is implied in the name *Onymacris* which appears to be a malformation of *Onychomacris* meaning large claws. The subgenus is feminine. *Melanonymacris* mirrors one of the morphologically defined groups identified by Penrith (1975).

Subgenus *Onymacris*

Type species *Adesmia candidipennis* Brême 1840: 112 (by subsequent designation of Allard 1885).

Diagnosis

All have tapering adeagi; elytra have parallel sculpture or are smooth; elytra always soft; thorax length less than three times the thorax width.

Subgenus *Melanonymacris*

Type species *Adesmia lobicollis* Fairmaire 1888: 183.

Diagnosis

Intercostal elytral sculpture rough; elytra hard; with one exception, *O. rugatipennis*, dorsoventral flattening of male elytra evident; the metathoracic femur as long or longer than the elytra in males with the exception of *O. hottentota*.

The groupings presented above have proved to be relatively robust through comparison (and congruence) with phylogenetic and phenetic analyses in this study, and a phylogenetic analysis by Penrith (1984). Several other authors have also provided evidence which corroborates the proposed subgenera and subgroups. In her incomplete key to the larvae of *Onymacris*, Schulze (1964) identified three species groups. The first group comprises a single White species *O. bicolor*, and the second, members of the Black group (*O. rugatipennis*, *O. multistriata*, *O. lobicollis*, *O. boschimana* and *O. plana*). An anomalous inclusion in the second group is the White species *O. marginipennis*. Schulze's third group links *O. laeviceps* with *O. unguicularis*.

Biochemical data, as well, may aid in the interpretation of the phylogeny of *Onymacris*. For example, McClain *et al.* (1985) discuss the occurrence of cuticular waxy blooms within the Adesmiini. Of the *Onymacris* species studied, *O. boschimana*, *O. plana*, *O. laeviceps* and *O. r. albostessellata* all show waxy blooms, whereas *O. unguicularis*, *O. marginipennis* and *O. r. rugatipennis* have no evidence of blooms. However, the occurrence of blooms is fairly widespread in the Adesmiini, and has also been shown to have strong ecological correlates (McClain *et al.* 1985). This character might therefore have developed in parallel and should be viewed cautiously. In his biochemical studies of cuticular hydrocarbons, Lockey (1982) also shows that the Black species *O. plana* and *O. rugatipennis* are more similar to each other than to the White *O. marginipennis*.

Broad groupings similar to the ones identified herein are also suggested by the hybridization experiments of Osberg (1983). However, since all of the above-mentioned biochemical and hybridization studies do not include all *Onymacris* species and realistic outgroups, final conclusions about species' relationships derived from these approaches are still pending.

5.6 Biogeography

Onymacris is a characteristic beetle genus of the Southwest Arid Subregion (Endrödy-Younga 1978), a faunal zone identifiable also for butterflies (Carcasson 1964), birds (Crowe & Crowe 1982) and mammals (Coetzee 1983). Gebien (1938) and Koch (1962) argued that the high species-level diversity and endemicity of the coleopteran fauna of the Namib, as well as ultra-psammophilous adaptations by some species, implied an extremely ancient (Cretaceous) origin for the Namib Desert. Biological data were thus used to substantiate geological hypotheses. However, Endrödy-Younga (1978, 1982a and 1982b) cites geological evidence to explain the present distribution of beetles in a desert which is relatively young (early to mid-Tertiary). Ward et al. (1983) also maintain that the extreme-arid environment and the present extensive dune systems may be of relatively recent origin. Endrödy-Younga (1978) suggests that Old World Adesmiini have psammophilous and xerophilous tendencies, which would have been preadaptations for inhabiting the Namib as the area became more arid and extensive dune systems developed. For this reason, he suggests that the present distribution of Onymacris (and other beetle genera from this subregion) reflects the relatively recent vicariant evolution of the group in dune 'pockets' and shifting dunes. As Onymacris species are flightless, the present dispersion of species may reflect relict distributions as well as recent ecological and geographical expansion.

Assuming that vicariance has played an important role in the evolution and biogeography of Onymacris, the extensive distribution of O. unguicularis might reflect the ancestral Namibian range of the genus. Speciation and present distribution could thus be explained by vicariance events related to geological, climatic and ecological fluctuations. Important vicariance events would have included the incision of major Namib rivers (Kuiseb, Swakop, Ugab, Kunene and Curoca) during wetter periods of the Plio-Pleistocene, and erosion and deposition of aeolian sands at different times (Ward *et*. *al*. 1983). Endrödy-Younga (1982a) suggests that isolated dune 'pockets', particularly at river mouths, and shifting dunes have played primary roles in the evolution and dispersion of *Onymacris* species.

Endrödy-Younga (1978) and Penrith (1984) maintain that many Namibian Coleoptera, adesmiine genera in particular, have their sister taxa to the south. The fact that some of likely primitive Black *Onymacris* species, *O*. *lobicollis*, *O*. *b*. *boschimana*, and *O*. *paiva* also occur in the south of the range of the genus (Figure 1) supports this hypothesis. These Black species all inhabit stable dunes or the sandy plains and inter-dunes (Penrith 1975), which are likely to have been the habitats of the ancestral *Onymacris* species prior to the accumulation of the sands of the dune-sea. Thus, the Black species proliferated due to their pre-adaptation to the arid and sandy environment.

The White species may be derived from fragmentation and subsequent allopatric divergence of proto-*unguicularis* stock which had originally dispersed into Namibia from the south. All White species are hyper-psammophilous, dune specialists, which also suggests that this group is highly derived. The possible hybridization between some of the White beetles (Penrith 1975, 1984) is further evidence of the recent evolution of this group. Fluctuations in pluvial conditions during the Quaternary, indicated by plant and animal remains, and the presence of Stone Age artefacts, may also have been important in modifying the ranges of certain species or in isolating populations of beetles.

The hypothesized biogeography of the subgenus *Onymacris* is corroborated by the cladogram (Figure 8). Once the major geographical barrier - the Orange River - had been crossed by proto-*laeviceps* stock, populations of beetles would have been able to disperse northward with the shifting dunes (Endrödy-Younga 1982a) giving rise to the subgenus. Ancestors of the Black species group may have only crossed the Orange River more recently. Subsequent bridgings by some Black species would explain the phylogeny of the *Melanonymacris* lineage.

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Appendix 1 Locality and sample size information for *Onymacris* species and subspecies used in the phenetic analyses. Gazetteers of the localities are found in Penrith (1975, 1977, 1979).

Species	Females N	Males N	Locality
O. bicolor	19	35	Angra Fria, Dunedin Star, Torres Bay, Sarusas, Rocky Point, Hoanib R., Unjab R.
O. boschimana boschimana	30	30	Goodhouse, Achab, Henkies R., Aggenys, Pofadder, Pella, Springbok, Nabeis.
O. boschimana subelongata	21	31	Kanaän, Awasib, Tsondabvlei, Excelsior, Namib Park, Namtib, Aus.
O. candidipennis	31	29	Foz do Cunene, Porto Alexandre, Curoca, Praia Rochas, Praia Pinda.
O. hottentota	30	30	Bogenfels, Pomona, Kolmanskop, Spencer Bay, Port Nolloth, Anigab, Holgat, Grootmis.
O. laeviceps	30	28	Lüderitz, Tsondabvlei, Awasib, Gobabeb, Harus Mts, Walvis Bay, Grasplaatz, Kanaän, Sossusvlei.
O. langi	26	34	Bethanie, Huab R., Hoanib, (Moçamedes, Lagoa da Carvalhoa, Espinheira).
(*O. langi langi*)	14	14	
O. lobicollis	28	31	Lüderitz, Klinghardt Mts, Lorelei, Plumpudding, Bogenfels, Haalenberg, Agate Beach, Obib, Rosh Piña.
O. marginipennis	31	28	Angra Fria, Möwe Bay, Dunedin Star, Khumib, Hoanib R., Unjab R., Swakopmund, Walvis Bay, Punta Albina.
O. multistriata	30	30	Tses, Keetmanshoop, Bethanie, Mariental, Noordoewer, Karasburg, Maltahoë, Koës, Gibeon, Mukorob.
O. paiva	29	31	Jakkalsputz, Kleinsee, Wallekraal, Strandfontein, Holgat, Hondeklipbaai, Buffelsrivier.
O. plana	26	30	Gobabeb, Lüderitz, Sossusvlei, Walvis Bay, Obib Mts, Harus Mts, Aus, Haalenberg, Tsondap, Homeb, Natab, Namtib.
O. rugatipennis	29	30	Namib Park, Felsenek, Namtib, Sossusvlei, Tsondap, Gobabeb, Walvis Bay, Rooibank, Kanaän, Awasib, Gorrasis.
O. unguicularis	29	24	Sylvia Hill, Bogenfels, Lüderitz, Dune 7, Rooibank, Gobabeb, Grasplaatz, Hottentot Bay, Anigab, Blueberg, Spencer Bay, Swakopmund.