

**Adaptation and constraint in the evolution of the physiology and behavior of the
Namib desert tenebrionid beetle genus *Onymacris***

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ABSTRACT.

We investigated the evolution of a number of physiological and behavioral characteristics in the Namib desert tenebrionid beetle genus *Onymacris* using a comparative phylogenetic approach. In particular we examined the adaptive hypotheses that stilting, wax blooms and fog basking behavior had evolved as specific adaptations within this group to deal with desert life. Some beetle species in the hot desert interior elevate their bodies above the substrate by straightening their legs (called stilting) to raise themselves out of the hot boundary layer of air. We tested the adaptive hypothesis that desert-interior species have longer legs (relative to body size) than beetles in the cooler coastal region to facilitate stilting. We found that, contrary to this hypothesis, long legs were found to be the ancestral state in this genus and that short legs were the derived state in coastal species. Congruent with an adaptive hypothesis, the phylogenetic approach showed that wax blooms on the exoskeleton, which reduce evaporative water loss, were more likely to evolve in beetles living in the hot desert interior than on coastal species. Some of these beetle species exhibit fog basking, i.e. they remove water from fog by condensation onto their exoskeletons. This behavior has evolved on two separate occasions. Using a squared parsimony approach, we found that there is perfect coadaptation between the body temperatures that the beetles prefer in the laboratory and those they achieve in the field. There was no significant correlation between critical thermal minima and maxima and preferred body temperatures. Some members of the genus, occupying the desert interior, have the highest body temperatures of any ectotherm. Lower body temperatures have secondarily evolved in coastal species.

Key words. Comparative method, phylogeny, beetles, Tenebrionidae, Namib desert, physiology, behavior.

Introduction

Small desert ectotherms live in harsh environments where there is likely to be strong selection on physiology and behavior (Schmidt-Nielsen 1964, Louw and Seely 1982). As a result, they have been subjected to an enormous amount of study of their adaptations to desert life. None of these studies has considered the role of phylogeny (Louw and Seely 1982, Louw 1990). This is particularly surprising in view of the fact that many such studies have not revealed any peculiar adaptations to desert existence (reviewed by Seely 1989, Louw 1990). Indeed, Slobodkin (1989) has suggested "that although the same basic physiological machinery is used by organisms that live in deserts, it is usually modified to cope with either the rich but episodic resources, or the more continuously available low quality resources that characterize desert ecosystems. In this context it would be interesting to know more about speciation in and around deserts, in particular to discover whether they act as sources of, or sieves for, evolutionary novelties". It is with this in mind that we examined some aspects of the physiology and behavior of a well-studied genus of Namib desert beetles, *Onymacris*, from a phylogenetic viewpoint.

Few studies have examined the role of phylogeny in physiology (Huey 1987, Huey and Bennett 1987) or phylogeny and behavior (Losos 1990). To date, none has examined the role of phylogeny in the evolution of both physiology and behavior of a group of organisms. It is necessary when studying the physiology of desert ectotherms to include behavioral studies with physiological ones because physiological effects on these organisms may frequently be mediated through behavioral thermoregulation (Hadley 1975, Casey 1981,

Heinrich 1993, Ward *et al.* submitted).

The study area

The Namib desert of southwestern Africa is similar in its environmental characteristics to west-coast deserts on other continents: the major form of precipitation is from advective fogs blowing from the ocean. This results in a gradient of decreasing humidity and increasing temperature from the coast inland. In the Namib, this gradient is particularly acute and leads to significant differentiation of the desert into a cool, foggy, coastal zone and a hot, dry inland region (Robinson and Seely 1980). For example, precipitating advective fog occurs approximately 120 days per year in the coastal dunes at Walvis Bay, while at Gobabeb, 56 km inland, the annual mean is 36 days of fog (Robinson and Seely 1980). This steep microclimatic gradient across the desert's width give rise to two differentiable beetle faunas, called "coastal" and "inland" faunas (Koch 1961, 1962). These two faunas provide a basis for comparison of adaptations to extremes of desert life.

The study species

One of the most species-rich tribes of tenebrionid beetles found in deserts of the world is the Adesmiini (Koch 1962). They are predominantly diurnal and are thus subject to extreme conditions of temperature and humidity. The genus *Onymacris* (Adesmiini) is one of the most widespread genera in the Namib desert and is almost entirely restricted to this desert

(Penrith 1975, 1984 - Fig. 1). *Onymacris* has been the subject of considerable taxonomic, phylogenetic, physiological and ecological study (e.g. Koch 1961, 1962, Penrith 1975, 1984, Seely *et al.* 1983, Hamilton and Seely 1976, Roberts *et al.* 1991, Ward 1991, Ward and Seely submitted, Ward *et al.* submitted). This genus provides an excellent example of a monophyletic group for which sufficient information is available regarding phylogeny, physiology and behavior to examine the roles of adaptation and constraint in the evolution of desert animals.

It has previously been shown that species in the genus *Onymacris*:

(1) Have the highest known body temperatures (hereafter T_b) of any ectotherm (Edney 1971, Hamilton 1975, Seely *et al.* 1988; Roberts *et al.* 1991, Ward 1991, Ward *et al.* submitted).

(2) Select T_b 's in the field that are highly positively correlated with preferred T_b 's in the laboratory ($r^2=0.80$ - Roberts *et al.* 1991).

(3) Occupy different habitats in a manner that appears to be at least partially related to the thermal characteristics of the habitats (Roberts *et al.* 1991).

(4) Have a variety of morphological adaptations that appear to be related to body temperature (Edney 1971, Hamilton 1975).

(5) Have unique ability among insects to absorb water vapor from unsaturated air in the gut using a Malpighian tubule fluid with an osmolality of 9 mOsm (Machin 1981).

(6) Are the fastest cursorial invertebrates (Nicolson *et al.* 1984); the fastest recorded species in this genus, *O. plana*, has a mean speed of 95 cm.s⁻¹.

All *Onymacris* species are diurnally-active and predominantly feed, as adults, on

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wind-blown detritus on the sand surface. The larvae of all species feed on roots and other plant material below the sand surface and are therefore not particularly amenable to study. For this reason, we will concern ourselves here with the adults only. All species in the genus are long-lived (several years) and active throughout the year. Adults of all species are apterous (wingless) and have fused elytra. Their only respite from the extreme climate on the surface is therefore gained by burying into the soft sand or occasionally by climbing dwarf shrubs where these are available (Seely and Mitchell 1987, Ward *et al.* submitted).

There are two distinct morphological groups of *Onymacris*, the all-black species (henceforth "black" species) and those species with white elytra (henceforth, "white" species)(Table 1). *O. marginipennis* has pale brown elytra, and is most similar to the "white" species in morphology and physiology (Penrith 1984, Roberts *et al.* 1991); for the sake of brevity, we shall consider it one of the "white" species here.

Onymacris species occupy sandy habitats ranging from dune slipfaces to sandy, dry riverine water courses and dry flood plains (Table 1). Some species in the genus occur in the cooler coastal region, while others occur in the hotter inland region. This facilitates comparison of coastal and inland species in terms of physiological, morphological and behavioral characteristics.

It has been hypothesized that *Onymacris* species inhabiting the inland part of the desert have evolved:

(1) Preferred T_b 's that match the T_b 's they are able to attain in the field (Roberts *et al.* 1991). This is known as perfect coadaptation (see Huey and Bennett 1987 for a discussion of variants on this).

(2) Longer legs (relative to body length) than coastal species to enable them to "stilt", i.e. straighten their legs to elevate their bodies above the substrate (Penrith 1984). It has been demonstrated both theoretically (Gates 1962, Dreisig 1990) and empirically (Medvedev 1965, Hamilton 1975, Broza *et al.* 1983) that stilting may be an effective way to control T_b in long-legged insect species because it may raise the body out of the boundary layer of hot air on the sand surface. For example, Medvedev (1965) has shown that adesmiine beetles in the Kara Kum desert of central Asia (Turkmenistan) may achieve a 3-21.5°C decrease in T_b in summer by raising the body 1 cm higher above the surface. Similarly, Edney (1971) has suggested that Namib desert tenebrionid beetles may be able to reduce T_b by about 4°C by this behavior.

(3) Wax blooms on their cuticles to reduce water loss (McClain *et al.* 1985, McClain and Gerneke 1990). McClain *et al.* (1985) have shown that species occurring in the dry interior portion of the Namib desert are more likely to develop blooms than species on the coast, and populations of species that occur in both regions are more likely to possess wax blooms in the inland region. This analysis, however, is not a phylogenetic one and may be due to chance association (Donoghue 1990, Maddison 1990). That is, if inland species in a particular clade are very common relative to coastal species, then the probability that a particular character (in this case, a wax bloom) would be associated with inland species would be rather high by chance alone. It is therefore necessary to establish whether the occurrence of wax blooms in inland species is greater than by chance alone based on the frequency within in the clade.

The above hypotheses are strictly adaptive: we wished to assess their rigor in the face

of phylogenetic assessment of their roles in the evolution of this genus.

An additional physiological feature that we wished to examine from a phylogenetic standpoint was the behavior known as fog basking. Two species inhabiting the coastal region, *O. unguicularis* and *O. bicolor*, possess an unusual behavior to collect water in this desert with no free water. They climb to the top of a dune during the early morning fog and orient their bodies with the tip of the abdomen pointed upwards and the head angled downwards. Water vapor from the fog precipitates on the abdomen and runs down the carapace into the mouth (Hamilton and Seely 1976, Seely 1979, Seely *et al.* 1983). We wished to establish whether or not this behavior has evolved on independent occasions.

Methods

The phylogeny of *Onymacris*, using qualitative morphological characters, is reliably elucidated using Wagner parsimony (Penrith 1984 - Fig. 2). We have also bootstrapped this phylogeny using PAUP (Swofford 1991) and produced the same phylogeny. No characters used in this phylogeny (or characters correlated with these) were used in the comparative analyses of morphological characters. We mapped the distribution of particular characters on the phylogeny with the program MacClade (Maddison and Maddison 1992).

Following Huey and Bennett (1987), we first assessed coadaptation of physiological and morphological characteristics of *Onymacris* using a comparative, nonphylogenetic analysis, known as an "equilibrium" analysis (Lewontin 1969, Lauder 1981). We regressed field body temperatures on preferred body temperatures, as well as critical thermal maxima

and minima, using data that we have published elsewhere (Seely *et al.* 1988, Roberts *et al.* 1991, Ward 1991, Ward *et al.* submitted). Perfect coadaptation is a 1:1 relationship between these traits.

We then used the phylogenetic approach championed by Lauder (1981), Ridley (1983), Felsenstein (1985), Huey (1987), Huey and Bennett (1987), and Harvey and Pagel (1991), among others. Here, perfect coadaptation is congruent ^{with} changes in physiology and morphology in magnitude and direction. We used parsimony as a criterion and an averaging algorithm where the value of a node is computed as the iterative average of the three nearest nodes (Cavalli-Sforza and Edwards 1964). This is a minimum-evolution approach that minimizes the squared change in thermal and morphological characteristics for each link in the tree, summed for all branches, and is similar, but not equivalent to, a maximum-likelihood estimate (Huey and Bennett 1987, Maddison 1991). In contrast to the equilibrium analysis, comparisons of characters are conducted by regressing the difference between value for a species and the value at the nearest node for each character. This is called a transformational analysis (Huey 1987). This approach, as used here, assumes that evolutionary change is punctuational at the specific level: i.e. differences in time between speciation events are considered unimportant. This assumption is made for expediency because the ages of the species are unknown.

We did not use intergeneric comparisons as Huey and Bennett (1987) did because, unlike the conservative rate of physiological evolution at the specific level for the lizards in their study, there are significant differences between species of *Onymacris* in a number of physiological characteristics (Roberts *et al.* 1991, Ward 1991).

The resulting regressions of these characteristics are based on non-independent data, which is a consequence of using the minimum-evolution approach. If times of divergence were known, Felsenstein's (1985) "Brownian motion" model could circumvent this problem. We also performed the analyses using the independent-contrasts method of Felsenstein (1985), assuming equal branch lengths (most branches are results of changes in a single morphological character). This latter technique can use number of changes as a proxy for time, assuming equal time is required for each character change (Losos 1990). The regressions from this latter technique use independent data; for this reason, it is usually preferred over the minimum-evolution approach (Harvey and Pagel 1991). There was no difference between the results obtained from the minimum-evolution and the independent-contrasts approaches. We present results using the former technique because it facilitates direct comparison with Huey and Bennett's (1987) analysis of physiological evolution of a lizard clade.

For the morphological analyses, we used the monophyletic group constituting the genus, but excluded *O. brainei* because insufficient data were available for this species.

We used *Physadesmia globosa* as the outgroup in the thermal analyses because it is a member of the genus most closely related to *Onymacris* (Penrith 1979), and because suitable thermal measurements were available for this species. There are no thermal data for many of the species of *Onymacris*, so we performed these analyses using a non-monophyletic assemblage of the species for which data were available (Huey and Bennet 1987, Losos 1990). That is, we retained the phylogeny but eliminated all branches for species for which there were no thermal data.

To determine whether changes in one character were associated with changes in another, we used Maddison's concentrated-changes test (Maddison 1990). In this test, the probability of various gains and losses in a dependent character occurring in the distinguished areas of the clade is determined based on the total number of gains and losses over the whole clade, under the null hypothesis that gains and losses are randomly distributed over the branches (Maddison 1990).

Thermal analyses

Five species of *Onymacris* have been the subject of especial attention as regards body temperature choices in laboratory and field, CT_{max} and CT_{min} (Seely *et al.* 1988, Roberts *et al.* 1991, Ward 1991, Ward *et al.* submitted). They are *Onymacris rugatipennis rugatipennis* (Haag), *O. plana* (Peringuey), *O. unguicularis* (Haag), *O. marginipennis* (Breme), and *O. bicolor* (Haag). In addition, these measurements were also taken for *Physadesmia globosa* (Haag), a member of the most closely-related genus (Penrith 1979). These beetles were chosen to represent a wide variety of morphologies and habits among the larger adesmiine tenebrionids in the Namib, and because they are found in habitats ranging from the coast to the hot, dry, eastern edge of the Namib.

Body temperature (T_b) was measured continually using indwelling copper-constantan thermocouples (40 gauge) implanted 2-3 mm to the right of the midline in the pro-thorax of each beetle (Roberts *et al.* 1991, Ward *et al.* submitted). The thermocouple wire was

supported from above, leaving locomotion relatively unimpeded. Thermocouples were connected to a Bailey Bat 12 temperature recorder in the field. Preferred T_b was determined by allowing the beetles (with implanted thermocouples) to select positions on an oval track (Kramm and Kramm 1972). The thermal gradient was created on this track by running copper pipes with hot and cold water in opposite directions under the track. Use of this gradient prevents the study animals from getting stuck in a corner and thus providing spurious readings. T_b was averaged continuous measurements over an eight-hour period (Roberts *et al.* 1991).

Results

Habitat

The coastal habitat is the ancestral habitat in this genus (Fig. 2). Two species, *O. plana* and *O. langi*, have both coastal and inland populations. *O. unguicularis*, the most widespread species (Luderitz to Angola - Fig. 1), is coastal although some have dispersed inland and maintained populations there in the last fifteen years (Louw and Seely 1982). The "white" species are all coastal, with the exception of *O. langi* which has coastal and inland populations. All "white" species occur in the northern part of the Namib (north of Walvis Bay (*O. marginipennis*); all others occur north of Torra Bay only - Fig. 1). The "black" species are found in the southern half of the Namib (Swakopmund southwards), with the exception of *O. unguicularis*.

Leg length and stilting

We constructed a qualitative character for leg length using the residuals from the regression of \log_{10} modal male posterior femur length on \log_{10} modal male elytra length (a measure of body size). This provides a measure of relative leg length that is independent of body size. A species was considered to have long legs (relative to body size) if it had a positive residual and *vice versa*. Tracing this character on the phylogeny of *Onymacris* indicates that long legs are the ancestral state in this genus, and that short legs have evolved independently on two occasions (*O. hottentota* and the "white" species) (Fig. 3).

All these short-legged species are coastal, suggesting that there is some association of short legs with this habitat. Maddison's correlated character change test shows that the probability of this occurring by chance is 0.044. Thus, this phylogenetic approach contradicts the hypothesis that the desert species have evolved long legs (relative to body size) because of the advantage to be gained by stilting to reduce T_b when environmental temperatures at the sand surface are high. Indeed, it appears that some species have evolved short legs to cope with coastal life. *O. hottentota* would be particularly interesting to study in this regard because it has independently evolved short legs; thus, the factor/s selecting for short legs may still be acting and may be elucidated by physiological and/or ecological study.

It should also be noted that the correlated character change test shows that the probability that long legs are associated with the desert-interior habitat is 0.0009. Thus, because long legs are ancestral in this genus, this indicates that long legs have a high probability of being retained in the desert interior. Selection against long legs in the desert

interior, in contrast with the situation on the coast, is probably weak.

The "equilibrium" approach suggests that there is perfect coadaptation of leg length and body size ($\log_{10} \text{Femur} = 0.70 \log_{10} \text{Elytra length} - 0.26$; $r^2 = 0.46$; $t = 3.07$; $p < 0.02$: vs. slope of 1 (=perfect coadaptation): $t = -1.31$; $0.2 > p > 0.1$). However, using the transformational approach, there is imperfect coadaptation of leg length and body size (elytra length) in *Onymacris* because the slope of this relationship is less than 1 ($\log_{10} \text{Femur} = 0.74 \log_{10} \text{Elytra} - 0.00$; $r^2 = 0.80$; $t = 6.61$; $p < 0.001$: vs. slope of 1: $t = -2.26$; $0.05 > p > 0.02$).

A quantitative analysis of the evolution of elytra length and leg length provides more resolution of the above-mentioned phenomenon. While short elytra length (=small body size) is the ancestral character in this genus, there is a general evolution of larger body size (Fig. 4). Contrastingly, there is evolution of longer femur length in the left side of the phylogeny and shorter femur length in the right side (Fig. 5). This is consistent with the qualitative character analysis using residuals of the femur length vs. elytra length regression, which suggests that short legs have evolved independently of changes in body size.

This phylogenetic perspective on the evolution of relative leg length is supported by data on the behavioral thermoregulation of the five best-studied species (Ward *et al.* submitted). Although stilting was more likely to occur at temperatures greater than 35°C, it was rarely recorded in the field. Of these species, only *O. bicolor* stilted at its highest T_b 's. *O. bicolor* is a short-legged coastal species, living in the coolest habitat. Stilting was not recorded in *O. rugatipennis*, which lives in one of the hottest habitats (Roberts *et al.* 1991). Stilting did not cause a net decrease in T_b in any of the five species (Ward *et al.* submitted).

Thus, there is little behavioral evidence to support the hypothesis that long legs should evolve in hot environments to improve the efficacy of stilting.

Fog basking

Fog basking has evolved on two independent occasions, in one "black" species, *O. unguicularis*, and one "white" species, *O. bicolor* (Fig. 6). In both cases, fog basking has evolved in coastal species. The absence of this behavior in *O. langi*, *O. candidipennis*, *O. marginipennis*, and *O. brainei* is not an observational artifact: one of the authors (MKS) has been resident in the Namib desert for 25 years, and has intensively surveyed and studied this behavior (e.g. Hamilton and Seely 1976, Hamilton and Seely 1976, Seely *et al.* 1983).

Wax blooms

In *Onymacris*, populations of *O. rugatipennis* (subspecies *albotessalata* only), *O. plana*, *O. boschimana* and *O. laeviceps* have wax blooms (McClain *et al.* 1985)(Fig. 7). Of the inland species, members of *O. multistriata* only do not have wax blooms. The probability that wax blooms in *Onymacris* are associated with the inland species is 0.005 (concentrated-changes test). Thus, the nonphylogenetic conclusions of McClain *et al.* (1985) that wax blooms develop in the dry, inland habitat are upheld with the phylogenetic approach.

It should be noted that wax blooms are not a necessary requirement of life in the

desert interior. For example, in addition to the absence of wax blooms in the inland species *O. multistriata*, no members of the subspecies *O. rugatipennis rugatipennis* possess wax blooms, yet the subspecies *O. r. albotessalata* does. These two subspecies of *O. rugatipennis* occur in adjacent habitats that are similarly hot and dry (Osberg *et al.* 1986, Hauffe 1988).

Coadaptation of CT_{Max}, CT_{min}, preferred and field body temperature

The slope of the regression of field on preferred T_b was not significantly different from 1 using both the equilibrium (Field $T_b = 0.68$ Preferred $T_b - 34.88$, $r^2 = 0.68$, $t = 2.52$, $p < 0.1$; vs. slope = 1 - $t = 1.18$; $p > 0.1$) and phylogenetic approaches ($t = 1.83$, $p > 0.1$ - Fig. 8), indicating perfect coadaptation between these characteristics. High body temperatures first evolve from the low body temperature in *P. globosa* in *O. rugatipennis* and *O. plana*, but then low body temperatures evolve thereafter in the coastal species (Fig. 9).

There was no significant relationship between CT_{max} or CT_{min} and field or preferred T_b , using both equilibrium and phylogenetic approaches. The probable reason for this is the very slight differences in the values of CT_{max} and CT_{min} between the species (Table 2).

Discussion

The value of the comparative phylogenetic approach

There is now a large number of recent studies that demonstrate the value of the comparative phylogenetic approach (reviewed by Harvey and Pagel 1991). However, it should be recalled that the comparative phylogenetic approach was once a cornerstone of evolutionary biology (see e.g. Huxley 1931, Lorenz 1952). The demise of this comparative approach was concomitant with the upsurge of experimental approaches that concentrated on adaptive features on organismal biology (e.g. in behavior - Tinbergen 1951; in physiology - Schmidt-Nielsen 1964).

Although well aware of the many pitfalls of the strict adaptationist line taken by many evolutionary biologists in the 1960's and 1970's (as parodied by Gould and Lewontin 1979), comparative biologists have sometimes fallen into the same trap that caught strict adaptationists, namely assuming that all is explained by the prevailing exemplar. An example of this is Stearns' phylogenetic-subtraction approach (1983), which removes effects due to phylogeny prior to the submission of evidence that phylogenetic constraints play a role in the evolution of the particular character (Harvey and Pagel 1991). It is now widely recognized that the adaptive and phylogenetic approaches are complementary (e.g. Lauder 1981, Huey 1987, Losos 1990, Harvey and Pagel 1991, Stearns 1992). There is clearly a distinct need for a more balanced approach that simultaneously examines the roles of adaptation and constraint in evolutionary biology (Lauder 1981, Huey and Bennett 1987, Huey 1987). Of

course, any discussion of the role of phylogeny and adaptation must necessarily be tempered with the observation that a cladogram is an hypothesis about the phylogeny of the clade being examined (e.g. Ridley 1983, Huey 1987). Thus, statements about the derived and ancestral conditions of characters are contingent upon the notion that the cladogram faithfully represents the phylogeny of the organisms being examined.

In our study, the phylogenetic approach proved useful in a number of ways. For example, one adaptive hypothesis proved to be inappropriate once viewed through a phylogenetic lens. That is, the hypothesized evolution of long legs from short legs to facilitate stilting in desert-interior species was rejected. It appears that short legs is the derived state in this genus. Contrastingly, the phylogenetic approach supported the adaptive hypotheses for the evolution of wax blooms in inland species and the perfect coadaptation of field T_b and preferred T_b . Knowledge of the phylogeny of *Onymacris* was also necessary to indicate that fog basking has evolved on two, rather than one, independent occasions.

Fog basking

Fog basking has evolved on two independent occasions, once in a "black" species and once in a "white" species. Both of these species are coastal, where they can make use of the precipitating advective fogs. Why should this analogous behavior have evolved independently? Why has it been lost in the other "white" species? This behavior may either be very costly and is therefore easily lost through natural selection, or it requires a single (or few) mutation that occurs frequently. All of the species that have apparently lost

this behavior (*O. marginipennis*, *O. brainei*, *O. candidipennis*, *O. langi*) have all or some populations in the coastal habitat. In addition, the detritus these beetles eat is very dry (Tschinkel 1973). Thus, it is hard to understand why they too would not gain from obtaining water through this behavior. We speculate that fog-basking behavior is controlled by a single mutation that is easily lost, perhaps through a negative genetic correlation.

Wax blooms

The phylogenetic approach adopted here supports the results of adaptive study of McClain *et al.* (1985) that wax blooms are more likely to evolve in desert-interior species. However, it is still necessary to consider why there has been a loss of wax bloom in *O. multistriata*, a species that inhabits the central Kalahari desert. This is most puzzling in the light of the strong adaptive value of these wax blooms in reducing water loss (McClain *et al.* 1985). Similarly, the absence of a bloom in the subspecies *O. r. rugatipennis* is equally hard to explain. Nonetheless, the results of this study point the way to new studies of the physiology of wax blooms and the need to incorporate phylogeny into such studies.

Long legs, hot habitats and stilting

The evolution of long legs in *Onymacris* is inconsistent with the hypothesis that long legs evolve to enhance stilting in the hot desert-interior habitats because long legs are the ancestral state in this genus, yet the coastal habitat is the ancestral habitat. This is supported

by behavioral data that indicate that stiling is rarely used as a cooling mechanism in these beetles (Ward *et al.* submitted). This may be because stiling is an ineffective cooling mechanism because of the over-riding influence of the particular convective conditions in this desert. If there is no forced convection at the surface, raising the body by about 1 cm by stiling is unlikely to be effective because the boundary layer will not be hotter than the layer above it (Ward *et al.* submitted). Conversely, if wind velocities are very high, thermal mixing will occur (the boundary layer will be broken up), equilibrating temperatures at and a few centimetres above the substrate; again there will be little benefit to stiling. Therefore, stiling may be effective at reducing T_b in a narrow range of wind velocities only. More effective strategies than stiling may be either to bury into the sand before the temperatures on the substrate get too high (Seely and Mitchell 1987) or to climb bushes to get higher above the substrate, as is the case in *O. rugatipennis* (Ward *et al.* submitted). Nonetheless, long legs are highly correlated with the inland habitat, suggesting that because long legs are ancestral, selection against long legs in these habitats is weak.

Additional support for the notion that convective conditions are of over-riding importance in the thermal physiology of these beetles is found in the study of Turner and Lombard (1990). They found that there was no difference in field T_b between "white" and "black" species of *Onymacris* of the same size under convective conditions normally experienced in the field. This indicates that convective conditions are more important than radiation effects on T_b ; if radiation had a more important effect on T_b , then white beetles should have lower equilibrium T_b than black beetles.

It should be noted that the above arguments are based on the assumption that selection

acts under "normal" conditions. Heinrich (1993) has pointed out that it is probable that selection has had its major effects under extreme conditions. Experimental examination of the effects of extreme conditions on these beetles is necessary to retrieve this latter argument from the panglossian morass.

While there is a biophysical reason why long legs might not be advantageous in this habitat, the evolution of short legs in some coastal species is hard to explain. We speculate that beetles with long legs incur a considerable cost in terms of breakage. It is known that some species of *Onymacris*, when kept in captivity on sand substrates different from their natural substrates, lose terminal leg segments through abrasion (Koch 1962). Indeed, beetles in the wild are frequently seen with missing terminal leg segments (pers. obs.). We suggest that when there is little advantage to be gained by possessing long legs in cool coastal habitats, selection favors short legs to minimize the cost of breakage.

Body temperatures

It is perhaps not surprising that preferred and field T_b are perfectly coadapted in these beetles. The selection pressure on T_b in small ectotherms in these hot habitats is likely to be very strong (Roberts *et al.* 1991). However, as Huey and Bennett (1987) pointed out in their study of Australian lygosomine skinks, partial or even antagonistic coadaptation may occur because of:

(1) Conflicting selection pressures with other aspects of the animal's life history (such as temperatures for optimal digestion).

- (2) Low heritability, negative genetic correlations, or weak selection (Falconer 1981).
- (3) Insufficient time for evolutionary equilibria to be established.
- (4) Burrowing and nocturnal activity that reduce selection pressures.

A fifth reason is that factors such as competition or predation may force the animals to be active at times when optimal T_b can not be achieved. Of course, if these factors are consistent in the long term, selection should favor evolution towards the T_b at which the animals are forced to be active. In deserts, there is a vast amount of spatial and temporal variation in the effects of abiotic (see Sharon 1980, Ward *et al.* 1992) and biotic factors (Seely 1978, 1985, Ward and Seely submitted) on organisms. It is conceivable that selection pressures are temporally and spatially variable and thus insufficient to drive T_b to new equilibria. Nonetheless, it appears that the above-mentioned factors are not of over-riding importance to the species of *Onymacris* studied thus far. Of course, a more complete statement about the coadaptation of field and preferred T_b requires examination of more species, especially in the left part of the clade from *O. rugatipennis* through *O. paiva* (Fig. 2). Examining more species will also help to elucidate whether the evolution of higher body temperatures in two inland species, *O. rugatipennis* and *O. plana*, and the subsequent evolution of lower T_b in the other, coastal species (Fig. 9) is due to correlations with habitat or due to phylogenetic factors.

In contrast to the pattern in *Onymacris*, *P. globosa* selects field T_b far below its preferred T_b (Fig. 9). Ward and Seely (submitted) have shown that *P. globosa* prefer the cool microhabitat under large *Acacia* trees in dry riverbeds where most of their preferred food, *Acacia* flowers, is located. In a series of removal experiments, we showed that

intraspecific competition forces some individuals of *P. globosa* to occupy the hot, unshaded microhabitat of open sand between these trees. We speculate that the high preferred T_b in *P. globosa* has been selected for to cope with conditions when intraspecific competition forces them to occupy hot habitats.

Why is there no relationship between CT_{max} and CT_{min} and preferred or field T_b ? There is very little variation among *Onymacris* species in either CT_{max} or CT_{min} (Table 2). Values for CT_{min} are set well below the low temperatures that the beetles usually encounter because they emerge from beneath the sand once substrate temperature exceeds CT_{min} only. Thus, it is not surprising that CT_{min} has not evolved in tandem with preferred T_b . Conversely, these beetles (particularly the inland species) frequently encounter substrate temperatures that are in excess of CT_{max} . For example, substrate temperatures encountered by *O. rugatipennis* frequently exceed CT_{max} for more than four hours in the middle of the day (Ward *et al.* submitted). These beetles avoid these temperatures either by burying or by climbing bushes (Ward *et al.* submitted). Thus, selection pressures on CT_{min} and CT_{max} may be low because the beetles can avoid extreme temperatures by behavioral means. This is not to say that selection on CT_{min} and CT_{max} is nonexistent; it is hard to imagine why else the limits to beetle activity, as determined by the difference between CT_{min} and CT_{max} (about 40°C on average), are so broad.

There are two other factors of possible importance in the control of body temperature in *Onymacris*:

- (1) Elevated transmittance to shortwave infrared radiation of the elytra, which may increase heat gain at the beginning and end of the day (Henwood 1975). This may increase

metabolic efficiency when air temperatures are low. However, because infrared radiation is more intense at midday when beetles have to retreat from the heat, this feature presumably is of benefit if it is compensated for by increased time for feeding and reproductive activity in the morning and evening and on cool days (Heinrich 1993). Thus far, this feature has only been detected in *O. plana* (Henwood 1975).

(2) Raised elytra (such as in *O. unguicularis*, *O. laeviceps* and *O. bicolor*), which may increase the size of the subelytral cavity. This subelytral cavity may act as a thermal buffer to reduce extreme temperatures experienced by the organs (Heinrich 1993). The thermal value of raised elytra has not been demonstrated experimentally.

Unfortunately, few species of *Onymacris* have been tested for either of these factors, preventing a phylogenetic analysis.

Why are *Onymacris* body temperatures so high ?

The species of *Onymacris* have the highest body temperatures of any ectotherm and maintain T_b in the upper part of the tolerated range (Seely *et al.* 1988, Roberts *et al.* 1991, Ward 1991). There are two main hypotheses to explain these high body temperatures:

(1) Hamilton (1975) has suggested that these beetles are "maxitherms"; that is, they maintain high body temperatures in order to maximize metabolic rate, which maximizes metabolic efficiency and enhances competitive ability and/or reproductive output.

(2) Heinrich (1977) has suggested that the environment constrains the beetles to withstand the high ambient temperatures frequently experienced. Because the enzymes that

are selected to withstand these high temperatures have a narrow range of activity, the beetles are forced to be active in the upper part of their tolerated range of air temperatures only.

Hamilton's (1975) maxithermy hypothesis has been tested experimentally. Ward (1991) surmised that if maxithermy is an adaptive strategy, the beetles would adopt it when there is a surfeit of food only. This is because an animal with a high metabolic rate would necessarily be wasting much-needed energy when faced with food deprivation. Selection should favor those animals that selected lower T_b to minimize energy expenditure when deprived of food. Thus, starved beetles should select lower T_b for activity. Beetles of the species *O. plana*, *O. rugatipennis* and *P. globosa* were starved over a six-week period and preferred T_b measured once a week on the thermal gradient described above (Methods). None of these species selected lower T_b over the period of the study and did not differ in preferred T_b from controls fed *ad libitum*. Therefore, there is no evidence to support the maxithermy hypothesis as an adaptive strategy.

Heinrich's (1977) hypothesis does not explain why these beetles have not evolved to become nocturnal: two genera in the tribe Adesmiini, *Epiphysa* and *Alogenius*, are nocturnal, while more recently derived genera including *Onymacris* are diurnal (Penrith 1979). Additionally, because the beetles can avoid extreme air temperatures on the surface by burying or climbing bushes, this hypothesis can not explain why high diurnal air temperatures are not avoided.

Does phylogenetic constraint control T_b ? It is plausible that the maxithermy hypothesis was once selected for and the beetles maintain high body temperatures through phylogenetic inertia. If this view is correct, placing them in conditions of food deprivation is

unlikely to affect preferred T_b because they seldom experience such conditions and selection pressure against maintaining such high T_b is low. In support of this argument, it has frequently been claimed that abiotic factors, such as weather, limit the abundance of many desert animals (e.g. Holm and Edney 1973, Noy-Meir 1973, Goodall 1976). Thus, their abundances may be kept at levels below the carrying capacity of the environment (Holm and Edney 1973). Additionally, competition between detritivorous insect species has not been demonstrated (Crawford 1991). However, it has recently been shown that intra- and interspecific competition affect the densities of beetles in some Namib communities (Ward and Seely submitted, Ward unpubl. data). Thus, food availability may be a limiting factor on populations.

An adaptive hypothesis that bears testing is that these beetles maintain high body temperatures in order to outrun their predators which either are not as fast as the beetles or have to expend excessive amounts of energy at high ambient temperatures (Wharton 1980, Seely 1985). This is, of course, an evolutionary lag argument. This argument begs the question why their predators have not evolved the ability to be more efficient at higher ambient temperatures, particularly because these beetles are among the most abundant Namib animal species.

We stress that the adaptive hypotheses for high body temperatures need to be fully explored before we fall back on the "default" phylogenetic-inertia hypothesis. However, there is some evidence that body temperatures may be contingent in part on historical factors, at least at the level of intercontinental comparison. Seely *et al.* (1988) have shown that tenebrionid beetles in the deserts of North America (Kenagy and Stevenson 1982,

Slobodchikoff 1983, Parmenter *et al.* 1989) experience far higher ambient temperatures than Namib or Saharan beetles, yet both Namibian and Saharan tenebrionids maintain far higher T_b . Further exploration of intercontinental differences in body temperatures should prove valuable in determining the role of history and phylogeny in the evolution of the physiological characteristics of desert tenebrionid beetles. Bell's (1989) nested analysis of covariance technique will be most useful for this, to tease out the effects of phylogeny (nested factors) and history (continent=covariate).

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Table 1. Microhabitats and elytra color of *Onymacris* species and the outgroup *Physadesmia globosa*.

| SPECIES | MICROHABITAT | ELYTRA COLOR |
|-------------------------|--|--------------|
| <i>O. unguicularis</i> | vegetationless dune slipfaces | Black |
| <i>O. multistriata</i> | vegetated red dunes | Black |
| <i>O. lobicollis</i> | vegetated coastal dunes and interdunes, sandy river banks | Black |
| <i>O. plana</i> | open sand and vegetation of lower dune slopes | Black |
| <i>O. laeviceps</i> | vegetationless dune slipfaces and vegetated dune bases | Black |
| <i>O. rugatipennis</i> | open sand of dry water courses (subsp. <i>rugatipennis</i>), vegetated dune bases and interdunes (subsp. <i>albotessalata</i>) | Black |
| <i>O. boschimana</i> | stable vegetated dunes and sparsely vegetated plains | Black |
| <i>O. hottentota</i> | vegetated dunes | Black |
| <i>O. paiva</i> | vegetated dunes and sandy plains | Black |
| <i>O. candidipennis</i> | vegetated dunes | White |
| <i>O. bicolor</i> | vegetationless dune slipfaces | White |
| <i>O. langi</i> | vegetated sand dunes and interdunes | White |
| <i>O. brainei</i> | vegetated dunes | White |
| <i>O. marginipennis</i> | vegetated dunes and river courses | Pale Brown |
| <i>P. globosa</i> | vegetation of dry water courses and gravel plains | Black |

Table 2. Mean CT_{max} and CT_{min} values for *Onymacris* and *P. globosa*.

| SPECIES | CT_{max} , °C | CT_{min} , °C |
|-------------------------|-----------------|-----------------|
| <i>O. plana</i> | 51 | 12 |
| <i>O. rugatipennis</i> | 50 | 10 |
| <i>O. unguicularis</i> | 49 | 9 |
| <i>O. marginipennis</i> | 48 | 10 |
| <i>O. bicolor</i> | 48 | 8 |
| <i>P. globosa</i> | 51 | 14 |

FIGURE CAPTIONS

Fig. 1. Distribution of *Onymacris* in southwestern Africa. All white species occur north of Torra bay. Black species, with the exception of *O. unguicularis*, occur from Swakopmund southwards.

Fig. 2. Regions occupied by *Onymacris*. Black = inland; clear = coastal.

Fig. 3. Relative leg lengths (qualitative character) of *Onymacris*. Black = long legs; clear = short legs.

Fig. 4. Elytra length (a measure of body size) plotted as a quantitative character on the phylogeny of *Onymacris*.

Fig. 5. Leg length plotted as a quantitative character on the phylogeny of *Onymacris*.

Fig. 6. Phylogeny of fog basking in *Onymacris*. Black = fog basker; clear = non-basker.

Fig. 7. Phylogeny of wax blooms in *Onymacris*. Black = wax bloom present; clear = no bloom.

Fig. 8. Coadaptation of field and preferred body temperatures in *Onymacris* using the minimum-evolution method. Values are the differences between the median body temperature of the species and the value of the nearest node.

Fig. 9. Preferred and field body temperatures of *Onymacris* and *P. globosa* plotted on the non-monophyletic cladogram. Preferred temperatures are written above field temperatures in each case.

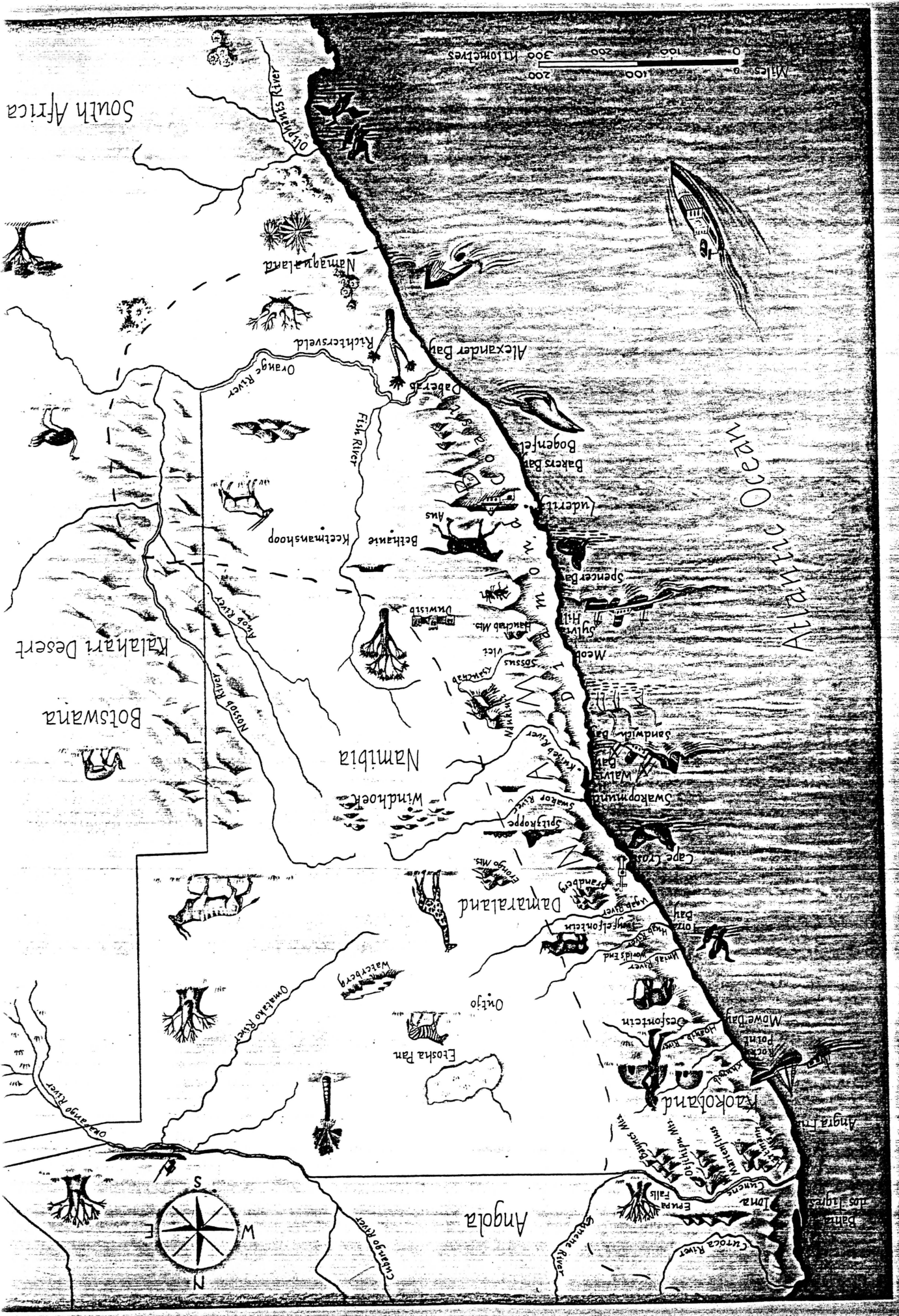


Fig. 2

HABITAT
0 coastal
1 inland

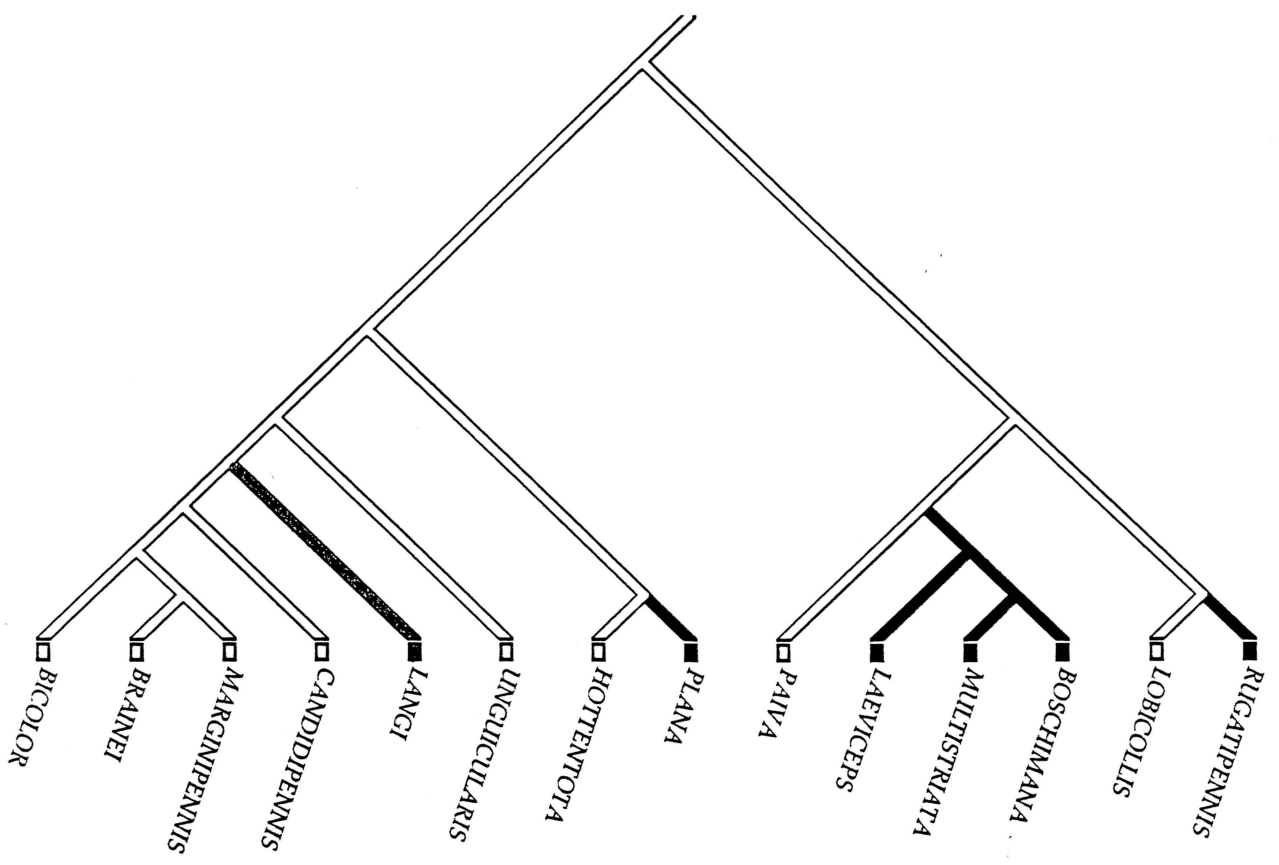
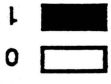


Fig. 3



LEG LENGTH

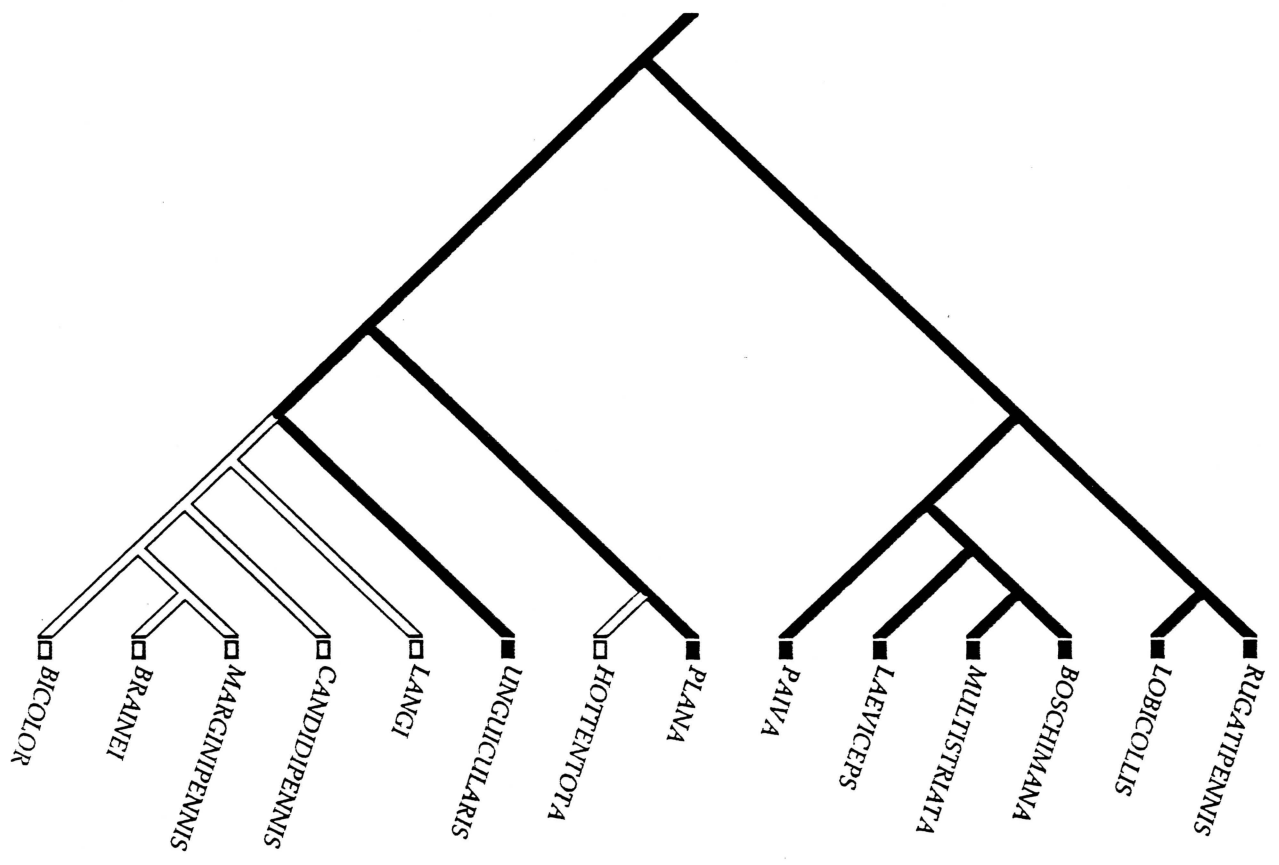
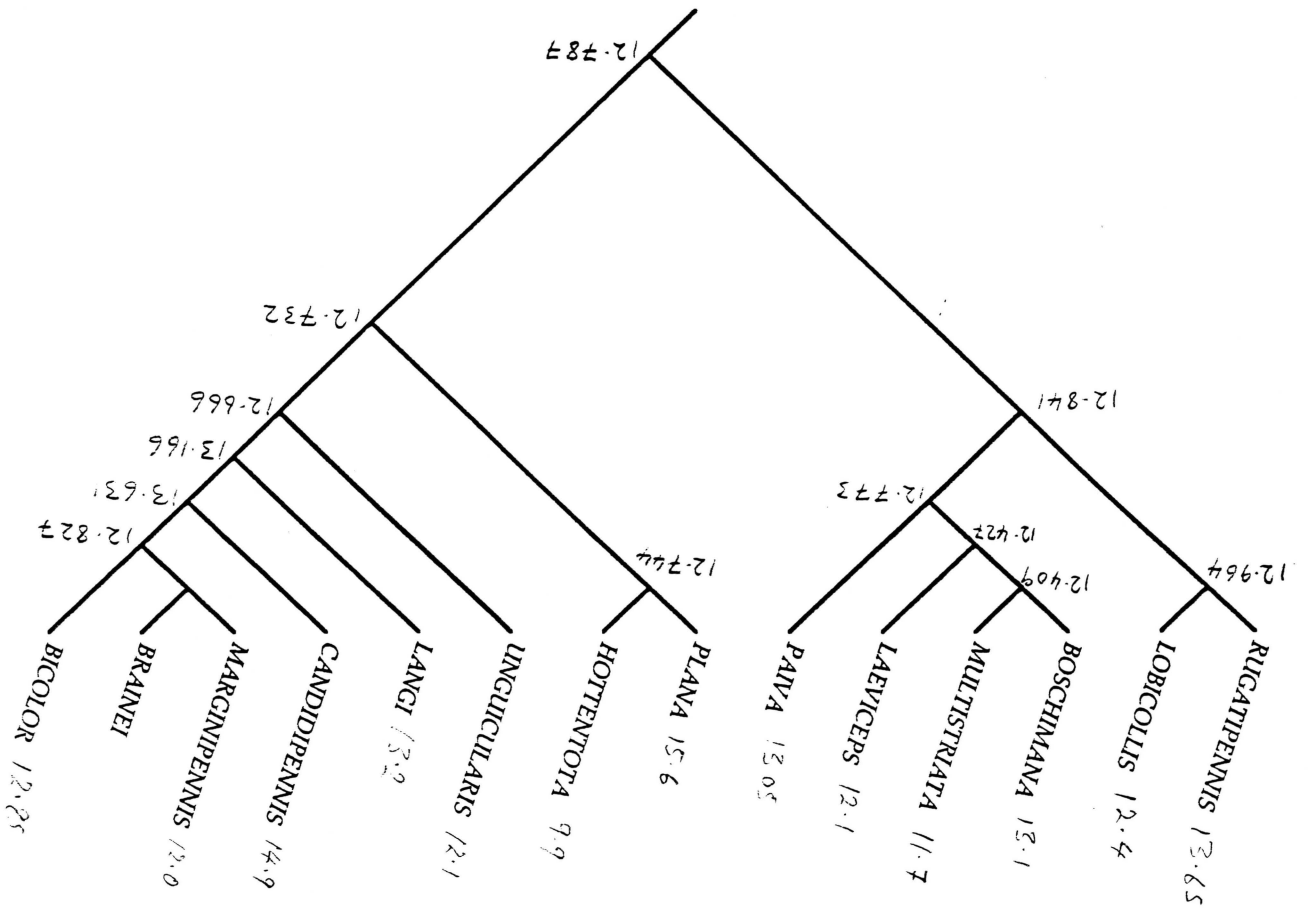
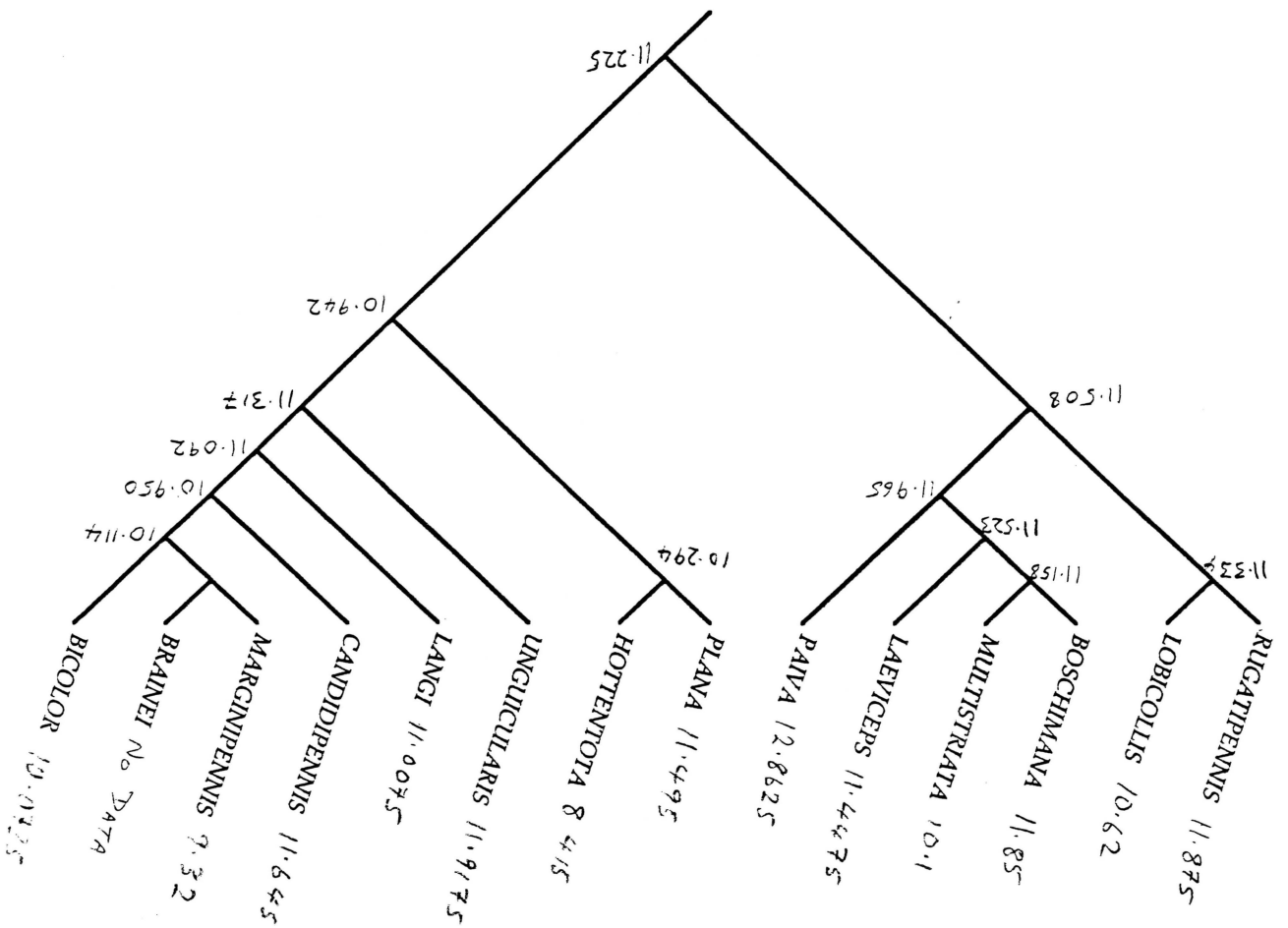


Fig. 4



Median Elytra length

Fig. 5



Femur length

FOG BASKING

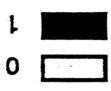


Fig. 6

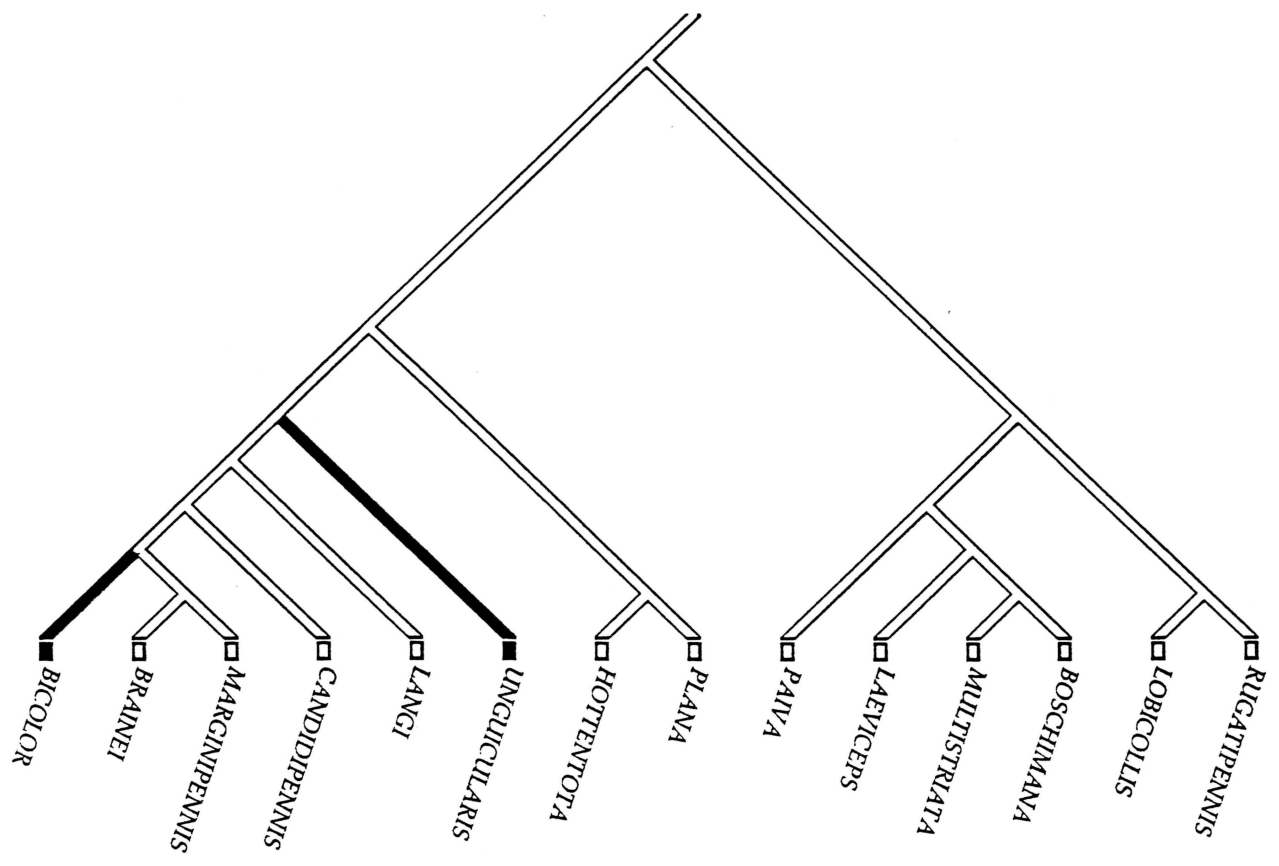


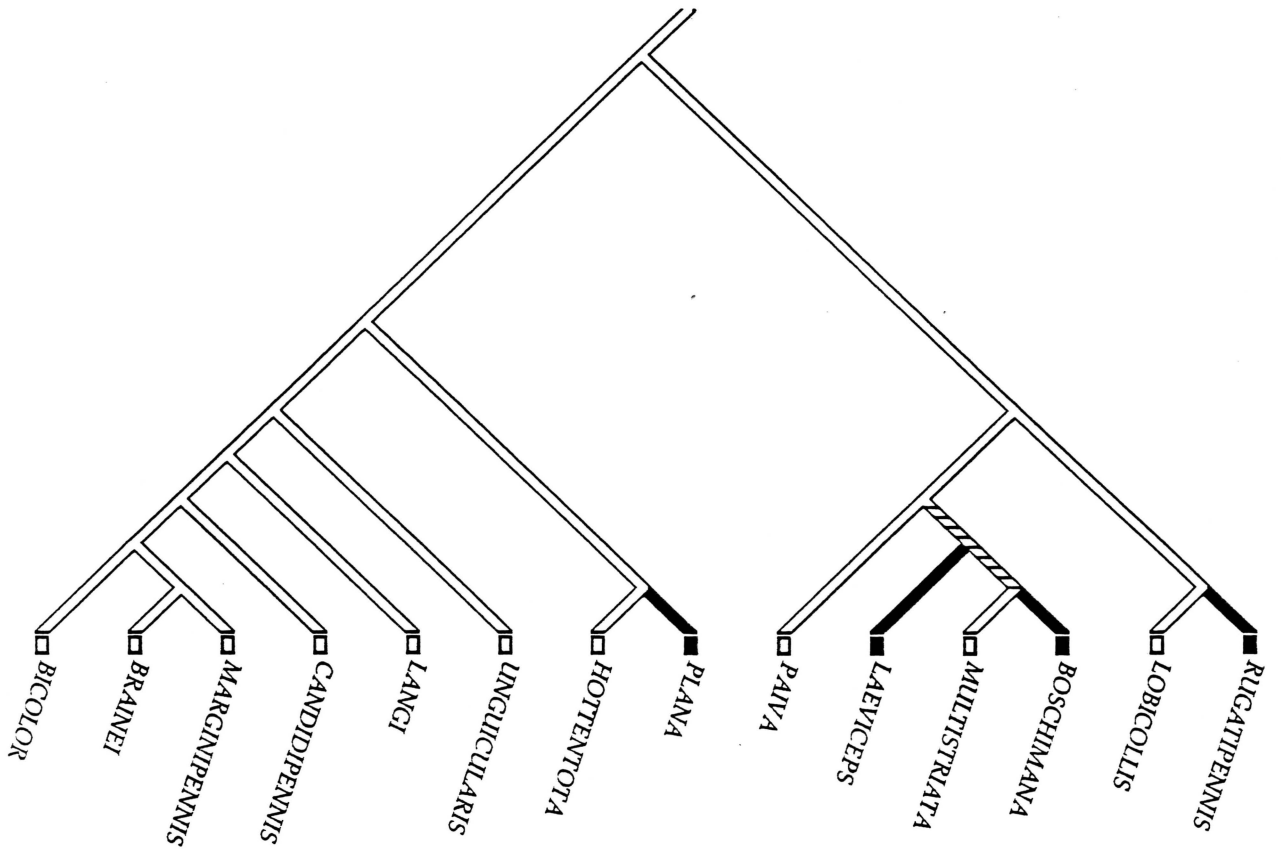
Fig. 7

WAX

0 No Wax

1 WITH WAX

equivocal



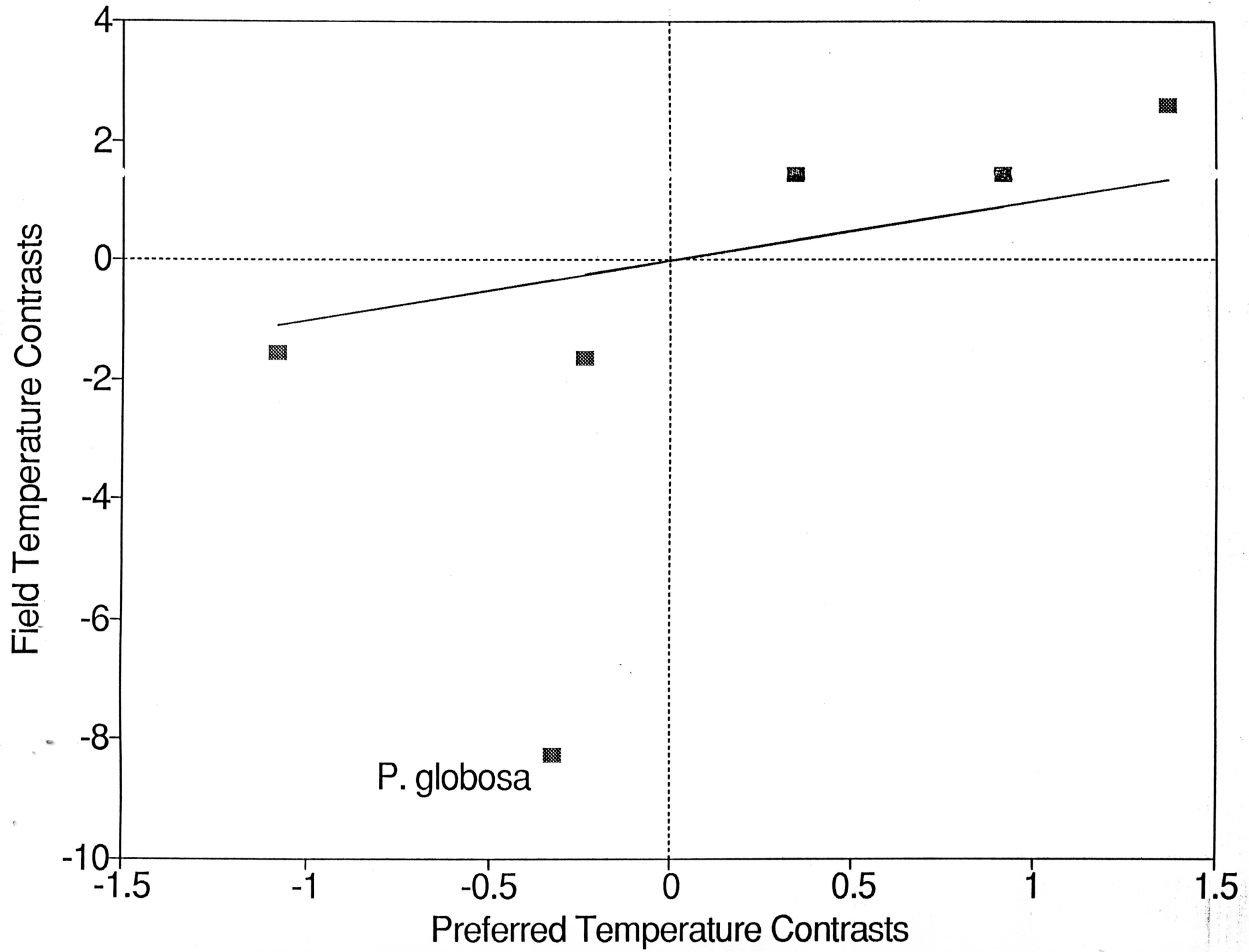


Fig. 8

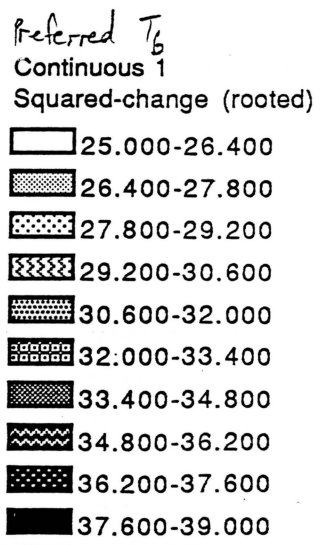
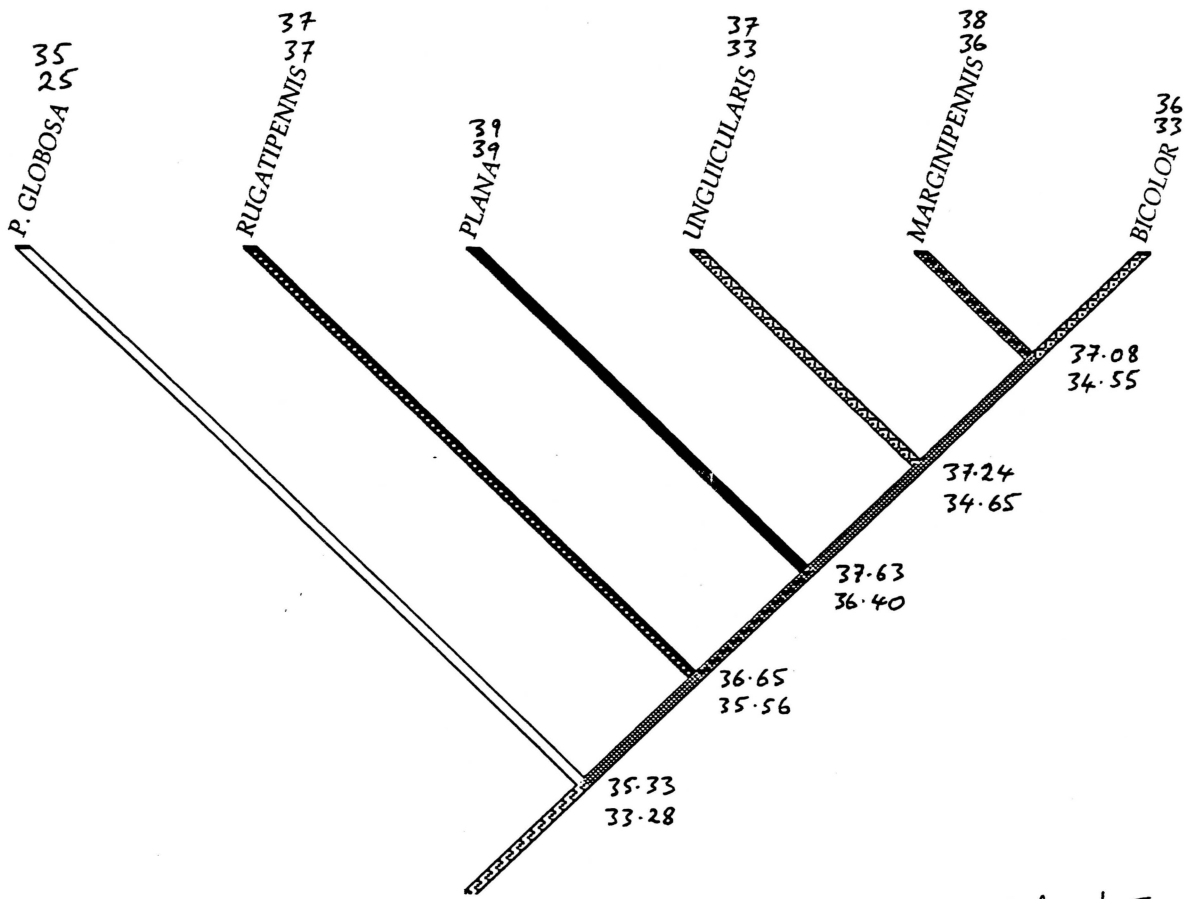


Fig. 9