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Phylogeny of *Geomydoecus* and *Thomomydoecus* pocket gopher lice (Phthiraptera: Trichodectidae) inferred from cladistic analysis of adult and first instar morphology

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Abstract. The phylogeny for all 122 species and subspecies of chewing lice of the genera *Geomydoecus* and *Thomomydoecus* (Phthiraptera: Trichodectidae) hosted by pocket gophers (Rodentia: Geomyidae) is estimated by a cladistic analysis of fifty-eight morphological characters obtained from adults and first instars. The data set has considerable homoplasy, but still contains phylogenetic information. The phylogeny obtained is moderately resolved and, with some notable exceptions, supports the species complexes proposed by Hellenthal and Price over the the last two decades. The subgenera *G. (Thaelerius)* and *T. (Thomomydoecus)* are both shown to be monophyletic, but the monophly of subgenus *T. (Jamespattonius)* could not be confirmed, perhaps due to the lack of first-instar data for one of its component species. The nominate subgenus of *Geomydoecus* may be monophyletic, but our cladogram was insufficiently resolved to corroborate this. Mapping the pocket gopher hosts onto the phylogeny reveals a consistent pattern of louse clades being restricted to particular genera or subgenera of gophers, but the history of the host–parasite association appears complex and will require considerable effort to resolve.

Introduction

The association between chewing lice of the genera *Geomydoecus* and *Thomomydoecus* (Phthiraptera: Trichodectidae) and their pocket gopher hosts (Rodentia: Geomyidae) presents a unique opportunity for the study of host–parasite relationships and cospeciation (Hellenthal & Price, 1991). Pocket gophers are fossorial rodents with fragmented distributions comprising small, genetically differentiated populations (Patton & Smith, 1989). This, coupled with the high degree of host specificity shown by *Geomydoecus* and *Thomomydoecus* lice (e.g. Hellenthal & Price, 1984a), raises the possibility that the gophers and their lice have cospeciated.

Support for the hypothesis of cospeciation has come from phylogenies constructed from allozyme data for a small sample of the gophers and their lice (Hafner & Nadler, 1988), which revealed substantial congruence between their evolutionary histories (Hafner & Nadler, 1988, 1990; Page, 1990). This data set is perhaps the best evidence to date for cospeciation in any host–parasite association, and has played a prominent role in the development of methods for reconstructing the history of host–parasite association (Page, 1990, 1993a, b) and for comparing genetic divergence between hosts and parasites (Hafner & Nadler, 1990; Brooks & McLennan, 1991: 310–317; Page, 1991). More recently, Hafner *et al.* (1994) have obtained mtDNA sequences from a sample of gophers and their lice which corroborates the evidence for cospeciation provided by the allozyme data.

To date, 122 species and subspecies of *Geomydoecus* and *Thomomydoecus* have been described, distributed among the two genera, four subgenera, and twenty-six species complexes (Hellenthal & Price, 1991, 1994). Hafner & Nadler (1988) sampled just ten louse species, which raises the question of how representative that sample was

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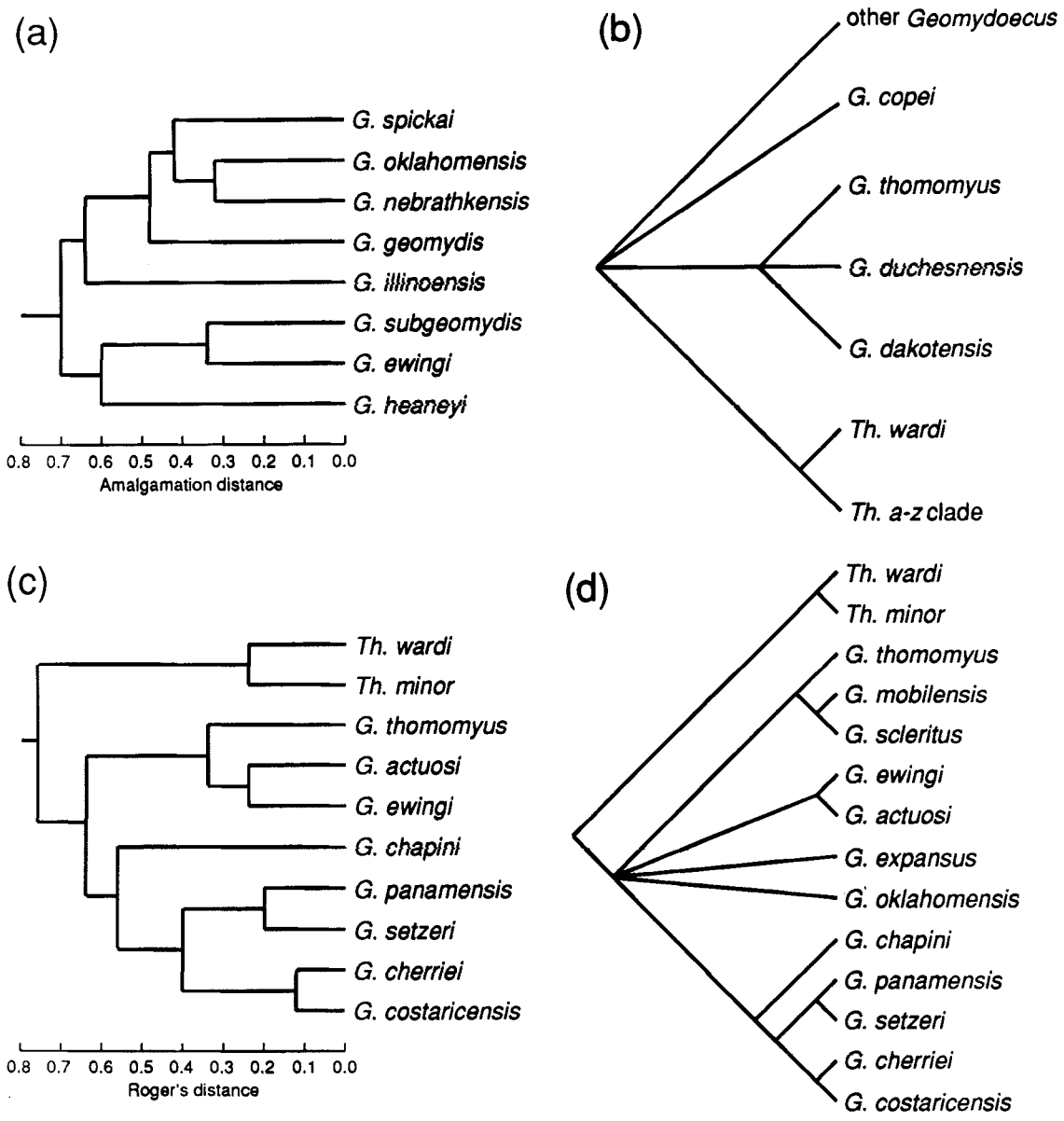


Fig. 1. Four trees summarizing relationships of various pocket gopher chewing lice: (a) UPGMA cluster analysis of male morphology of lice belonging to the *geomydis* complex (after Timm & Price, 1980: fig. 15); (b) Lyal's (1985: fig. 34) cladistic analysis of *Geomydoecus* and *Thomomydoecus* taken from his cladogram for the Trichodectidae; (c) UPGMA analysis of allozyme data (after Hafner & Nadler, 1988: fig. 2); and (d) strict consensus tree for eighty equally parsimonious trees computed from allozyme data (after Nadler & Hafner, 1993: fig. 1).

of the overall pattern of association between gophers and lice. Indeed, all previous efforts to infer the phylogeny of the lice have typically been limited by the number of taxa sampled.

The earliest attempt to infer pocket gopher louse relationships was Timm & Price's (1980) phenetic analysis of the adult morphology of lice belonging to the *geomydis* complex (Fig. 1a). The first cladistic analysis of *Geomydoecus* and *Thomomydoecus* was published by Lyal (1985), as part of his study of relationships within the Trichodectidae. Lyal concluded that *Geomydoecus* and *Thomomydoecus* together were monophyletic and that *Neotrichodectes* is their sister taxon, but could not confirm the monophyly of either *Geomydoceus* or *Thomomydoecus* with respect to each other (Fig. 1b). Because Lyal's focus was on the relationships among the Trichodectidae, he did not attempt a detailed analysis of the gopher lice.

Hafner & Nadler's (1988) study of cospeciation between gophers and lice was based on a UPGMA analysis of allele frequencies at thirty-one loci in the gophers, but only fourteen loci in the lice (Fig. 1c). Their use of UPGMA was justified by the clock-like structure of the data (see Page, 1990). Later, they added four more taxa to the same data set (Fig. 1d) and presented both parsimony and

UPGMA analyses (Nadler & Hafner, 1993). Although representing a small sample of lice (fourteen species from nine complexes), their data supported the monophyly of both *Geomydoceus* and *Thomomydoecus* (see also Nadler & Hafner, 1989). More recently, Demastes & Hafner (1993) collected allozyme data from some representatives of the *geomydis* complex, and obtained a tree largely congruent with that of Timm & Price (1980).

In this paper we attempt to estimate the phylogeny of all 122 louse species and subspecies, based on morphology of the adults and first instars. We hope that locating the small number of lice for which molecular data are available in this broader phylogenetic framework will shed more light on host–parasite relationships between gophers and their lice, and will suggest which louse complexes would be most profitably sampled next using molecular techniques. Our other motivation is to provide an estimate of louse phylogeny that is independent of those derived from allozyme and mitochondrial DNA sequence data (Hafner *et al.*, 1994).

Materials and Methods

Terminal taxa. The terminal taxa are the 122 species and subspecies delimited by R.D.P. and R.A.H. over the last 20 years (see Hellenthal & Price, 1991, 1994, for reviews).

Adults. Hellenthal & Price (1994) illustrate the diversity of adult pocket gopher louse morphology. The bulk of the data used in this study came from the morphometric data base assembled by R.D.P. and R.A.H. over the last 20 years and maintained by R.A.H. (see Hellenthal & Price, 1980). The data base consists of measurement and count data for fifty-five characters (Table 1) for 14,641 individual lice. For our analysis we used species (or subspecies) means for each character. Although the data base is large, not all the characters necessarily contain phylogenetic information, nor were they collected with that purpose in mind. Their primary use has been in discriminating between morphologically very similar terminal taxa.

First instars. During the brushing of adult pocket gopher lice off prepared museum skins to serve as the basis for the extensive studies published over the last 20 years, R.D.P. concurrently collected large numbers of immature lice, which were slide-mounted and housed in the University of Minnesota entomology collection. The resulting collection comprises first, second and third instars for nearly all 122 recognized louse taxa. The chaetotaxy of the first instars of pocket gopher lice is extremely well organized and relatively simple, yet diverse, facilitating cross-taxon comparisons. Price & Hellenthal (1994) describe this instar, and provide a key to the first instars of the twenty-six pocket gopher louse complexes.

Because some gopher taxa host more than one louse taxon, there is the potential for associating first instars with the wrong species or subspecies. However, in almost all cases individual gophers were found that hosted only a single species, enabling the identity of the first instar to be established with certainty. The most difficult situation, and the only real problem among all these lice, arose in associating the first instars of the *mexicanus* and the *coronadoi* complexes, both of which invariably co-occurred on the same individual gopher. Fortunately, the co-occurrence of a species of the *coronadoi* complex with one of the *mcgregori* complex, whose identity had been previously ascertained, enabled the allotment of this louse to the proper taxon and clarification of the identity of the other paired louse taxa.

Outgroup. In Lyal's (1985) cladistic analysis, *Neotrichodectes* is the sister taxon to the gopher lice. Because of the difficulty in establishing homologies between characters of the only first instar of this genus available (*N.minutus*) and the gopher lice, and the variation in adult *Neotrichodectes* morphology, we abandoned the use of an outgroup to root our tree, and chose instead to root the phylogeny between the two louse genera, *Thomomydoecus* and *Geomydoecus*. The assumption that these two genera are monophyletic with respect to each other (and consequently that the root of the gopher louse tree lies between them) is supported by Nadler & Hafner's (1993) allozyme data.

Character coding. Cladistic analysis typically requires discrete characters, and the use of morphometric data is controversial (see review by Stevens, 1991). Our approach has been to use the morphometric data to delimit reasonably discrete clusters of taxa that are internally homogenous for a particular character. These clusters correspond to the states of that character. For the first instar data, this was done manually by RDP prior to analysis. In cases where taxa had more than one state for a given character, we used the modal state, as the software used to construct the phylogeny (Farris, 1988) requires taxa to have only one character state.

For the adult data, we used bivariate plots to explore the relationship between pairs of variables, and histograms to obtain frequency distributions. Because of the wide variation in louse size (TOT LGTH for adult males ranges from 1037 to 1979 μm), where necessary we plotted variables against HD WDTH to control for size. To illustrate our approach we provide examples below of how some adult characters were coded.

Price & Emerson (1971: 230) noted that the male scape occurs in three types: '(a) with a distinct protuberance on the posterior margin..., (b) with a tendency for a much less developed convexity on the posterior margin..., and (c) with the posterior margin essentially straight...' A bivariate plot of SCP MDWD against SCP EDWD (Fig. 2) shows that for the bulk of the lice SCP EDWD ≈ SCP MDWD, but there is a distinct group of lice for which SCP MDWD > SCP EDWD, and a few lice lie in between these two groups. These groups correspond to the three scape types noted by Price & Emerson, and hence were coded as three separate states of the same character (45).

A similar but less clear-cut example concerns the relative size of the inner marginal temple (MG TMP) seta in males and females (character 43). Typically they are subequal in size but in one group of lice the value of MG TMP for the male is larger than that of the female, whereas in a second group the males have relatively much smaller setae than

Table 1. Measurement and count variables in the adult louse data base maintained by R. A. Hellenthal.

Character code	Description
Females	
G100 TG7	Number of setae of length ≥100 microns on tergite 7
GS LGTH	Genital sac length (microns)
GS WDTH	Genital sac width (microns)
GSLP LTH	Genital sac loop length (microns)
HD LGTH	Head length (microns)
HD WDTH	Head (temple) width (microns)
LNS TG6	Longest setae of medial 10 on tergite 6 length (microns)
LNS TG7	Longest setae of medial 10 on tergite 7 length (microns)
LNS TG8	Longest setae of medial two on tergite 8 length (microns)
MG TMP	(Inner) marginal temple seta length (microns)
NGS LPS	Number of genital sac loops
PSLTG IN	Posterior (last) tergite inner lateral seta length (microns)
PSLTG MD	Posterior (last) tergite middle lateral seta length (microns)
PSLTG OT	Posterior (last) tergite outer lateral seta length (microns)
PTX WDTH	Prothorax width (microns)
SET SGPL	Number of setae on subgenital plate
SET STN2	Number of setae on sternite 2
SET STN3	Number of setae on sternite 3
SET STN4	Number of setae on sternite 4
SET STN5	Number of setae on sternite 5
SET STN6	Number of setae on sternite 6
SET STN7	Number of setae on sternite 7
SET TG2	Number of setae on tergite 2
SET TG3	Number of setae on tergite 3
SET TG4	Number of setae on tergite 4
SET TG5	Number of setae on tergite 5
SET TG6	Number of setae on tergite 6
SET TG7	Number of setae on tergite 7
SMG TMP	Submarginal temple seta length (microns)
TOT LGTH	Total length (microns)
Males	
GEP LGTH	Genital endomeral plate length (microns)
GEP WDTH	Genital endomeral plate width (microns)
GPA WDTH	Genital parameral arch width (microns)
HD LGTH	Head length (microns)
HD WDTH	Head (temple) width (microns)
MG TMP	(Inner) marginal temple seta length (microns)
PTX WDTH	Prothorax width (microns)
SCP EDWD	Scape distal end width (microns)
SCP LGTH	Scape length (microns)
SCP MDWD	Scape medial width (microns)
SET STN2	Number of setae on sternite 2
SET STN3	Number of setae on sternite 3
SET STN4	Number of setae on sternite 4
SET STN5	Number of setae on sternite 5
SET STN6	Number of setae on sternite 6
SET STN7	Number of setae on sternite 7
SET STN8	Number of setae on sternite 8
SET TG2	Number of setae on tergite 2
SET TG3	Number of setae on tergite 3
SET TG4	Number of setae on tergite 4
SET TG5	Number of setae on tergite 5
SET TG6	Number of setae on tergite 6
SET TG7	Number of setae on tergite 7
SMG TMP	Submarginal temple seta length (microns)
TOT LGTH	Total length (microns)

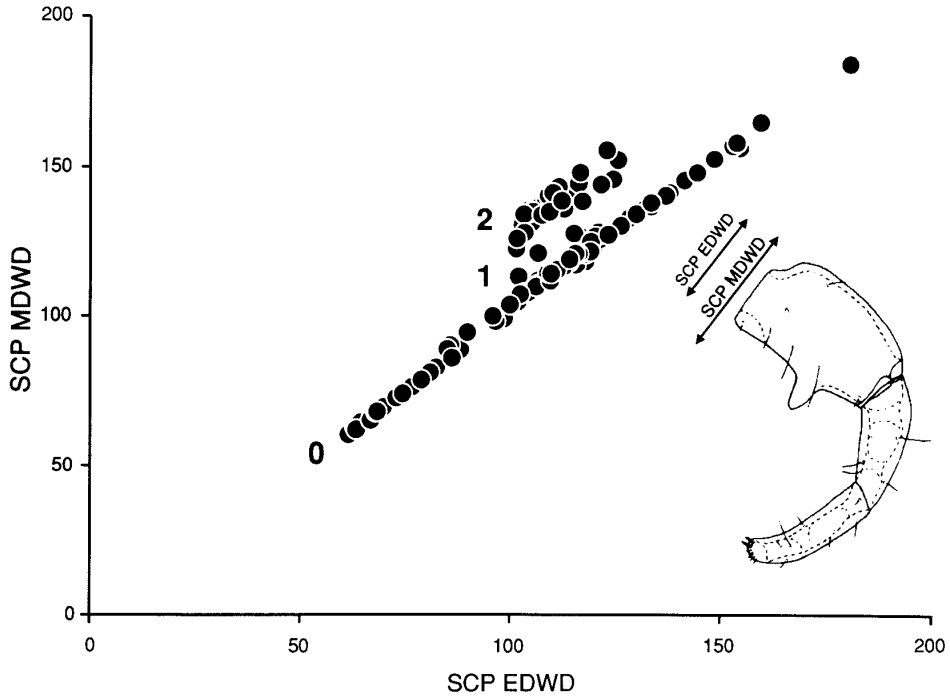


Fig. 2. Relationship between medial (SCP MDWD) and distal (SCP EDWD) width of male scape in *Geomydoecus* and *Thomomydoecus* (units μm), showing the three character states (0–2) delimited for character 45.

their females (Fig. 3). Although the existence of three clusters seems clear, the edges of those clusters are slightly fuzzy, making it difficult to decide to which cluster a taxon belongs (and hence which character state it bears). In this instance we chose ratios between the two measurements that appeared to give the cleanest separation of taxa.

Some characters were obtained from raw counts, such as the mean number of setae on tergite 7 in males (SET TG7). Fig. 4 shows a histogram of SET TG7 for all lice for which males are known. This distribution is clearly bimodal and was coded as a binary character (50) with two states: (0) SET TG7 $\leq$ 13.5 and (1) SET TG7 $>$ 13.5. Much of the morphometric data base consists of setal counts on the abdominal segments of both sexes (Table 1). Because of the strong correlation between setal counts on adjacent abdominal segments (typically $r \geq 0.9$), these counts are unlikely to be independent and hence only a single segment showing a particular pattern was coded. This means that a large part of the data base is of limited value for cladistic analysis.

Once discrete character states were delimited, characters that described shape (e.g. character 55) were treated as unordered. Characters developed from the morphometric data base were treated as ordered to preserve the relative similarity of taxa possessing different states. Appendices 1 and 2 list the characters, their states, and their distribution.

Tree construction and interpretation. The computer program Hennig86 (Farris, 1988) was used to search for most parsimonious cladograms for the data, primarily because of its speed (Platnick, 1989). Given the large number of terminal taxa, finding the most parsimonious tree was not computationally feasible so we employed heuristic methods. Initial starting trees were obtained using the *mhennig** command. The *bb** ('branch-breaking') command was then used to rearrange those trees in the attempt to find a more parsimonious tree (or trees).

Preliminary searches revealed considerable amounts of homoplasy in the data. Because phylogenetic programs will obtain trees even for random data, we used the phylogenetic tail probability (PTP) test of Faith & Cranston (1991) to check that the data matrix contained significant hierarchical structure. The original data matrix was permuted 100 times and an estimate of the length of the most parsimonious tree for each matrix was obtained using the *hennig* command in Hennig86. The length of the tree for the original data (also found using *hennig*) was compared with this distribution.

The high degree of homoplasy shown by some characters suggested that not all characters are equally informative. Various weighting schemes have been proposed to reflect the relative phylogenetic value of different characters (Farris, 1969; Carpenter, 1988; Sharkey, 1989). We used successive approximations character weighting (Farris, 1969). This method assigns weights to characters based on their fit on the most parsimonious tree(s). These weights, computed as the product of the character consistency and retention indices (= the rescaled consistency index; Farris, 1989), are scaled to lie in the range 0–10, and are then

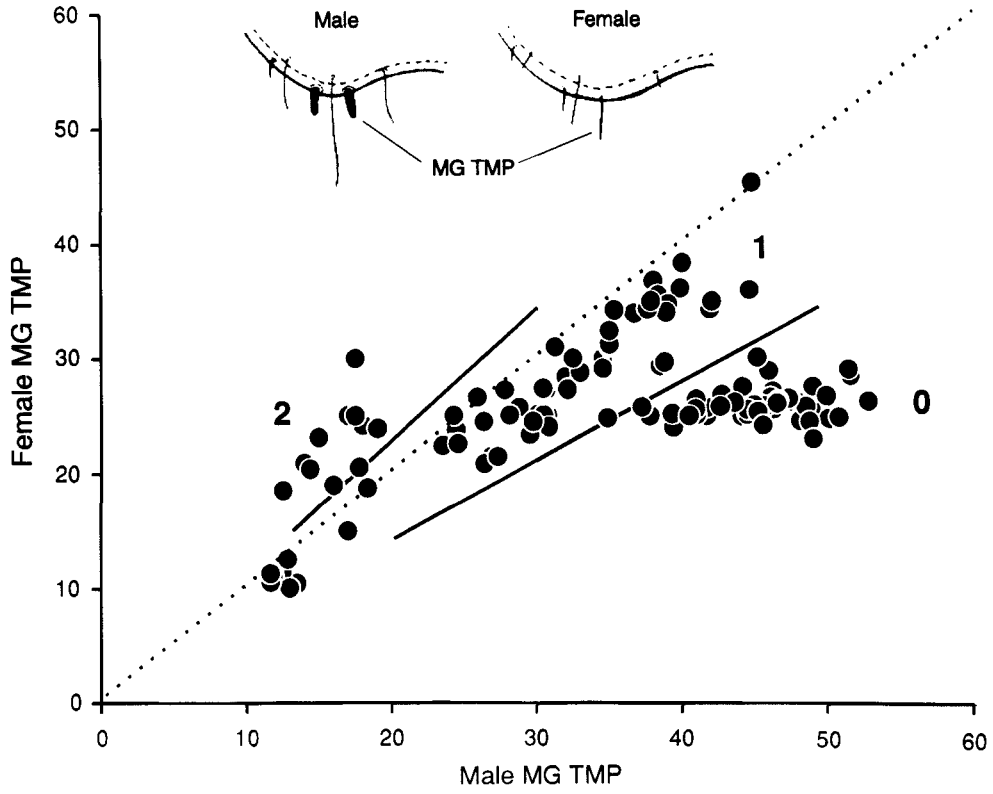


Fig. 3. Relationship between length of inner margin temple seta (MG TMP) in adult male and female *Geomydoecus* and *Thomomydoecus* (units μm), showing the three characters states (0–2) delimited for character 43. The dotted line represents equal lengths of the seta in male and female lice.

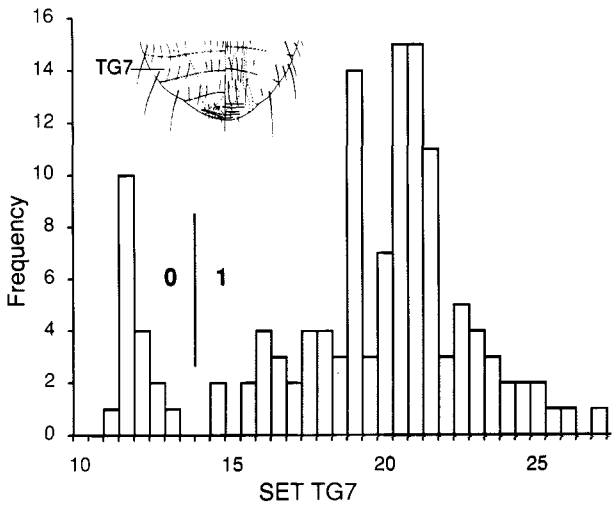


Fig. 4. Frequency distribution of mean numbers of setae on tergite 7 (SET TG7) in adult male *Geomydoecus* and *Thomomydoecus*. Two character states (0 and 1) were recognized for this character (50).

applied to the original data and new trees computed. This procedure is repeated until the trees no longer change.

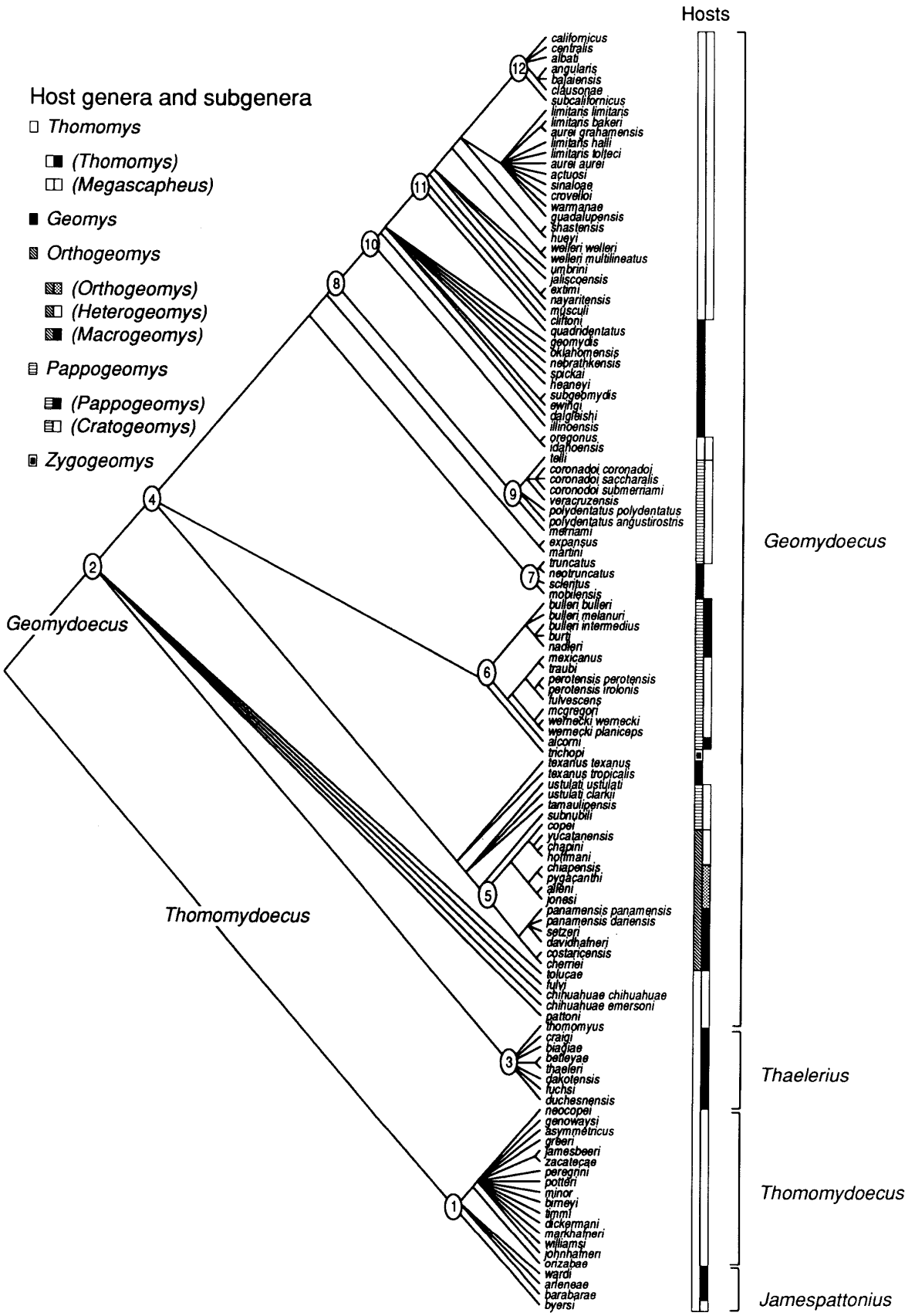
Results

Cladistic analysis

The shortest trees found by Hennig86 had a length of 613 steps (consistency index, CI = 0.22; retention index, RI = 0.82), of which only the first 1319 could be stored in our computer's memory. Despite the amount of homoplasy in the data, the PTP test revealed significant ($P < 0.01$) cladistic structure: all trees generated from the permuted matrices had lengths between 1785 and 1890 steps, compared to the 638 steps required for the original data. Using successive approximations weighting, Hennig86 retained 1314 trees with weighted length 866 (CI = 0.52, RI = 0.92); again more trees were found than could be stored in memory. The strict consensus of the trees retained by the program is shown in Fig. 5, and the final character weights obtained by successive weighting are given in Appendix 1.

Using this tree we now discuss the evidence for the groups it contains. For each supporting character we list

Fig. 5. Strict consensus of the 1314 most parsimonious trees for the lice obtained using successive approximations weighting. The louse genera and subgenera recognized by Hellenthal & Price (1994) are indicated, as are the pocket gopher host genera and subgenera. For discussion of each numbered clade see text.


Hosts
Host genera and subgenera
Thomomys
(Thomomys)
(Megascapheus)
Geomys
Orthogeomys
(Orthogeomys)
(Heterogeomys)
(Macrogeomys)
Pappogeomys
(Pappogeomys)
(Cratogeomys)
Zygogeomys
Geomydoecus
Thomomydoecus
californicus centralis albati angularis bajaensis clausonae subcalifornicus limitaris limitaris limitaris bakeri aurei grahamensis limitaris halli limitaris tolteci aurei aurei actuosi sinaloae crovelloi warrenae guadalupensis shastensis hueyi welleri welleri welleri multilineatus umbrini jaliscoensis extimi nayaritensis musculi clifioni quadridentatus geomydis oklahomensis nebrathkensis spickai heaneyi subgeomydis ewingi dalquesti illinoensis oregonus idahoensis telli coronadoi coronadoi coronadoi saccharalis coronodoi submerriami veracruzensis polydentatus polydentatus polydentatus angustirostris merriami expansus martini truncatus neotruncatus sclerurus mobilensis bulleri bulleri bulleri melanuri bulleri intermedius burti nadleri mexicanus traubi perotensis perotensis perotensis irolonis fulvescens mcgregori wetmorei wetmorei wetmorei planiceps alcorni trichopi texanus texanus texanus tropicalis ustulati ustulati ustulati clarkii tamaulipensis subnubilis copei yucatanensis chapini hottmani chiapensis pygacanthi alfordi jonesi panamensis panamensis panamensis dariensis setzeri davidhalmeri costaricensis cherriei toluca fulvi chihuahuae chihuahuae chihuahuae emersoni pattoni thomomyus craigi bladiae bottyae thaleri dakotensis fuchsi duchesnensis neocopei genowaysi asymmetricus greeni jamesbeeri zacatecae peregrini potteri minor bameyi timmi dickermani markhalmeri williamsi johnhalmeri onzabae wardi arleneae barabarae byersi
Geomydoecus
Thaelerius
Thomomydoecus
Jamespattonius

the corresponding state shared by the clade being discussed, so that 1^2 means character 1, state 2. A state marked with an asterisk (*) is unique to most or all members of that clade, the absence of an asterisk means that some taxa in other clades also posses that state (hence it does not uniquely diagnose the different clades.

1. *Thomomydoecus*. The basal split in the cladogram is between the genera *Thomomydoecus* and *Geomydoecus*, which is where we chose to root the tree. The first instars of *Thomomydoecus* lice all have two short setae on each side of the terminal segment ($*2^3$) and small temple widths ($*19^1$). Males have relatively short scapes (49^0, except *T.byersi*), possess a pair of grouped setae on tergites II and III (54^1, found elsewhere only in *G.copei*) and have distinctive genitalia (characters 53, 55 and 56). Within the genus there is little support for the complexes recognized by Hellenthal & Price (1991), although the lice belonging to the nominate subgenus do form a clade. Monophyly of the subgenus *Jamespattonius*, created for the *wardi* complex (Hellenthal & Price, 1989c) is not confirmed. Three species of *Jamespattonius (arleneae, barbarae* and *wardi*) form an unresolved polytomy with *T. (Thomomydoecus)*, and have first instars lacking very long lateral setae on segment VI (1^2), and the males having moderately wide parameral arches (53^2). Unfortunately the first instar of *T. (J.) byersi* is unknown, making the assignment of this taxon to *Jamespattonius* by Hellenthal & Price (1984b) difficult to test. The first instars of *T. (Thomomydoecus)* possess intermediate sternal seta on segment III (32^1), whereas the males have relatively few setae on tergite VII (50^0), narrow parameral arches (53^0), and distinctive genitalia (55^8 and 56^4). Lice of this subgenus are hosted by gophers belonging to *Thomomys (Megascapheus)*.

2. *Geomydoecus*. The genus *Geomydoecus* is split basally into the *thomomyus* complex, the *tolucae* complex, and clade 4. Lice from the *tolucae* complex (Price & Hellenthal, 1979) form an unresolved polytomy at the base of *Geomydoecus*. Hellenthal & Price (1991: 195) suggested *tolucae* lice, hosted by *Thomomys (Megascapheus)*, were closest to the *oregonus* complex (discussed below), but this is not borne out in the cladistic analysis. In particular, lice from the *tolucae* complex retain the relatively long medial setae on tergite VIII of the female ($34^{2,3}$) found also in *Thomomydoecus* and *G. (Thaelerius)*.

3. *Geomydoecus (Thaelerius)*. The subgenus *Thaelerius* was created by Hellenthal & Price (1994) to accommodate the *thomomyus* complex (Hellenthal & Price, 1989b), which comprises eight distinctive lice characterized by first instars lacking submarginal temple seta 4 ($*5^2$), having short median metanotal setae ($*12^2$), and adults with short inner marginal temple setae (46^0), long submarginal temple setae (47^4), and distinctive male genitalia (55^9 and 57^1). This clade is restricted to gophers belonging to the nominate subgenus of *Thomomys*.

Relationships within the *thomomyus* complex are largely unresolved (Fig. 5), with the exception of the consistent grouping of *G.betleyae* and *G.thaeleri*: first instars of both these lice lack median sternal seta on segment IX (16^1) and have short submarginal head seta 3 (24^1).

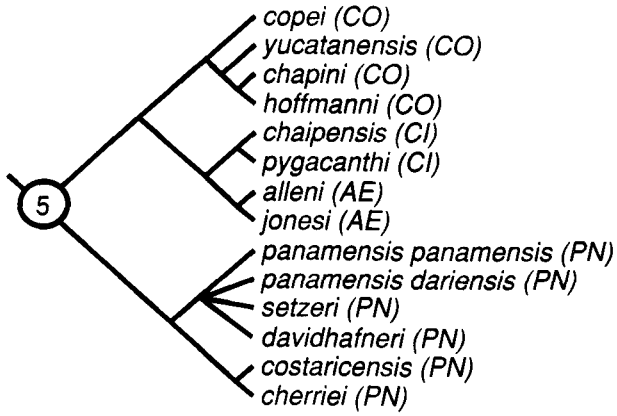


Fig. 6. Clade 5. Species complex abbreviations: copei (CO), *chiapensis* (CI), *alleni* (AE) and *panamensis* (PN).

4. Clade 4 comprises *Geomydoecus (Geomydoecus)*, with the exclusion of the *tolucae* complex (Price & Hellenthal, 1979) whose exact placement is unresolved. In Fig. 5 this clade is divided into three subclades.

5. This clade (Fig. 6) comprises the lice hosted by *Orthogeomys* gophers. Lice of the *texanus* complex (Price & Hellenthal, 1975b) form a paraphyletic assemblage below this clade, despite being unique among pocket gopher lice in possessing very long lateral metanotal setae (3^1) in the first instar. Clade 5 is united by having first instars with small marginal temple seta 4 (8^2), large temple widths (19^{3-5}), a lack of intermediate sternal setae on segment III (32^1), females with few setae on sternite II ($39^{0,1}$), and males and females with the submarginal temple seta distinctly medial with respect to the marginal temple seta ($*44^1$). Females of the *panamensis* complex (Price *et al.*, 1985) all have a notch in the anterior margin of the genital sac ($*42^1$). The *copei* lice (Price & Hellenthal, 1976) are distinctive, with the males superficially resembling *Thomomydoecus* males, and in Fig. 6 they group with the *chiapensis* and *alleni* complexes (Price & Hellenthal, 1988a). The *chiapensis* and *alleni* complexes are found on *O. (Orthogeomys)*, the *copei* complex is found on *O. (Heterogeomys)*, and the *panamensis* complex is restricted to *O. (Macrogeomys)*.

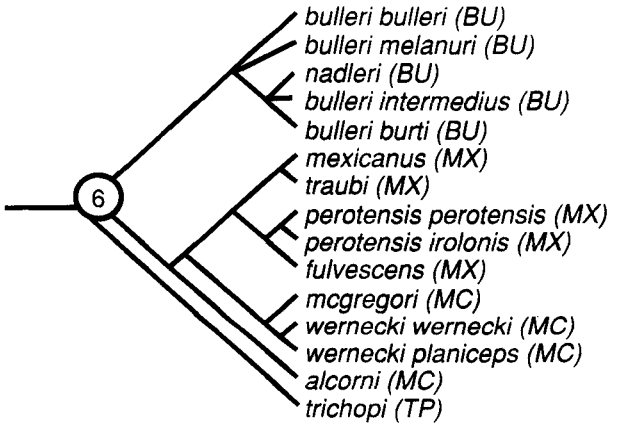


Fig. 7. Clade 6. Complex abbreviations: *bulleri* (BU), *mcgregori* (MC), *mexicanus* (MX) and *trichopi* (TP).

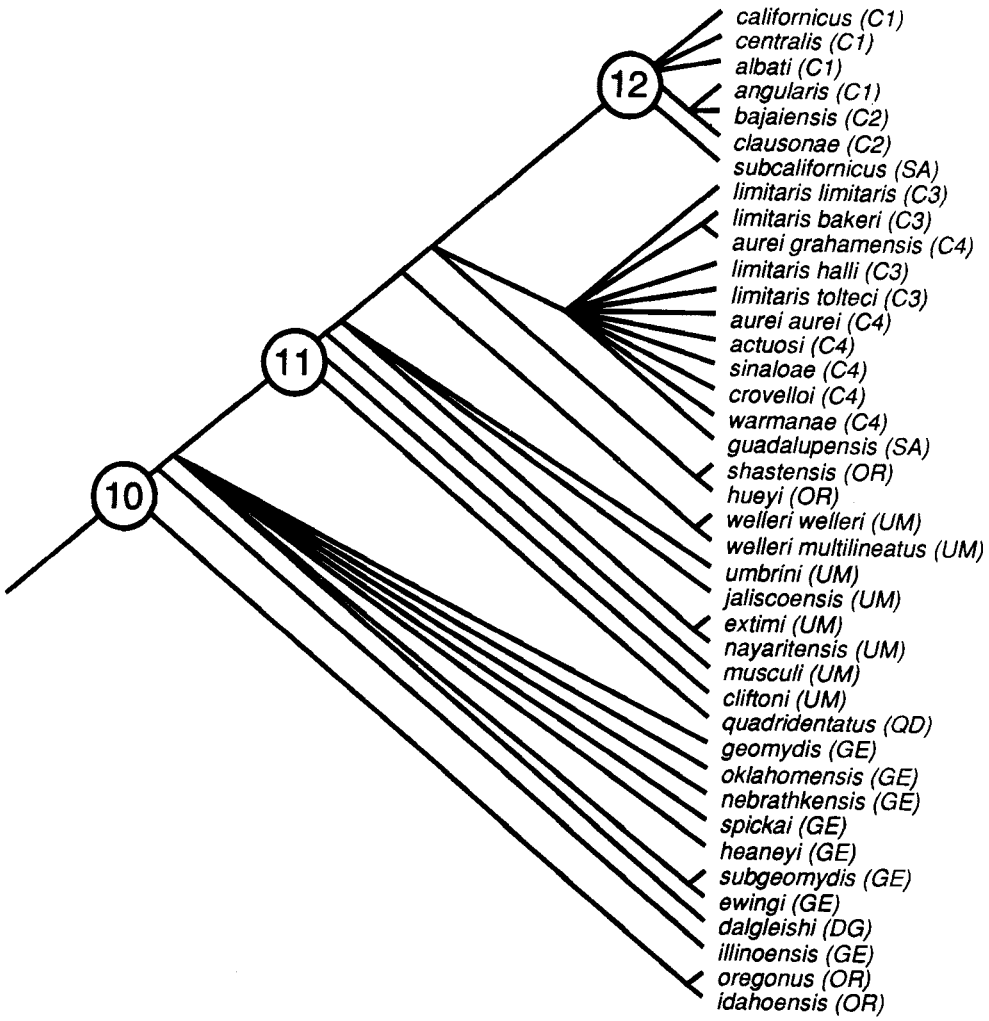


Fig. 8. Clade 10 and subclades 11 and 12. Complex abbreviations: *californicus* (C1–C4), *dalgleishi* (DG), *geomydis* (GE), *oregonus* (OR), *quadridentatus* (QD), *subcalifornicus* (SA) and *umbrini* (UM).

6. Clade 6 (Fig. 7) includes the *bulleri*, *mexicanus* and *mcgregori* complexes (Price & Hellenthal, 1989a, b). The *bulleri* complex and *G.alcorni* parasitize *Pappogeomys (Pappogeomys)* gophers, the *mcgregori* and *mexicanus* complexes (with the exception of *G.alcorni*) are hosted by *P. (Cratogeomys)* gophers. The clade is diagnosed by first instars with well-developed marginal temple seta 5 ($*23^2$), females with setal formula 2 + 2 + 2 on the posterior tergite (41^0), moderately long submarginal temple setae (47^2), and the *bulleri* and *mcgregori* males sharing a similar endomeral plate morphology (56^3). The first instars of *mcgregori* and *mexicanus* lice generally have moderately long intermediate sternal setae on segments V ($14^{3,4}$) and VII ($31^{2,3}$).

The *mcgregori* complex appears paraphyletic as *G.alcorni* is the sister taxon to both the remaining *mcgregori* lice and the *mexicanus* complex. *G.alcorni* lacks the large number of setae found on the male sternite VIII ($*51^2$) possessed by the remaining *mcgregori* and *mexicanus* lice. In the *mexicanus* complex, females have small genital sacs (40^1), and the males have relatively short bodies (48^1), with the exception of *G.traubi*, lack genital sac spines (52^0) and have distinctive genitalia (53^2, 55^0, 56^0).

G.trichopi, the sole member of the *trichopi* complex (Price & Hellenthal, 1989b), is the sister group to clade 6.

7. The *scleritus* (Price, 1975; Price & Timm, 1979) and *truncatus* complexes (Hellenthal & Price, 1989a) are sister, although there is only weak evidence for this relationship, namely the similar tergal setation segments I–VI of the first instar (9^3), and the medium sized female genital sac (40^2, except in *G.scleritus*). Both complexes are hosted by *Geomys* gophers.

8. Clade 8 is diagnosed by the small size of the male inner marginal temple seta relative to that of the female (43^0) and the presence of a long dorsal head seta ($*58^1$) in the female. Its sister group is the two members of the *expansus* complex (Price & Hellenthal, 1975a), found on *Pappogeomys (Cratogeomys)* gophers.

9. Clade 9 comprises the *coronadoi* and *telli* complexes. The *coronadoi* complex as defined by Price & Hellenthal (1989b) is paraphyletic as it excludes *G.telli*. The latter was described by Price & Hellenthal (1988b: 215) as standing

apart from all other *Geomydoecus*. However, although its female genital sac morphology is unique (*42^2), *G.telli* shares a number of features with the *coronadoi* complex, including the distinctive sculpturing of the ventral temple surface in the first instar (4^3), relatively long male scape (49^2), and short inner and outer posterior tergal setae in the female ($37^{0,1}$ and *38^0). Clade 9 parasitizes gophers belonging to *Pappogeomys (Cratogeomys)*.

10. Clade 10 (Fig. 8) contains the large *californicus* (Price & Hellenthal, 1981a) and *umbrini* (Price & Hellenthal, 1981b) complexes which parasitize *Thomomys (Megascapheus)* gophers, as do the *oregonus* and *subcalifornicus* complexes. The remaining lice are hosted by *Geomys*. With the exception of the four *oregonus* lice and *G.illinoensis*, all males in this clade have a small to large posterior projection on the scape (*$45^{1,2}$).

Although the eight members of the *geomydis* complex are hosted by gophers belonging to the *Geomys bursarius* complex (Timm & Price, 1980), they do not form a clade although they are adjacent to each other on the tree (Figs 5 and 8), together with *Geomydoecus dalgleishi* (Timm & Price, 1979), a parasite of *Geomys personatus fuscus*.

The *oregonus* complex (Price & Hellenthal, 1980) is polyphyletic. *G.hueyi* and *G.shastensis* parasitize *Thomomys bottae* gophers and group with the *californicus* complex, also hosted by *T.bottae* (see Hellenthal & Price, 1984a). *Geomydoecus oregonus* and *G.idahoensis* infest *Thomomys bulbivorus* and *T.townsendii*, respectively, and are sister taxa to the rest of clade 10.

The *subcalifornicus* complex (Hellenthal & Price, 1980) is also polyphyletic. *Geomydoecus subcalifornicus* is part of clade 12, whereas *G.guadalupensis* is part of an unresolved assemblage in clade 11 comprising the *aurei* (C4) and *limitaris* (C3) subcomplexes of the *californicus* complex, to which it is geographically closer (Hellenthal & Price, 1984a: figs 3 and 5).

11. Clade 11 comprises primarily the *californicus* and *umbrini* complexes which are hosted by *Thomomys* gophers, and is diagnosed by first instars having two or more intermediate sternal setae on each side per segment (*6^2), having long lateral setae on segments IV (26^1) and V (33^1), and females with 13 + setae on sternite II (39^2). Interestingly, *G.quadridentatus* (Hellenthal & Price, 1989a), a parasite of *Geomys arenarius*, also belongs in this clade.

12. Clade 13 comprises the *californicus* (C1) and *bajaiensis* (C2) subcomplexes of the *californicus* complex and one member of the *subcalifornicus* complex (*G.subcalifornicus*).

Discussion

We do not pretend that the tree presented here is the definitive gopher louse phylogeny. The data set contains considerable homoplasy, and probably supports many thousands of equally parsimonious trees (we managed to retain only the first 1300 before our computer ran out of memory in which to store the trees). Despite this, there is sufficient cladistic structure, as shown by the PTP test, for us to feel justified in attempting a cladistic analysis.

The phylogeny is in good accord with the existing louse taxonomy, with only a few complexes being clearly not monophyletic, notably the *oregonus* and *subcalifornicus* complexes, which are polyphyletic. The *texanus, tolucae* and *geomydis* complexes appear to be paraphyletic. When compared to previous hypotheses of gopher louse relationships, our cladistic analysis agrees with the relationships within clade 5 (hosted by *Orthogeomys*) found by Hafner & Nadler (1988) and Nadler & Hafner (1993). The relationships within *Geomydoecus* shown Nadler & Hafner's fig. 3 agree closely with our Fig. 5, except for the placement of *G.thomomyus*, which their tree places well within *Geomydoecus*, rather than basally as in our tree. However, the relative order of branching for the *scleritus* complex and *expansus*, relative to the *geomydis* complex and *G.actuosi*, is the same as in our Fig. 5.

The pattern of host associations reveals numerous cases of correspondence between putatively monophyletic clades of lice and genera or subgenera of pocket gophers. This suggests that shared history has played an important role in the evolution of the gopher–louse association. However, the repeated occurrence of different lineages of lice on the same gophers suggests the history of this host–parasite association is complex. Hafner & Nadler (1988) suggested that, while cospeciation predominates, at least some of the lice they sampled had undergone host switches, whereas Page (1990, 1993a, b) suggested much of the apparent incongruence between gopher and louse phylogenies may be due to independent speciation of the lice, followed by lineage sorting (analogous to lineage sorting of genes).

Establishing the relative roles of these, and other, processes in this host–parasite assemblage will require robust, fully resolved gopher and louse phylogenies. We hope that the preliminary phylogeny reported here will encourage further efforts towards improving our estimate of the louse phylogeny, using both morphological and molecular characters. There is considerable scope for more detailed morphological work (for example SEM microscopy), and DNA sequencing is an obvious source of new data. However, we note that the two research fields of systematics and coevolution may require different sampling strategies if resources are limited. Rapid testing of our phylogeny as a whole would be best undertaken by sampling one or two lice from each species complex (taking appropriate care when there is no evidence for the monophyly of a given complex). However, because of the complexity of the host–parasite relationships, a coevolutionary study would gain more from exhaustively sampling all lice (and their hosts) within a particular clade, rather than sampling phylogenetically widely scattered taxa.

Lastly, we hope our efforts with the lice will inspire mammalogists to attempt a similarly comprehensive phylogenetic analysis of the pocket gopher hosts.

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References

Brooks, D.R. & McLennan, D.A. (1991) *Phylogeny, Ecology, and Behavior*. Chicago University Press.

Carpenter, J.M. (1988) Choosing among equally parsimonious cladograms. *Cladistics*, **4**, 291–296.

Demastes, J.W. & Hafner, M.S. (1993) Cospeciation of pocket gophers (*Geomys*) and their chewing lice (*Geomydoecus*). *Journal of Mammalogy*, **74**, 521–530.

Faith, D.P. & Cranston, P.S. (1991) Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. *Cladistics*, **7**, 1–28.

Farris, J.S. (1969) A successive approximations approach to character weighting. *Systematic Zoology*, **18**, 374–385.

Farris, J.S. (1988) *Hennig86, version 1.5. Computer program and documentation*. Port Jefferson Station, New York.

Farris, J.S. (1989) The retention index and the rescaled consistency index. *Cladistics*, **5**, 417–419.

Hafner, M.S. & Nadler, S.A. (1988) Phylogenetic trees support the coevolution of parasites and their hosts. *Nature*, **332**, 258–259.

Hafner, M.S. & Nadler, S.A. (1990) Cospeciation in host–parasite assemblages: comparative analysis of rates of evolution and timing of cospeciation. *Systematic Zoology*, **39**, 192–204.

Hafner, M.S., Sudman, P.D., Villablanca, F.X., Spradling, T.A., Demastes, J.W. & Nadler, S.A. (1994) Disparate rates of molecular evolution between cospeciating hosts and parasites. *Science*, **265**, 1087–1090.

Hellenthal, R.A. & Price, R.D. (1980) A review of the *Geomydoecus subcalifornicus* complex (Mallophaga: Trichodectidae) from *Thomomys* pocket gophers (Rodentia: Geomyidae), with a discussion of quantitative techniques and automated taxonomic procedures. *Annals of the Entomological Society of America*, **73**, 495–503.

Hellenthal, R.A. & Price, R.D. (1984a) Distributional associations among *Geomydoecus* and *Thomomydoecus* lice (Mallophaga: Trichodectidae) and pocket gopher hosts of the *Thomomys bottae* group (Rodentia: Geomyidae). *Journal of Medical Entomology*, **21**, 432–446.

Hellenthal, R.A. & Price, R.D. (1984b) A new species of *Thomomydoecus* (Mallophaga: Trichodectidae) from *Thomomys bottae* pocket gophers (Rodentia: Geomyidae). *Journal of the Kansas Entomological Society*, **57**, 231–236.

Hellenthal, R.A. & Price, R.D. (1989a) *Geomydoecus* (Mallophaga: Trichodectidae) from the Texas and desert pocket gophers. *Proceedings of the Entomological Society of Washington*, **91**, 1–8.

Hellenthal, R.A. & Price, R.D. (1989b) *Geomydoecus thomomyus* complex (Mallophaga: Trichodectidae) from pocket gophers of the *Thomomys talpoides* complex (Rodentia: Geomyidae) of the United States and Canada. *Annals of the Entomological Society of America*, **82**, 286–297.

Hellenthal, R.A. & Price, R.D. (1989c) The *Thomomydoecus wardi* complex (Mallophaga: Trichodectidae) of the pocket gopher, *Thomomys talpoides* (Rodentia: Geomyidae). *Journal of the Kansas Entomological Society*, **62**, 245–253.

Hellenthal, R.A. & Price, R.D. (1991) Biosystematics of the chewing lice of pocket gophers. *Annual Review of Entomology*, **36**, 185–203.

Hellenthal, R.A. & Price, R.D. (1994) Two new subgenera of chewing lice (Phthiraptera: Trichodectidae) from pocket gophers (Rodentia: Geomyidae), with a key to all included taxa. *Journal of Medical Entomology*, **31**, 450–466.

Lyal, C.H.C. (1985) A cladistic analysis and classification of trichodectid mammal lice (Phthiraptera: Ischnocera). *Bulletin of the British Museum (Natural History), Entomology*, **51**, 187–346.

Nadler, S.A. & Hafner, M.S. (1989) Genetic differentiation in sympatric species of chewing lice (Mallophaga: Trichodectidae). *Annals of the Entomological Society of America*, **82**, 109–113.

Nadler, S.A. & Hafner, M.S. (1993) Systematic relationships among pocket gopher chewing lice (Phthiraptera: Trichodectidae) inferred from electrophoretic data. *International Journal for Parasitology*, **23**, 191–201.

Page, R.D.M. (1990) Temporal congruence and cladistic analysis of biogeography and cospeciation. *Systematic Zoology*, **39**, 205–226.

Page, R.D.M. (1991) Clocks, clades, and cospeciation: comparing rates of evolution and timing of cospeciation events in host-parasite assemblages. *Systematic Zoology*, **40**, 188–198.

Page, R.D.M. (1993a) Genes, organisms, and areas: the problem of multiple lineages. *Systematic Biology*, **42**, 77–84.

Page, R.D.M. (1993b) Parasites, phylogeny and cospeciation. *International Journal for Parasitology*, **23**, 499–506.

Patton, J.L. & Smith, M.F. (1989) Population structure and the genetic and morphological divergence among pocket gopher species (genus *Thomomys*). *Speciation and its Consequences* (ed. by D. Otte and J. A. Endler), pp. 284–304. Sinauer, Sunderland, Mass.

Platnick, N.I. (1989) An empirical comparison of microcomputer parsimony programs. II. *Cladistics*, **5**, 145–161.

Price, R.D. (1975) The *Geomydoecus* (Mallophaga: Trichodectidae) of the southeastern USA pocket gophers (Rodentia: Geomyidae). *Proceedings of the Entomological Society of Washington*, **77**, 61–65.

Price, R.D. & Emerson, K.C. (1971) A revision of the genus *Geomydoecus* (Mallophaga: Trichodectidae) of the New World pocket gophers (Rodentia: Geomyidae). *Journal of Medical Entomology*, **8**, 228–257.

Price, R.D. & Hellenthal, R.A. (1975a) A reconsideration of *Geomydoecus expansus* (Duges) (Mallophaga: Trichodectidae) from the yellow-faced pocket gopher (Rodentia: Geomyidae). *Journal of the Kansas Entomological Society*, **48**, 33–42.

Price, R.D. & Hellenthal, R.A. (1975b) A review of the *Geomydoecus texanus* complex (Mallophaga: Trichodectidae) from *Geomys* and *Pappogeomys* (Rodentia: Geomyidae). *Journal of Medical Entomology*, **12**, 401–408.

Price, R.D. & Hellenthal, R.A. (1976) The *Geomydoecus* (Mallophaga: Trichodectidae) from the hispid pocket gopher (Rodentia: Geomyidae). *Journal of Medical Entomology*, **12**, 695–700.

Price, R.D. & Hellenthal, R.A. (1979) A review of the *Geomydoecus tolucae* complex (Mallophaga: Trichodectidae) from *Thomomys* (Rodentia: Geomyidae), based on qualitative and quantitative characters. *Journal of Medical Entomology*, **16**, 265–274.

Price, R.D. & Hellenthal, R.A. (1980) The *Geomydoecus oregonus* complex (Mallophaga: Trichodectidae) of the western

United States pocket gophers (Rodentia: Geomyidae). *Proceedings of the Entomological Society of Washington*, **82**, 25–38.

Price, R.D. & Hellenthal, R.A. (1981a) A review of the *Geomydoecus californicus* complex (Mallophaga: Trichodectidae) from *Thomomys* (Rodentia: Geomyidae). *Journal of Medical Entomology*, **18**, 1–23.

Price, R.D. & Hellenthal, R.A. (1981b) Taxonomy of the *Geomydoecus umbrini* complex (Mallophaga: Trichodectidae) from *Thomomys umbrinus* (Rodentia: Geomyidae) in Mexico. *Annals of the Entomological Society of America*, **74**, 37–47.

Price, R.D. & Hellenthal, R.A. (1988a) *Geomydoecus* (Mallophaga: Trichodectidae) from the Central American pocket gophers of the subgenus *Orthogeomys* (Rodentia: Geomyidae). *Journal of Medical Entomology*, **25**, 331–335.

Price, R.D. & Hellenthal, R.A. (1988b) A new species of *Geomydoecus* (Mallophaga: Trichodectidae) from *Pappogeomys* (Rodentia: Geomyidae) pocket gophers in Jalisco, Mexico. *Journal of Entomological Science*, **23**, 212–215.

Price, R.D. & Hellenthal, R.A. (1989a) *Geomydoecus bulleri* complex (Mallophaga: Trichodectidae) from Buller's pocket gopher, *Pappogeomys bulleri* (Rodentia: Geomyidae), in westcentral Mexico. *Annals of the Entomological Society of America*, **82**, 279–285.

Price, R.D. & Hellenthal, R.A. (1989b) *Geomydoecus* (Mallophaga: Trichodectidae) from *Pappogeomys* and *Zygogeomys* pocket gophers (Rodentia: Geomyidae) in central Mexico. *Journal of Medical Entomology*, **26**, 385–401.

Price, R.D. & Hellenthal, R.A. (1994) Taxonomic importance of first-instar chewing lice (Phthiraptera: Trichodectidae) from pocket gophers (Rodentia: Geomyidae). *Annals of the Entomological Society of America*, in press.

Price, R.D. & Timm, R.M. (1979) Description of the male of *Geomydoecus scleritus* (Mallophaga: Trichodectidae) from the southeastern pocket gopher. *Journal of the Georgia Entomological Society*, **14**, 162–165.

Price, R.D., Hellenthal, R.A. & Hafner, M.S. (1985) The *Geomydoecus* (Mallophaga: Trichodectidae) from the central American pocket gophers of the subgenus *Macrogeomys* (Rodentia: Geomyidae). *Proceedings of the Entomological Society of Washington*, **87**, 432–443.

Sharkey, M.J. (1989) A hypothesis-independent method of character weighting for cladistic characters. *Cladistics*, **5**, 63–86.

Stevens, P.F. (1991) Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany*, **16**, 553–583.

Timm, R.M. & Price, R.D. (1979) A new species of *Geomydoecus* (Mallophaga: Trichodectidae) from the Texas pocket gopher, *Geomys personatus* (Rodentia: Geomyidae). *Journal of the Kansas Entomological Society*, **52**, 264–268.

Timm, R.M. & Price, R.D. (1980) The taxonomy of *Geomydoecus* (Mallophaga: Trichodectidae) from the *Geomys bursarius* complex (Rodentia: Geomyidae). *Journal of Medical Entomology*, **17**, 126–145.

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Appendix 1. Characters used in the cladistic analysis. For each character the table lists its final weight assigned by successive approximation character weighting, the character states, and for multistate characters whether the character was treated as ordered or unordered. For explanation of abbreviations for measurement and count variables used to define adult character states, see Table 1. For characters 56 and 57 the number(s) in **boldface** after each state refers to the corresponding figure(s) in Hellenthal & Price (1994).

	Weight	Description
First instars		
1	1	Very long lateral seta on segment VI. Present (1); absent (2).
2	6	Marginal setae on terminal segment. None (1); one very long seta each side (2); two short setae each side (3). Unordered.
3	4	Lateral metanotal seta. Very long, >200 μm (1); short <90 μm (2).
4	6	Sculpturing of ventral temple surface. No conspicuous 'bumps' or sculpturing (1); wide area of dark 'bumps' (2); narrow elongate area of dark 'bumps' (3); sparse 'bumps' only near margin (4); small bumps in short rows (5). Unordered.
5	10	Submarginal temple seta 4. Present (1); absent (2).
6	10	Intermediate sternal setae. Not more than one seta each side per segment (1); two or more setae each side on some segments (especially II, III, and often IV) (2).
7	3	Seta on coxa III. Large, thick, at least 20 μm long (1); medium, moderately thick, 10–20 μm long (2); short, fairly slender, ≤10 μm long (3); slender, ≥25 μm long (4). Unordered.
8	4	Marginal temple seta 4. Prominent, conspicuously longer and thicker than adjacent setae (1); small, little different from adjacent setae (2).
9	1	Median tergal setae on I–VI. All uniformly medium to long, extending to or overlapping base of following seta (1); all uniformly shorter, not extending to base of following seta (2); anterior setae prominent, posterior very short to minute (3); all very short to minute, often difficult to discern (4). Unordered.
10	0	Median tergal seta on VII. Absent (1); present (2).
11	1	Median tergal seta on VIII. Absent (1); present (2).
12	10	Median metanotal seta. Very long, >200 μm (1); short <110 μm (2).
13	2	Intermediate sternal setae on II. Absent (0); present (1).
14	1	Median length of intermediate sternal seta on V. 5–15 μm (1), 17–25 μm (2); 27–35 μm (3); 37–45 μm (4). Ordered.
15	0	Size of median sternal setae on IV–V relative to corresponding intermediate setae. Roughly comparable in size (1); distinctly larger (2).
16	1	Median sternal seta on IX. Absent (1); present (2).
17	2	Relative sizes of sternal setae on II–VII. Similar in size (1); VII shorter than II–VI (2); VI–VII shorter than II–III or II–IV (3); II, II–III or II–IV shorter than others (4); V much longer than others (5). Unordered.

18	0	Submarginal sternal seta on VII: Long to very long, extending across at least two segments (1); medium, extending from ½ to 1½ segments (2); short to minute, not extending over ½ segment (3). Ordered.
19	1	Mean temple width (μm). 240–262 (1); 264–310 (2); 311–340 (3); 344–360 (4); 381–395 (5); 433–482 (6). Ordered.
20	0	Median length of mid-dorsal head seta 1 (μm). 5–25 (1); 27–50 (2); 52–75 (3); 77–140 (4). Ordered.
21	0	Median length of mid-dorsal head seta 2 (μm). 5–10 (1); 12–20 (2); 22–32 (3); 52–62 (4). Ordered.
22	0	Median length of pronotal seta (μm). 7–25 (1); 27–50 (2); 52–77 (3); 82–112 (4). Ordered.
23	10	Marginal temple seta 5. Very short to minute, usually <10 μm long (1); well-developed, 15–25 μm long (2).
24	0	Median length of submarginal head seta 3 (μm). 10–22 (1); 25–40 (2); 42–62 (3). Ordered.
25	0	Median length of dorsal antennal pedical seta (μm). 27–45 (1); 47–65 (2); 67–85 (3); 87–112 (4). Ordered.
26	1	Lateral seta on segment IV. Short (0); long (1).
27	0	Length of submarginal tergal seta on VII relative to submarginal tergal seta on VIII. Comparable (1); much shorter (2).
28	1	Submarginal tergal seta on II–V. Uniformly long, extending well onto following segment (1); uniformly short, not extending onto following segment (2); uniformly very long, extending at least onto second following segment (3); II–III or II–IV very long, IV–V or V much shorter (4). Unordered.
29	1	Intermediate tergal setae. Long (1); medium (2); short (3). Ordered.
30	4	Very long lateral seta on segment VII. Present (1); absent (2).
31	1	Median length of intermediate sternal seta on VII. 5–17 μm (1), 20–37 μm (2); 42–57 μm (3); 67–120 μm (4). Ordered.
32	3	Intermediate sternal setae on III. Absent (0); present (1).
33	1	Lateral seta on segment V. Short (0); long (1).
Adults (F, M, or both)		
34(F)	3	Mean length of medial two setae on tergite VIII (LNS TG8/HD WDTH). <0.09 (0); 0.09–0.20 (1); 0.20–0.27 (2); >0.27 (3). Ordered.
35(F)	0	Mean number of genital sac loops (NGS LPS). None (0); ≤2 (1); 3–5 (2); 6–9 (3); 10–11 (4); 12+ (5); Ordered.
36(F)	1	Mean length of medial setae on tergite VII (LNS TG7/HD WDTH). ≤0.18 (0); 0.18–0.25 (1); 0.25–0.35 (2); 0.35+ (3). Ordered.
37(F)	2	Length of posterior (last) tergite inner lateral seta (PSLTG IN/HD WDTH). ≤0.07 (0); 0.07–0.15 (1); 0.15–0.225 (2); 0.225–0.27 (3); 0.27+ (4). Ordered.
38(F)	3	Length of posterior (last) tergite outer lateral seta (PSLTG OT/HD WDTH). ≤0.10 (0); 0.10–0.23 (1); 0.23+ (2). Ordered.
39(F)	2	Mean number of setae on sternite II (SET STN2). ≤7 (0); 7–9.5 (1); 9.5–13 (2); 13+. Ordered.
40(F)	2	Length of genital sac (GS LGTH) relative to total body length (TOT LGTH). ≤0.09 (1); 0.09–0.12 (2); 0.12+ (3); Ordered.
41(F)	4	Arrangement of lateral setae on posterior (last) tergite. 2+2+2 (0); 3+3 (1); 1+4+1 (2); Unordered.
42(F)	10	Anterior margin of genital sac. Smooth, gently curved (0); with prominent central notch (1); conspicuous anterior protrusion (2). Unordered.
43	2	Relative size of male and female inner marginal temple seta (male MG TMP/female MG TMP). <0.7 (0); 0.7–1.15 (1); >1.15 (2).
44	10	Position of submarginal temple seta with respect to marginal temple seta. Lateral (0); medial (1).
45(M)	3	Posterior margin of male scape. Straight, SCP EDWD/SCP MDWD <1.10 (0); weakly developed convexity, SCP EDWD/SCP MDWD 1.10–1.15 (1); distinct protuberance, SCP EDWD/SCP MDWD >1.15 (2). Ordered.
46(M)	2	Size of inner marginal temple seta (MG TMP/HD WDTH). ≤0.035 (0); 0.035–0.076 (1); >0.076 (2). Ordered.
47(M)	2	Size of submarginal temple seta (SMG TMP/HD WDTH). <0.09 (0); 0.09–0.15 (1); 0.15–0.21 (2); 0.21–0.28 (3); >0.28 (4). Ordered.
48(M)	1	Length of body relative to head length (HD LGTH/TOT LGTH). ≤0.25 (0); >0.25 (1).
49(M)	3	Relative male scape length (SCP LGTH/HD WDTH). <0.31 (0); 0.31–0.45 (1); >0.45 (2). Ordered.
50(M)	4	Mean number of setae on tergite VII (SET TG7). ≤13.5 (0); >13.5 (1).
51(M)	1	Mean number of setae on sternite VIII (SET STN8). <5 (0); 5–7 (1); >7 (2). Ordered.
52(M)	1	Number of genital sac spines. No spines (0); two (1); three (2); four (3); five (4); six (5); eight or more (6). Ordered.
53(M)	2	Relative width of genital parameral arch (GPA WDTH/HD WDTH). <0.19; (1) 0.19–0.24 (2); 0.24–0.31 (3); >0.31 (4). Ordered.
54(M)	4	Grouped setae on tergites II and III. Absent (0); present (1).
55(M)	10	Genital parameral arch shape. Semicircular, lacking any posterior projection (0, **64**); medial posterior apical projection flanked by smaller projections (1, **19**); with marked medial thickening (2, **14**, **16**); posterior margin truncated (3, **62**); thick, with lateral 'shoulders' and broad apical projection (4, **63**); gently curved, with medial, typically triangular, apical projection (5, **18**, **65**); medial apical projection bulbous (6, **15**); thick, anterior margin straight, long apical projection (7, **58**); irregularly curved, asymmetrical (8, **24–30**); posterior margin produced, no apical projection (9, **20**). Unordered.
56(M)	8	Genital endomeral plate shape. Ovoid (0, **94**), diamond (1, **93**); elongated diamond (2, **19**); anterior margin straight, with dorsal thickening, apically bluntly triangular (3, **101–104**); irregular, asymmetrically curved (4, **33–44**); triangular, sometimes with small to moderate apical bifurcation (5, **20**, **92**, **96–100**, **105–114**); deep terminal bifurcation (6, **95**); posterior margin rounded with small indentation (7); elongated triangle (8); long, anterior margin straight with medial depression or projection (9, **22–23**, **31–32**). Unordered.
57(M)	10	Shape of genital sac spines. Variable, generally stout (0, **69–91**); slender, curved (1, **54–57**); small, triangular (2). Unordered.
58(F)	10	Outer mid-dorsal head seta. Short (0); long (1).

Appendix 2. Data matrix for pocket gopher chewing lice. The louse taxa are arranged by species complex, with the nominate species in each species complex marked with an asterisk (*). The name of the species complex to which a taxon lacking an asterisk belongs can be found by going up the table until a taxon with an asterisk is encountered. For a description of each character see Appendix 1. Taxa for which the state of a given character could not be ascertained, either because the feature was missing (e.g. the first instar is unknown), or the character is inapplicable (e.g. shape of genital spines in a taxon with no spines) are marked indicated by '?'

Taxon	Character 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	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
*californicus**	1	1	2	2	1	2	1	1	1	1	1	1	1	4	1	1	1	1	2	4	4	4	1	3	2	1	1	1	1	1	4	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
centralis	1	1	2	2	1	2	1	1	1	1	1	1	1	4	1	1	1	1	2	3	3	3	1	3	1	1	1	1	1	1	3	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
albati	1	1	2	2	1	2	1	1	1	1	1	1	1	4	1	1	1	1	2	3	3	3	1	2	1	1	1	1	1	1	3	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
angularis	1	1	2	2	1	2	1	1	1	1	1	1	1	4	1	1	2	1	2	3	3	3	1	2	2	1	1	1	1	1	3	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
bajaensis	1	1	2	2	1	2	1	1	1	1	1	1	1	4	1	1	2	1	2	3	4	4	1	2	2	1	1	1	1	1	3	1	1	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
clausonae	1	1	2	2	1	2	1	1	1	1	1	1	1	4	1	1	2	1	2	3	4	4	1	2	1	1	1	1	1	1	2	1	1	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
limitans limitans	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	2	3	1	1	1	1	2	2	3	1	1	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
l. bakeri	1	1	2	2	1	2	1	1	1	2	2	1	1	2	2	1	1	2	2	2	2	2	1	1	1	0	2	2	3	1	1	1	0	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
l. halli	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	2	3	1	1	1	1	2	2	3	1	2	1	1	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
l. tolteci	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	2	3	1	1	1	1	2	2	3	1	2	1	1	1	4	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
aurei aurei	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	2	2	1	1	1	1	2	2	3	1	2	1	1	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
a. grahamensis	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	3	2	1	1	2	0	2	2	3	1	1	1	0	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
actuosi	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	3	3	1	1	1	1	2	2	3	1	1	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
sinaloae	1	1	2	2	1	2	1	1	1	2	1	1	1	3	1	1	1	2	2	2	2	3	1	1	1	1	2	2	3	1	2	1	1	1	4	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
crovelloi	1	1	2	2	1	2	1	1	1	2	1	1	1	3	2	1	1	1	2	2	2	3	1	1	1	1	1	1	3	1	1	1	1	1	2	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
warmanae	1	1	2	2	1	2	1	1	1	2	1	1	1	1	2	1	1	1	2	1	2	3	1	1	1	1	1	1	3	1	1	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	5	3	0	5	5	0	1
*umbrini**	1	1	2	2	1	2	1	1	1	1	1	1	1	2	1	1	1	1	2	3	3	3	1	1	1	1	2	1	2	1	2	1	1	1	3	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
musculi	1	1	2	2	1	2	1	1	1	2	1	1	1	2	1	1	1	1	2	2	3	2	1	1	1	1	2	1	2	1	1	1	1	1	2	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
cliftoni	1	1	2	2	1	2	1	1	1	2	1	1	1	2	2	1	1	2	2	2	2	2	1	1	1	1	2	2	3	1	1	1	1	1	4	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
jaliscoensis	1	1	2	2	1	2	1	1	1	2	1	1	1	2	1	1	1	1	3	3	3	3	1	1	1	1	2	1	2	1	2	1	1	1	4	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
extimi	1	1	2	2	1	2	1	1	1	2	1	1	1	4	1	1	1	1	3	4	3	3	1	1	2	1	1	3	1	1	2	1	1	1	3	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
nayaritensis	1	1	2	2	1	2	1	1	1	1	1	1	1	3	1	1	1	1	3	3	3	3	1	1	1	1	1	4	1	1	2	1	1	1	4	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
welleri welleri	1	1	2	2	1	2	1	1	1	2	1	1	1	3	1	1	1	2	2	1	2	2	1	1	1	1	2	1	2	1	2	1	1	1	2	1	3	1	3	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
w. multilineatus	1	1	2	2	1	2	1	1	1	2	1	1	1	3	2	1	1	1	2	1	2	3	1	1	1	1	2	1	1	1	2	1	1	1	3	1	3	1	3	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
*subcalifornicus**	1	1	2	2	1	2	1	1	1	2	1	1	1	4	1	1	1	1	2	3	3	4	1	1	1	1	1	1	2	1	2	1	1	1	5	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	3	3	0	5	5	0	1
guadalupensis	1	1	2	2	1	2	1	1	1	1	1	1	1	2	2	1	1	1	2	2	2	3	1	1	1	1	2	2	3	1	1	1	1	1	3	1	2	1	3	3	1	0	0	0	2	1	3	0	1	1	1	3	3	0	5	5	0	1
*quadridentatus**	1	1	2	2	1	2	1	1	1	2	1	1	1	3	1	1	2	1	2	2	3	3	1	1	1	0	1	2	3	1	2	1	0	1	1	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	3	3	0	5	5	0	?
*geomydis**	1	1	2	4	1	1	1	1	1	2	1	1	1	1	2	1	1	3	2	3	3	2	1	2	2	0	2	2	3	1	1	1	0	1	4	1	2	1	2	3	1	0	0	0	1	1	1	0	1	1	1	5	3	0	5	5	0	1
illinoensis	1	1	2	1	1	1	1	1	1	2	1	1	1	1	2	1	1	2	2	3	2	2	1	2	1	0	1	2	3	1	1	1	0	1	2	1	2	1	2	3	1	0	0	0	0	1	1	0	1	1	1	5	3	0	5	5	0	1
oklahomensis	1	1	2	4	1	1	1	1	1	2	1	1	1	1	2	1	1	3	2	3	3	2	1	2	1	0	2	2	3	1	1	1	0	1	1	1	2	1	2	3	1	0	0	0	2	1	1	1	1	1	1	5	3	0	5	5	0	1
nebrathkensis	1	1	2	4	1	1	1	1	1	2	1	1	1	1	2	2	1	2	2	2	2	2	1	1	1	0	2	2	3	1	1	1	0	1	1	1	2	1	2	3	1	0	0	0	1	1	1	0	1	1	1	5	3	0	5	5	0	1
spickai	1	1	2	4	1	1	1	1	1	2	1	1	1	1	2	1	1	3	2	3	3	2	1	2	2	0	2	2	3	1	1	1	0	1	1	1	2	1	2	3	1	0	0	0	2	1	1	1	1	1	1	5	3	0	5	5	0	1
heaneyi	1	1	2	4	1	1	1	1	1	2	1	1	1	1	2	1	1	2	2	3	3	2	1	3	1	0	1	1	3	1	1	1	0	1	1	1	2	1	2	3	1	0	0	0	2	1	1	0	1	1	1	5	3	0	5	5	0	1
subgeomydis	1	1	2	2	1	1	1	1	2	2	1	1	1	1	1	1	3	3	2	2	2	2	1	1	1	0	2	2	3	1	1	1	0	1	2	1	2	1	2	3	1	0	0	0	1	1	1	0	1	1	1	5	3	0	5	5	0	1
ewingi	1	1	2	2	1	1	1	1	2	2	1	1	1	1	1	1	3	3	2	2	2	2	1	1	1	0	2	2	3	1	1	1	0	1	2	1	2	1	2	3	1	0	0	0	1	1	1	0	1	1	1	3	3	0	5	5	0	1
*truncatus**	1	1	2	1	1	1	1	1	3	2	1	1	1	1	1	1	3	3	2	1	2	1	1	2	4	0	2	2	3	1	1	1	0	1	1	1	2	1	2	2	1	0	0	0	0	1	0	1	1	1	1	5	3	0	3	7	0	0
neotruncatus	1	1	2	1	1	1	1	1	3	2	1	1	1	1	1	1	3	3	2	1	2	1	1	1	3	0	2	2	3	1	1	1	0	1	1	1	2	1	2	2	1	0	0	0	0	1	0	1	1	1	1	5	3	0	5	5	0	0
*telli**	1	1	2	3	1	1	1	1	4	1	1	1	1	2	2	2	4	3	3	2	2	2	1	2	2	0	2	2	3	1	2	1	0	1	0	1	1	0	2	3	1	2	0	0	0	1	1	0	2	1	1	5	3	0	5	5	0	1
*dalgleishi**	1	1	2	4	1	1	1	1	1	2	1	1	1	1	2	1	1	3	2	2	3	2	1	2	1	0	1	1	3	1	1	1	0	1	0	1	2	1	2	3	1	0	0	0	2	1	1	1	1	1	1	5	3	0	5	5	0	1
*coronadoi coronadoi**	1	1	2	3	1	1	1	1	4	1	1	1	1	2	1	1	2	3	2	2	2	1	1	1	2	0	2	2	3	1	1	1	0	1	2	1	0	0	2	3	1	0	0	0	0	1	1	0	2	1	1	5	3	0	5	5	0	1
c. saccharalis	1	1	2	3	1	1	1	1	4	1	1	1	1	2	1	1	1	3	2	2	3	2	1	1	4	0	2	2	3	1	2	1	0	1	2	1	0	0	2	3	1	0	0	0	0	1	1	0	2	1	1	5	3	0	5	5	0	1
c. submerriami	1	1	2	3	1	1	1	1	4	1	1	1	1	2	1	1	4	3	2	2	3	2	1	1	3	0	2	2	3	1	2	1	0	1	2	1	0	0	2	3	1	0	0	0	0	1	1	0	2	1	1	5	3	0	5	5	0	1
merriami	1	1	2	3	1	1	2	1	4	1	1	1	1	1	2	1	1	3	2	2	2	1	1	2	2	0	2	2	3	1	1	1	0	1	5	1	1	0	2	3	1	0	0	0	0	1	1	0	2	1	1	5	3	0	5	5	0	1
veracruzensis	1	1	2	3	1	1	1	1	4	1	1	1	1	3	1	1	4	2	2	1	2	1	1	1	1	1	1	1	1	1	2	1	1	1	3	1	1	0	2	3	1	0	0	0	0	1	1	0	1	1	1	5	3	0	5	5	0	1
polydentatus polydentatus	1	1	2	3	1	1	2	1	4	1	1	1	1	1	2	1	4	3	2	1	2	1	1	1	1	0	2	2	3	1	1	1	0	1	2	1	1	0	2	3	1	0	0	0	0	1	1	0	2	1	1	6	3	0	5	5	0	1
p. angustirostris	1	1	2	3	1	1	2	1	4	1	1	1	1	2	2	1	4	3	2	1	2	2	1	2	3	0	2	2	3	1	1	1	0	1	2	1	1	0	2	3	1	0	0	0	0	1	1	0	2	1	1	6	3	0	5	5	0	1
*expansus**	1	1	2	3	1	1	2	1	4	1	1	1	1	3	2	1	1	1	2	3	2	2	1	2	3	0	1	4	3	1	2	1	1	1	2	1	2	1	2	3	1	0	1	0	0	1	1	0	1	1	1	5	3	0	5	5	0	0
martini	1	1	2	3	1	1	2	1	4	1	1	1	1	3	2	1	1	1	2	2	2	2	1	2	4	1	1	4	3	1	2	1	1	1	3	1	2	1	2	3	1	0	0	0	0	1	1	0	1	1	1	5	3	0	5	5	0	0
*bulleri bulleri**	2	1	2	2	1	1	2	1	2	1	1	1	1	1	2	1	1	3	2	1	2	2	2	2	2	0	2	2	3	1	1	1	0	1	5	1	2	1	2	3	0	0	1	0	0	1	2	0	1	1	1	5	3	0	5	3	0	0
b. melanuri	2	1	2	2	1	1	2	1	2	1	1	1	1	1	1	1	1	3	3	1	1	1	2	1	1	0	2	2	3	1	1	1	0	1	5	1	1	1	2	3	0	0	1	0	0	1	2	0	1	1	1	5	3	0	5	3	0	0
b. intermedius	2	1	2	2	1	1	2	1	2	1	1	1	1	1	2	1	1	3	2	2	1	2	2	2	4	0	2	2	3	1	1	1	0	1	5	1	2	1	1	3	0	0	1	0	0	1	2	0	1	1	1	5	3	0	5	3	0	0
burti	2	1	2	2	1	1	2	1	4	1	1	1	1	1	1	1	1	3	3	2	2	2	2	3	4	0	2	2	3	1	1	1	0	1	5	1	2	1	1	3	0	0	1	0	0	1	2	0	1	1	1	5	3	0	5	3	0	0
nadleri	2	1	2	2	1	1	2	1	2	1	1	1	1	1	2	1	1	3	2	1	2	1	2	2	3	0	2	2	3	1	1	1	0	1	5	1	2	1	1	3	0	0	1	0	0	1	1	0	1	1	1	5	3	0	5	3	0	0
*mexicanus**	1	1	2	1	1	1	3	2	1	2	2	1	0	4	1	1	1	2	2	2	1	?	2	2	4	1	1	1	1	1	3	1	1	1	0	0	2	2	0	1	1	0	1	0	0	1	2	1	1	1	2	0	2	0	0	0	?	0
perotensis perotensis	1	1	2	1	1	1	2	1	1	2	2	1	0	4	1	1	1	1	2	2	2	2	2	2	4	0	2	1	1	1	3	1	1	1	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1	2	0	1	0	0	0	?	0
p. irolonis	1	1	2	1	1	1	2	1	1	2	1	1	0	2	1	1	1	3	2	1	1	2	2	2	4	1	2	1	1	1	2	1	1	1	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1	2	0	1	0	0	0	?	0

Appendix 2. (*Cont.*)

traubi	1	1	2	1	1	1	3	2	1	2	1	1	0	3	1	1	1	2	3	1	1	2	2	2	4	1	2	2	2	1	2	1	1	0	0	0	1	2	0	1	0	0	1	0	0	1	2	1	1	1	2	1	2	0	1	2	2	0
fulvescens	1	1	2	1	1	1	2	1	1	2	1	1	0	2	1	1	1	2	3	2	2	3	2	3	4	1	1	4	1	1	2	1	1	1	0	0	1	1	1	1	0	0	1	0	0	1	2	1	1	1	2	0	1	0	4	1	?	0
*oregonus**	1	1	2	1	1	1	2	1	1	2	1	1	1	1	2	2	1	2	3	2	3	2	1	2	3	1	2	1	3	1	1	1	0	1	3	1	2	1	2	3	1	0	0	0	0	1	2	0	1	1	1	5	3	0	5	5	0	1
idahoensis	1	1	2	1	1	1	2	1	1	2	1	1	1	1	2	2	1	3	2	2	3	2	1	2	3	1	2	1	3	1	1	1	0	1	3	1	2	1	3	3	1	0	0	0	0	1	3	0	1	1	1	5	3	0	5	5	0	1
shastensis	1	1	2	5	1	2	4	1	1	2	1	1	1	3	2	2	1	1	2	3	2	3	1	3	3	1	1	1	1	1	2	1	1	1	3	1	2	1	3	3	1	0	0	0	0	1	3	0	1	1	1	5	3	0	5	5	0	1
hueyi	1	1	2	5	1	2	4	1	1	1	1	1	1	3	1	2	2	1	2	3	3	4	1	2	2	1	1	1	2	1	2	1	1	1	4	1	2	1	3	3	1	0	0	0	0	1	3	0	1	1	1	5	3	0	5	5	0	1
*tolucae**	1	1	2	1	1	1	3	1	1	2	2	1	1	1	2	2	1	3	2	1	2	1	1	3	4	0	2	2	3	1	1	1	0	2	0	1	3	1	3	3	1	0	0	0	0	1	3	0	1	1	1	5	3	0	2	5	0	0
fulvi	1	1	2	1	1	1	3	1	1	2	2	1	0	1	2	2	5	3	2	1	2	1	1	3	4	0	2	2	3	1	1	0	0	2	0	2	3	1	2	3	1	0	0	0	0	2	4	0	1	1	1	5	3	0	2	5	0	0
chihuahuae chihuahuae	1	1	2	1	1	1	3	1	1	2	2	1	1	1	2	2	4	3	2	1	1	1	1	3	3	0	2	2	3	1	1	1	0	3	0	3	4	1	2	3	1	0	1	0	0	2	3	0	1	1	1	5	3	0	2	5	0	0
c. emersoni	1	1	2	1	1	1	3	1	1	2	2	1	1	1	2	2	4	3	2	1	1	2	1	3	4	0	2	2	3	1	1	1	0	3	0	3	4	1	2	3	1	0	1	0	0	2	2	0	1	1	1	5	3	0	5	5	0	0
pattoni	1	1	2	1	1	1	3	1	1	2	2	1	0	1	2	2	4	3	2	2	2	?	1	3	4	0	2	2	3	1	1	0	0	2	0	2	3	1	1	3	1	0	1	0	0	2	3	0	1	1	1	5	3	0	6	5	0	0
*texanus texanus**	1	1	1	1	1	1	3	1	2	1	1	1	0	1	1	1	1	3	3	1	2	1	1	2	4	0	2	2	3	1	1	1	0	1	1	1	2	1	2	3	1	0	1	0	0	1	0	0	1	1	1	3	3	0	5	5	0	0
t. tropicalis	1	1	1	1	1	1	3	1	2	1	1	1	0	1	1	1	2	3	2	1	1	1	1	2	4	0	2	2	3	1	1	1	0	1	1	1	2	1	2	3	1	0	1	0	0	1	0	0	1	1	1	3	3	0	5	5	0	0
ustulati ustulati	1	1	1	1	1	1	3	1	2	1	1	1	0	2	1	1	1	1	3	1	1	2	1	3	4	0	1	2	2	1	2	0	0	1	1	1	2	1	1	3	1	0	1	0	0	1	0	0	1	1	1	3	3	0	5	5	0	0
u. clarki	1	1	1	1	1	1	3	1	2	1	1	1	0	2	1	1	1	1	2	1	2	2	1	3	4	0	1	2	2	1	2	0	0	1	1	1	2	1	1	3	1	0	1	0	0	1	0	0	1	1	1	3	3	0	5	5	0	0
tamaulipensis	1	1	1	1	1	1	3	1	2	1	1	1	0	3	1	1	1	1	3	1	2	4	1	3	4	0	1	2	2	1	3	0	0	1	1	2	3	1	1	3	1	0	1	0	0	1	0	0	1	1	1	3	3	0	5	5	0	0
subnubili	1	2	1	1	1	1	3	1	2	1	1	1	0	2	1	1	1	1	2	1	1	2	1	3	4	0	1	2	2	1	2	0	0	0	1	0	2	1	1	3	1	0	1	0	0	1	0	0	1	1	0	3	3	0	5	5	0	0
*trichopi**	2	2	2	1	1	1	3	1	1	2	2	1	0	1	2	1	4	3	2	1	1	1	1	2	4	0	2	2	3	1	1	1	0	1	2	1	1	1	2	3	1	0	1	0	0	1	2	0	1	1	1	5	3	0	5	3	0	0
*copei**	1	1	2	1	1	1	3	2	4	2	2	1	0	3	1	1	1	1	4	1	2	1	1	2	4	0	1	2	3	1	2	0	0	1	0	0	3	2	0	2	1	0	1	1	0	0	0	1	1	0	0	0	0	1	7	8	?	0
yucatanensis	1	1	2	1	1	1	3	2	4	2	2	1	0	3	1	1	1	3	5	1	2	1	1	1	4	0	2	2	3	1	2	0	0	0	1	3	3	1	0	2	1	0	2	1	0	0	0	1	1	1	1	0	0	0	7	8	?	0
chapini	1	1	2	1	1	1	3	2	4	2	2	1	0	3	1	1	1	3	5	2	2	1	1	2	4	0	2	2	3	1	2	0	0	0	1	3	3	1	0	2	1	0	2	1	0	0	0	1	0	1	1	0	0	0	7	8	?	0
hoffmani	1	1	2	1	1	1	3	2	4	2	2	1	0	3	1	1	1	3	5	1	2	1	1	2	4	0	2	2	3	1	2	0	0	0	1	3	3	1	0	2	1	0	2	1	0	0	0	1	0	1	1	0	0	0	7	8	?	0
*panamensis panamensis**	2	1	2	1	1	1	3	2	4	2	1	1	0	2	1	1	1	3	4	2	2	1	1	3	4	0	2	2	3	1	1	0	0	0	0	1	2	1	1	3	1	1	2	1	0	1	0	1	1	1	1	5	3	0	5	5	0	0
p. dariensis	1	1	2	1	1	1	3	2	4	2	1	1	0	2	1	1	1	3	5	2	2	1	1	2	4	0	2	2	3	1	2	0	0	0	0	1	2	1	1	3	1	1	2	1	0	1	0	1	1	1	1	5	3	0	5	5	0	0
setzeri	1	1	2	1	1	1	3	2	4	2	1	1	0	2	1	1	1	3	3	1	1	1	1	1	4	0	2	2	3	1	1	0	0	0	0	1	2	1	1	3	1	1	2	1	0	1	0	1	1	1	1	5	2	0	5	5	0	0
davidhafneri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	2	1	1	3	1	1	2	1	0	1	0	1	1	1	1	5	3	0	5	5	0	0
costaricensis	1	1	2	1	1	1	3	2	4	2	1	1	0	2	1	1	1	3	4	1	2	1	1	1	4	0	2	2	3	1	2	0	0	0	0	1	2	1	1	3	1	1	2	1	0	1	0	1	1	1	1	3	2	0	5	6	0	0
cherriei	1	1	2	1	1	1	3	2	4	2	1	1	0	2	1	1	1	3	3	1	1	1	1	1	4	0	2	2	3	1	2	0	0	0	0	1	2	1	1	3	1	1	2	1	0	1	0	1	1	1	1	2	3	0	5	6	0	0
*sclerotus**	1	1	2	1	1	1	3	1	4	2	1	1	1	1	1	1	3	3	2	2	2	1	1	3	4	0	2	2	3	1	1	1	0	1	3	2	2	1	1	3	1	0	1	0	0	1	1	1	1	1	1	5	3	0	5	5	0	0
mobilensis	1	1	2	1	1	1	3	1	4	2	1	1	1	1	1	1	3	3	2	2	2	1	1	3	4	0	2	2	3	1	1	1	0	1	3	1	2	1	1	2	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0
*chiapensis**	2	1	2	1	1	1	3	2	4	1	1	1	0	3	1	1	1	1	6	4	2	1	1	2	4	1	1	2	2	1	3	0	1	1	1	1	2	1	0	3	1	0	2	1	0	1	?	1	1	1	1	5	3	0	5	5	0	0
pygacanthi	2	1	2	1	1	1	3	2	4	1	1	1	0	4	1	1	1	1	6	4	3	1	1	2	4	1	1	2	2	1	3	0	1	1	1	0	2	1	0	3	1	0	2	1	0	1	0	1	1	1	1	5	3	0	5	5	0	0
*alleni**	1	1	2	1	1	1	3	2	2	1	1	1	0	3	1	1	1	1	6	4	3	1	1	3	4	1	1	4	2	1	4	0	1	0	0	1	2	1	0	3	1	0	1	1	0	0	0	1	1	1	1	3	3	0	5	7	0	0
jonesi	1	1	2	1	1	1	3	2	2	1	1	1	0	3	1	1	1	1	6	4	2	1	1	3	?	1	1	4	2	1	4	0	1	0	0	1	2	1	0	3	1	0	1	1	0	0	0	1	1	1	2	3	3	0	5	7	0	0
*mcgregori**	1	1	2	1	1	1	4	1	2	1	1	1	0	3	1	1	1	1	3	1	2	2	2	3	4	1	1	4	1	1	2	1	1	1	1	1	2	1	2	3	0	0	1	0	0	1	2	0	1	1	2	4	3	0	5	3	0	0
wernecki wernecki	1	1	2	1	1	1	4	1	2	2	1	1	0	3	1	1	1	1	3	1	2	2	2	3	4	1	1	4	1	1	2	1	1	1	2	1	2	1	2	3	0	0	1	0	0	1	2	0	2	1	2	5	3	0	5	3	0	0
w. planiceps	1	1	2	1	1	1	4	1	2	2	1	1	0	3	1	1	1	2	4	1	1	3	2	3	4	1	1	4	1	1	3	1	1	1	3	0	2	1	2	3	0	0	1	0	0	1	2	0	2	1	2	5	3	0	5	3	0	0
alcorni	1	1	2	1	1	1	2	1	1	2	1	1	0	3	1	1	1	1	2	2	1	?	2	2	3	1	1	4	1	1	2	1	1	1	4	1	2	1	2	3	0	0	1	0	0	1	2	0	1	1	1	5	3	0	5	3	0	0
*neocopei**	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	1	1	8	4	?	0
genowaysi	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
asymmetricus	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	2	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
green	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	1	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
jamesbeeri	1	3	2	1	1	1	3	1	1	2	2	1	0	1	2	2	4	3	1	2	1	?	1	2	2	0	2	2	3	1	1	1	1	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
peregrini	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	2	1	2	2	0	2	2	3	1	1	1	1	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	0	0	0	1	8	4	?	0
potteri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	2	2	2	2	1	0	0	1	0	0	2	0	0	0	0	0	0	0	1	8	4	?	0
*minor**	1	3	2	1	1	1	3	1	4	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	1	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
birneyi	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
zacatecae	1	3	2	1	1	1	3	1	1	2	2	1	0	1	2	2	4	1	1	1	1	2	1	3	1	0	2	2	3	1	1	1	1	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
timmi	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	2	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
*dickermani**	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
markhafneri	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	0	0	0	1	8	4	?	0
williamsi	1	3	2	1	1	1	3	1	3	2	2	1	0	1	2	2	4	3	1	1	1	2	1	3	2	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	0	0	0	1	0	0	1	8	4	?	0
orizabae	1	3	2	1	1	1	3	1	1	2	2	1	0	1	2	2	4	3	1	1	1	1	1	2	2	0	2	2	3	1	1	1	0	2	0	2	2	1	2	?	2	0	1	0	0	2	0	0	0	0	0	0	0	1	8	4	?	0
johnhafneri	1	3	2	1	1	1	3	1	4	2	2	1	0	1	2	2	4	3	1	1	1	1	1	1	1	0	2	2	3	1	1	1	0	2	0	2	2	2	2	?	0	0	1	0	0	2	0	1	0	0	0	0	0	1	8	4	?	0
*wardi**	2	3	2	1	1	1	3	1	4	2	2	1	0	1	1	2	4	3	1	1	1	2	1	2	2	0	2	2	3	2	1	0	0	2	0	2	2	1	2	1	0	0	1	0	0	2	0	0	0	0	1	0	2	1	5	9	?	0
arleneae	2	3	2	1	1	1	3	1	4	2	2	1	0	1	1	2	4	3	1	1	1	?	1	2	2	0	2	2	3	2	1	0	0	2	0	2	2	1	2	1	0	0	1	0	0	2	0	0	0	1	1	0	2	1	5	9	?	0
barbarae	2	3	2	1	1	1	3	1	4	2	2	1	0	1	1	2	4	3	1	1	1	2	1	2	2	0	2	2	3	2	1	0	0	2	0	2	2	1	2	1	0	0	1	0	0	2	0	0	0	1	1	0	2	1	5	9	?	0
byersi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	2	2	1	2	1	0	0	1	0	0	2	0	0	1	1	2	0	1	1	5	9	?	0
*thomomyus**	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	2	4	3	2	1	1	1	1	1	1	0	2	2	3	2	1	0	0	2	0	1	3	2	2	1	0	0	1	0	0	0	4	0	1	1	1	3	3	0	9	5	1	0
craigi	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	2	4	3	2	1	1	1	1	2	1	0	2	2	3	2	1	0	0	2	0	1	4	2	2	1	0	0	1	0	0	0	4	0	1	1	1	3	3	0	9	5	1	0
biagiae	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	2	4	3	2	1	1	1	1	2	1	0	2	2	3	2	1	0	0	2	0	1	3	2	2	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0
betleyae	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	1	4	3	2	1	1	1	1	1	2	0	2	2	3	2	1	0	0	2	0	1	3	2	2	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0
thaeleri	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	1	4	3	2	1	1	1	1	1	1	0	2	2	3	2	1	0	0	2	0	1	3	2	2	1	0	0	1	0	0	0	4	0	1	1	1	5	3	0	9	5	1	0
dakotensis	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	2	4	3	2	1	1	1	1	2	1	0	2	2	3	2	1	0	0	2	0	1	3	2	2	2	0	0	1	0	0	0	4	0	1	1	2	5	3	0	9	5	1	0
fuchsi	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	2	4	3	2	1	1	1	1	2	1	0	2	2	3	2	1	0	0	2	0	1	3	2	2	1	0	0	1	0	0	0	4	0	1	1	1	5	3	0	9	5	1	0
duchesnensis	2	1	2	1	2	1	3	1	1	2	2	2	0	1	2	2	4	3	2	1	1	1	1	1	1	0	2	2	3	2	1	0	0	2	0	1	3	2	2	1	0	0	1	0	0	0	4	1	1	1	1	0	3	0	9	5	?	0