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Multivariate analysis applied to a classification problem in dytiscid beetles (Coleoptera: Dytiscidae)

Curtis Y. Takahashi
San Jose State University

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**MULTIVARIATE ANALYSIS APPLIED TO A CLASSIFICATION PROBLEM IN
DYTISCID BEETLES (COLEOPTERA: DYTISCIDAE)**

A Thesis

Presented to

The Faculty of the Department of Biology

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Curtis Y. Takahashi

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APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

Dr. Ronald E. Stecker

Dr. William E. Bros

Dr. J. Gordon Edwards

Dr. Vida C. Kenk

APPROVED FOR THE UNIVERSITY

ABSTRACT

MULTIVARIATE ANALYSIS APPLIED TO A CLASSIFICATION PROBLEM IN DYTISCID BEETLES (COLEOPTERA: DYTISCIDAE)

by Curtis Y. Takahashi

This thesis addresses the problem of species identification for the predaceous diving beetle species pairs, Deronectes panaminti (Fall)/ D. coelamboides (Fall) and D. grammicus Sharp / D. titulus Leech, both of which have been proposed as races of each other. The data were subjected to Principal Component Analysis and the resulting component scores if significant were analyzed by t-test to verify the dichotomy of the two species. Despite apparent morphological similarities between D. panaminti/D. coelamboides, the separation of the two species remains intact. However, Principal Component Analysis did not reveal differences between sexes for the measurements taken. Principal Component Analysis did not identify any suitable characters from those measured with which to clarify the relationship between D. grammicus / D. titulus.

Acknowledgments:--I would like to thank the members of my committee, Ron Stecker, J. Gordon Edwards, William Bros, and Vida Kenk for their patience during this project. Many thanks to the National Park Service for their permission to collect in the Death Valley National Monument. I would also like to thank David Kavanaugh, Norman Penny, and Roberta Brett for access to the California Academy of Sciences collection. Special thanks to Robert Roughley for his advice and encouragement (and for suggesting the project), Cliff Ramos for allowing me time to work on my thesis, and my dearest thanks to Elizabeth Goff for her support and encouragement.

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Multivariate Analysis Applied to a Classification Problem in Dytiscid Beetles
(Coleoptera: Dytiscidae)

Introduction

The beetles (Order: Coleoptera) are among the most numerous of insect orders, comprising an estimated 5,000,000 species. Many groups are not well understood within the order. While some groups are well known due to their economic importance or their aesthetic appearance, others have been infrequently studied compared to other groups. One such group is the family Dytiscidae (predaceous diving beetles). Small in size and easily overlooked, many members of this group have been poorly studied and questions remain to be answered regarding their systematics. This study is intended to clarify the confusion of the relationships between D. panaminti (Fall)/D. coelamboides (Fall) and D. grammicus Sharp/D. titulus Leech.

The Dytiscidae are some of the most widespread of aquatic insects, occurring on most of the world's major land masses (excluding Antarctica) and many islands in between (Zimmerman, 1970). The family includes 4 subfamilies, 15 tribes, and 153 genera (Nilsson & Angus, 1992), 40 of which occur in the Nearctic region (Anderson 1985). They are found in a variety of habitats ranging from alpine areas to the desert floor of Death Valley, North America.

The most recent revision of the hydroporine genus Deronectes (Sharp)

was in 1982 by Zimmerman. Within his "depressus" group, he proposed that the closely related species D. panaminti and D. coelamboides are races of a single, wide-ranging species. D. grammicus and D. titulus were also proposed as representing a single species.

In 1923, Fall placed the entire genus as a subgroup of the genus Hydroporus, making it the largest Nearctic genus. Balfour-Browne (1940) distinguished the subgenera Deronectes, Potamonectes and Stictotarsus, within the genus Deronectes. Other authors (Nilsson & Angus, 1992) grant Stictotarsus Zimmermann 1919, full generic standing.

Zimmerman and Smith (1975) describe the genus Deronectes to be a "fairly cohesive group," all except 2 members being confined to the western and southwestern parts of the North American continent. Zimmerman separates Deronectes from Hydroporus by an "incised midline of the hind coxal processes, by the absence of a marked pronotal declivity, and by the general lack of any large punctures on the ventral surface and dorsum except for linear series on the elytra and margins of the pronotum." Zimmerman (1982) placed Deronectes grammicus, D. titulus, and the related D. neomexicanus within the subgenus Stictotarsus. Nilsson and Angus (1992) place D. panaminti, D. coelamboides, D. grammicus, and D. titulus within the genus Stictotarsus, their contention being that there are no true "Deronectes" in North America. Roughley (1993, personal communication)

places the North American members of (previously) Deronectes within Potamonectes (Zimmermann 1921), and elevates Potamonectes to full generic status.

Deronectes panaminti are small, pale dytiscids which were first described from the Panamint Mountains near the Death Valley National Monument by Fall. They are the smallest members of the genus in North America (Zimmerman & Smith, 1975). In his work with Smith, Zimmerman stated that the range of D. panaminti was narrowly sympatric with respect to that of D. coelamboides, being found primarily in the Death Valley area of California (most being recorded at Salt Creek and Bad Water). Anderson (1985) in his paper on Great Basin dytiscids, places D. panaminti in what he terms his "endemic" species category, stating that it is only known from Death Valley and its surrounding area.

In his later work, Zimmerman (1982) revised his and Smith's earlier statement, saying that the range should now be considered to be broadly sympatric based upon specimens of D. panaminti collected in the Chiricahua Mountains and Wilcox Playa in Arizona.

The mesotibia of male members of D. panaminti are modified, possessing a marked declivity (see Fig. 1) which Fall stated may assist in holding the female during mating. This character helps to differentiate these beetles from other members of Deronectes.

D. coelamboides is a larger beetle than D. panaminti, similar in many of its characteristics. It, too, was first described by Fall in his monograph on the Hydroporus of North America. It has been found from California to New Mexico, Arizona and Baja California, Mexico. These beetles also possess the modification of the male mesotibia, suggesting that they are very closely related to D. panaminti.

D. grammicus was first described by Sharp (1887) in his monograph on the dytiscids of North America. A distinguishing characteristic is the possession of a highly punctate metatibia, which, according to Leech (1945), serves to separate it (and D. titulus) from the other members of Deronectes. D. titulus was described by Leech in 1945 as being quite similar to D. grammicus in most respects except for the color of the head, which is red.

Zimmerman (along with Smith) suggested that D. grammicus and D. titulus were races of one another, based upon lack of distinguishing morphological characteristics. In his 1982 work, he gave no additional evidence to substantiate his speculations regarding the relationship between D. grammicus and D. titulus.

In previous revisions of other dytiscids, Zimmerman (1970) used some numerical measurements in his descriptions. In his revision of the genus Laccophilus, characters used included total length, elytral length, total width,

and pronotal width. Of these 4 measures, Zimmerman found that the measure of pronotal width proved to be the most reliable.

The purpose of this study is to clarify the confusion of the identity of the D. panaminti/D. coelamboides, D. grammicus/D. titulus species pairs. The studies performed by Zimmerman (1975, 1982) make no use of modern statistical methods, such methods evaluating (according to Zimmerman) "...differences which are too subtle to be used in species identifications." In this case, where the species in question are morphologically similar in appearance, every avenue of determination available should be explored.

MATERIALS AND METHODS

Handling of Specimens:

The specimens examined were obtained from various institutions including the California Academy of Sciences, the University of California at Berkeley, The University of California at Davis, San Francisco State University, San Jose State University, Cornell University, the collection of the State of California, Department of Food and Agriculture, and specimens from the private collections of Deborah Lynn Mead of San Francisco State University and Gilbert Challet of the Orange County Vector Control District. Fresh specimens for dissection were collected by the author at the California State University Desert Studies Center at Zzyzx Springs, California and at the Death Valley National Monument, Inyo County, California.

Collections of live specimens were made using a standard aquatic collection net by sweeping the aquatic vegetation and bottom sediments at habitat locations. The easiest way to obtain specimens from the sample was to allow the beetles to emerge from the exposed material. Specimens crawl to the bottom edges of the net where they can be removed by hand. Some specimens were preserved when collected, while others were retained alive to observe reproductive behavior and to dissect later.

The beetles can be kept alive for months by feeding them live brine shrimp (available at most pet stores). Tubifex sp. worms may be substituted, but they foul the water quickly and so the water must be changed frequently. Those beetles that expired were placed in 80% ethanol and were saved for later study.

Morphometric Measurements:

Measurements of the beetles were made using an American Optical binocular dissecting scope fitted with a measuring reticle (100 divisions, metric, numbered every 1/10th) at 10X or 30X (leg characteristics of D. panaminti/coelamboides were measured at 30X). The measurement methods were modified from those used by Zimmerman and Smith (1975) and those of Zimmerman (1970).

Measurements were defined as follows (see Figs. 1 and 2):

Total Length (TL): The distance measured from the front of the head to the apex of elytra.

Total Width (TW): The distance across the widest visible area of the body, just behind the midpoint (if the elytra were separated, twice the value of a single elytron was substituted).

Head Width (HW): The distance across the head.

Pronotum to Elytral Length (PEL): The distance from the leading edge of the pronotum to the apex of the elytra.

Pronotal Width (PW): The distance across the widest part of the pronotum. Zimmerman found this to be the most stable of the measurements, being little affected by distortion of other parts of the body.

Pronotal Length (PL): The distance from the front edge to the posterior margin of the pronotum along the median line.

Pronotal Margin (PM): The length of the side of the pronotum, measured along the edge.

Profemoral Length (PFL): The length of the protrochanter plus profemur.

Protibial Length (PTL): The length of the protibia.

Mesofemoral Length (MFL): The length of the mesotrochanter plus mesofemur.

Mesotibial Length (MTL): The length of the mesotibia.

Metafemoral Length (MFL): The length of the metatrochanter plus metafemur.

Metatibial Length (MTL): the length of the metatibia.

Body Depth (BD): The height of the body at it's deepest part, from a lateral view.

Sex: This may be determined by the shape and size of the mesotibiae in D. panaminti and D. coelamboides.

MATERIAL EXAMINED:

Deronectes grammicus:

USA: Texas, 20 miles south of Alpine, 12-May-1927, J.O. Martin, 1

specimen. MEXICO: Chihuahua, Zaragosa, 9-Oct-1975 (753), J.R.

Zimmerman, 2 specimens. Bachinava, 10-April-1975 (765), J.R.

Zimmerman, 2 specimens. ZAC, 10 miles southwest of Zacatecas, 21-Oct-

1972, 1 specimen. S.L.P. Porvenis (W.N. Mexcuitic), 22-Oct-1980, 1

specimen. Mexico, El Oro, 9-May-1964, P. Reyes, 2 specimens.

Deronectes titulus:

PARATYPE, USA. TEXAS, Green Valley, Jul-1926. H.P. Chandler. 1 specimen, male. TEXAS: 20 miles south of Alpine, 12-May-1927, J.O. Martin. 2 specimens. Brewster, 3-May-1927, J.O. Martin. 35 specimens.

Deronectes panaminti:

USA, CALIFORNIA, INYO Co: Post Office Springs, near Ballarat, 25 Apr-1980, G. Challet, 13 males, 5 females. Salt Creek, 3-May-1969, G. Challet, 2 males, 3 females. Salt Creek, 3-May-1964, G. Challet, 2 males, 1 female. Salt Creek, 27-Dec-1963, R. Bandar, 1 male. Salt Creek, Miller & Calhoun, 1 male. Salt Creek, 21-Mar-1967, H.B. Leech, 7 males, 7 females. Bad Water, 3-May-1969, G. Challet, 2 males, 2 females. Bad Water, 2-Feb-1951, H.E. Stookey, 1 female. Bad Water, 14-Apr-1938, J.J. duBois, 1 male. Bad Water, 1-April (no year given), H.B. Leech, 1 male. Bad Water, 22-Feb-1937, Allyn G. Smith, 5 males, 4 females. Bad Water, H.P. Chandler, No. 8 Expo. 5-Apr-1946, 1 female. Bad Water, 6-April-1936, Van Dyke Collection, 1 female. Post Office Springs @ Ballarat, 25-April-1980, G. Challet, 2 females, Post Office Springs @ Ballarat, 30-April-1982, G. Challet, 1 male. Post Office Springs @ Ballarat, 30-April-1982, G. Challet, 2 females. Death Valley, 3-Apr-1942, H. Vander Aay, 1 female. Death Valley National Monument, alt -250 feet, 21 Mar-1967, H.B. Leech, 2 males, 2 females. Stream West of Harmony Borax Works, elevation -250 feet, 21-Mar-1967, H.B. Leech, 7 males, 2 females. SAN BERNARDINO Co: Saratoga Springs, 19-May-1972, G. Challet, 2 males, 2 females. Saratoga Springs, 19-May-1972, 1 male. KERN Co: 6 miles south of Shoshone, 3-June-1967, 1 male.

Deronectes coelamboides:

USA. NEVADA: Springdale, 18-Mar-1948, R. Coleman, 2 males. CALIFORNIA, INYO Co.: Saline Valley, 3-Apr-1960, Joe Selacek, saline pools adjacent to west side of lake, 19 males, 23 females. Tecopa, alkaline North Francis (or Grimshaw) Lake, 24-Mar-1964, 2 males, 1 female. North Grimshaw Lake, Stop 64-13, Tecopa, 24-Mar-1964, H.B. Leech, 1 female. SAN BERNARDINO Co: Cronese Valley, 3-Apr-1953, J.W. Mac Swain, 1 male. Death Valley National Monument, Saratoga Spring, 23-Mar-1967, H.B. Leech, 1 female. Mojave Water Camp, 30-Apr-1937, H.B. Leech, 6 males, 9 females. Afton, 25-Jun-1967, T. Danielson, 3 females. Mojave River, Afton, 17-Mar-1968, 3 females. NEW MEXICO: Grants, 21-Sept-1944, Elevation 5,000 SW, H.P. Chandler, 2 males, 1 female. New Mexico,

Th. 1 male. 97, Aug, A. Fenyes Collection, 1 male. Dexter, 10-Mar-1936, J.G. Needham, 4 males 1 female. ARIZONA: O.P.C. National Monument, 11-Apr-1953, A & H Dietrich, 7 males, 3 females.

Dissection Methods:

Dissection of specimens was accomplished by first pinning a specimen in a watch glass filled with hardened paraffin. A minuten pin was placed between the elytra just behind the pronotal disc to secure the specimen to the paraffin, then the elytra and flight wings were removed. The abdominal tergites were then removed by separating them from the rest of the abdomen by cutting the intersegmental membranes and pulling them off with forceps. These were also discarded, care being taken not to disturb the internal organs. The reproductive systems of some of the beetles were preserved in glycerine. Male genitalia were removed and mounted onto glass microscope slides. Some specimens were cleared in 10% KOH and mounted on glass microscope slides using permount. Reproductive systems were lightly stained after removal using chlorazol black E, a chitin stain, to prepare for drawing.

Analysis of data:

According to Daly (1985), "Morphometrics is the measurement and analysis of form." The forms involved can be of virtually anything, an object, a geographical feature, parts of the body, anything that can be

quantified. Morphometrics is a constantly changing discipline its practitioners range from ecologists to sociologists to health professionals. The only commonality is in the use of certain statistical functions that can be used for many purposes, such as describing patterns of relationship between multiple variables.

Insects are excellent subjects for morphometric analysis. Unlike softer organisms which can become deformed when preserved, the rigidity of the insect exoskeleton makes accurate measurement easy. Also, an insect's mode of life is reflected in the form of its exoskeleton (Daly 1985).

Morphometric analysis is a very useful tool when applied correctly. When researchers have difficulties in reaching conclusions about species' affinity based upon classical methods, statistical methods can help reveal patterns of affinity or discrimination that were previously difficult to see.

Because the analysis was to describe the measured variables of beetles, Principal Component Analysis (PCA) was used to describe the data describing the measurements of the beetles. PCA is a means of explaining variance-covariance of a system through a few linear combinations of values of the original data matrix (Johnson & Wichern 1992). The objectives of a PCA are data reduction and interpretation. Even though many components may be required to reproduce the total variability of a system, the system's variability can sometimes be reproduced by a smaller number of principle

components. In PCA, objects are defined as a series of "axes" which each represent a separately measured attribute (variable). Then, those axes which best describe the relationship between the individuals involved are chosen and the scores along those axes are tested for significant differences.

Discriminant analysis was considered for the initial analysis of the measurements taken, but this presupposed that the two groups were separate. In light of the question asked: "Do the individuals in the sample belong to one or two groups?", it was felt that PCA was the more appropriate choice for identifying proper variables and discriminant analysis for assigning groups to beetles of questionable affiliation, should differences prove significant.

RESULTS AND DISCUSSION

According to Pimentel (1993), measurements involved in multivariate analysis should include enough characters to summarize the system while excluding extraneous variables. If they can, then the principal components can be used to replace the original variables and the original data set is reduced to one comprised of the principal components.

The first step in the analysis of the dytiscid data was to construct a Pearson's correlation matrix using SYSTAT (version 5.03). The output is a matrix showing the correlations between the variables measured (see Table 1). Variables with multiple cross-correlations of greater than 0.70 (with

other variables) were removed. If more than one variable with an equal number of cross correlations was present, the variable with the lowest variance/mean was removed (the ones with larger variance/mean ratios are better discriminators). When all cross-correlates were removed, the remaining variables were those that were uncorrelated and would give a better PCA. The results of the PCA are shown in Table 2. The component loadings explain the influence that each of the 4 retained variables has on each of the principal components (greater value meaning greater contribution to the component). For the first principal component, all four of the retained variables (PW, PM, PL and BD) contribute significantly to the variance scores along the first principal component (the component giving the best overall explanation for the data, explaining 58.1% of the total variance). For the second principal component (the component giving the next best explanation of the data, explaining 17.8% of the total variance), PL is the most significant contributor, and the third component (explaining 12.4% of the total variance) is influenced most by the value of PM. The fourth principal component (explaining 11.7% of the total variance) shows an inverse relationship between PW and BD. Because each of the four principal components accounted for over 10% of the total variance explained, all were retained.

These four lines (principal components) describe most of the variation

in the data collected for the original data set. Because the object of the study was to determine if separation of species is warranted, a t-test was run on each of the four principal component scores to test for H_0 (that the variances are equal and that the sample came from one, single population).

Analysis of D. panaminti/D. coelamboides Data:

The results of the correlation matrix are shown in Table 1. After cross correlated variables were removed, PCA was run on the remaining 4 variables (PM, PL, PW, and BD). The results of the PCA are shown in Table 2. Because each of the principal components explained more than 10% of the total variance, all four were then tested by t-test for confirmation of H_0 . T-test showed that factors 1 and 3 rejected the H_0 ($p < 0.025$) indicating that the variance between the scores did not come from a single population (Table 3). So for factors 2 and 4, we cannot rule out that the data taken were from a single population.

Looking again at Table 2, it can be seen that factor 1, whose component loadings are all over 0.3, is indicative of whole body size. Factor 3 is mainly a measure of PM and BD. A t-test of the raw data scores shows that PM/BD is a good measure of species affiliation ($p = 0.001$). A plot of the relationship between factor 1 and factor 3 is shown in Figure 3. As shown, individual beetles with a large body size and a high value of PM/BD are indicative of D. coelamboides; those with a low body size and a low

PM/BD ratio are indicative of D. panaminti.

Next, because sex affiliations were known, a PCA was run grouped by sex. As shown in table 4, principal components 3 and 4 show a rejection of H_0 grouped by sex. Looking at the component loadings again, components 3 and 4 are influenced most strongly by PM/BD and PW/BD, respectively.

T-tests on ratios for the variables involved showed that we could not reject H_0 (see Table 5). So, while PCA can discriminate between D. panaminti and D. coelamboides, it cannot discriminate between sexes within those species involved.

Analysis of D. grammicus/D. titulus Data:

The results of the Pearson Correlation Matrix are shown in Table 6. Note that there are no cross correlates to be removed. Because no variables were removed, all 14 variables were used in the PCA analysis. The results of the PCA are shown in Table 7. Factor 1 accounts for 44.09% of the total variance in the system; factors 2 and 3 account for 9.51% and 8.53% of the total variance. T-tests run on all factors (see Table 8) showed rejection of H_0 ($p < .025$) only for factor 1 (the first principal component). As can be seen from the component loadings in Table 7 (the first three principal components), all loadings were positive and most contributed significantly (above 0.30) to the first principal component. This tells us that overall body size is important for the first principal component. Therefore, total body size

is the only significant discriminator (for the variables measured) for separation of D. grammicus/D. titulus. Without any diagnostic variables, I cannot give any further information to contribute to the diagnosis of the two beetles.

Internal Characters:

Specimens of D. grammicus and D. titulus are not common, so available specimens are rare. For this reason, no work on the internal anatomy of these beetles was performed. All subsequent discussion of internal anatomy will be confined to D. panaminti and D. coelamboides.

It was hoped that dissection of the internal reproductive organs of the beetles would give additional characters on which to base a species discrimination. However, the internal arrangement of male reproductive organs is very similar between D. panaminti and D. coelamboides. The diagram in Figure 4 can be applied to either D. panaminti or D. coelamboides. The structure is comprised of a bilobed spermatheca, with connections to the testes. This arrangement is common among hydroporines.

Attempts to observe reproductive behavior were unsuccessful. Specimens were maintained alive for up to two months in hopes of rearing larvae. Larvae have been collected by the author, but none has been successfully reared to adulthood. Pupal sites have also been elusive. Internal examinations of beetles kept alive and those preserved immediately

on-site showed that during the spring, ovarian development was insufficient to permit laying of eggs.

Observations/Additions to Distribution:

Zimmerman in his 1982 revision of the Deronectes of the Southwestern United States and Mexico, stated that the elytral markings of D. panaminti are "...quite weak, confined mostly to posterior half of elytra..." In specimens I have examined, the elytral vittae can be exceptionally weak. However, the same patterning can be observed on specimens of D. coelamboides. The best indication of species identification is the contrast in size between the two species, D. panaminti being 3.5-4.00mm in total length, and D. coelamboides being 4.1 to 4.8mm in length.

Also in his 1982 work, he stated that D. coelamboides had not yet been reported from Mexico. In the collection of the California Department of Food and Agriculture, there is a specimen (identified by Zimmerman) that comes from Baja California, Norte. Speaking with the collector, he informed me that the area is similar to that of the site of previous finds because it is a highly saline environment.

Field observations of D. panaminti and D. coelamboides show similar habitat preferences. I have collected these beetles in areas with a high concentration of borate salts (corroborated by habitat tags on many museum

specimens). At both the Zzyzx Springs research station and Bad Water (Death Valley), the beetles preferred shallow banks with dense vegetative material. They did not occur in more open areas. At Salt Creek (Death Valley National Monument), where there was running water, the beetles preferred the shallow areas of the creek, often swimming along the edge, among the debris. Beetles also occurred in greater numbers under rocks in the stream compared to the open water. Larvae were observed swimming in areas relatively free of vegetation in the ponds at Bad Water, moving between and over salt formations searching for food items. Pupae were not found in the springtime at Death Valley. It is possible that larvae may pupate under the salt formations that serve as a shoreline at the pools which occur at Bad Water.

The analysis of measured variables, when coupled with distribution records, retains the dichotomy for D. coelamboides/panaminti (Fall). The same variables applied to the analysis of D. grammicus Sharp /D. titulus Leech were not adequate to give any further information upon which to base an opinion.

Appendix:

Original Species Descriptions:

Source: Fall, 1923

"111. *H. coelamboides* new species.

Rather elongate, oblong oval, moderately convex; testaceous, head and thorax somewhat rufescent, immaculate; elytra with numerous narrow blackish vittae, which are interrupted at sides and show a tendency to coalesce here and there on the disk. Body beneath black; antennae and legs rufotestaceous, the former with the outer joints infusate. Integuments finely alutaceous, feebly shining above opaque beneath, the elytra with a few fine, scattered hairs, detectable on close examination. Punctuation fine, dense, uniform in distribution; prothorax with a series of coarser punctures along the front margin, and a few similar ones near the base; elytra with the usual series of coarser punctures, which are however quite inconspicuous; body beneath excessively densely punctate and feebly wrinkled. The prothorax is much narrower than the elytra at base, the outline strongly discontinuous, sides subparallel posteriorly, the hind angles obtuse and almost rounded. Middle coxae narrowly separated, prosternal process narrow, strongly declivous (ascending) in front.

Length, 4.15 to 4.6 mm.; *width*, 2 to 2.25 mm.

Described from two examples taken at Albuquerque, New Mexico, Dec. 3, 1901; type in my collection. I am unable to determine the sex with certainty. The middle tarsi are narrow, the front tarsi distinctly broader, joints 1-3 of nearly equal width; claws simple, slender, equal.

112. *H. panaminti* new species

Elongate oval, moderately convex, testaceous; head and thorax immaculate, elytra with numerous narrow more or less coalescent fuscous vittae. Antennae and legs testaceous, the former scarcely infusate apically; body beneath brownish (probably immature). Integuments finely alutaceous, above closely finely punctate, feebly shining, pubescence virtually wanting; beneath very finely and densely punctate, the abdomen at middle less densely so and somewhat shining. Coarser punctures of prothorax and elytra, as in the preceding species, quite inconspicuous.

Length, 3.4mm.; *width*, 1.65 mm.

This species is represented in my collection by a single example taken by Koebele in the Panamint Valley, California. The specimen is doubtless a male, for although the middle tarsi are quite narrow and the front tarsi only

moderately dilated, with slender simple claws, the middle tibiae are sinuate on their inner margin and strongly thickened apically, and the middle femora are subangulate on their lower edge. *Panaminti*, though smaller, is very similar in most features to *coelamboides*, but is not quite so densely punctate above, while the abdominal punctures are distinctly spaced medio-basally and the surface moderately shining. The tarsi in my two specimens of *coelamboides* are almost precisely the same as in the present species, which in view of other similarities would seem to indicate that they too are males. If this surmise be correct, the sexual modifications of the middle femora and tibiae in *panaminti* will serve as distinguishable traits."

Deronectes grammicus was first described by Sharp in 1887. The original description reads:

"2(A). *Deronectes grammicus* (p.27)

Suboblongus, opacus, ferrigineus, supro nigro-testaceo variegato, elytris lineis elongatis ornatis; dense minuteque punctatus; elytris stria suturali posterius abbreviata striaque juxta hanc magis profunda et elongata; antennis pedibusque testaceis, illis extrorsum tibiisque fuscis, tarsis piceis. Long. 5 1/2, lat. 3 millim.

Hab. MEXICO, near the city (Hoge). One example.

This remarkable *Deronectes* is of more elongate form than any of the others of our region, and is readily distinguished by the numerous elongate lines of colour on the elytra. The antennae are elongate; the head is yellow, with the margins of the eyes black; the thorax is yellow, black on the front margin, and with a large double black mark at the base; the elytra bear alternate lines of black and yellow colour, and are spotted with yellow at the sides. The hind coxal cavities are very distinctly separated."

The original description of *Deronectes titulus* is as follows (Leech, 1945):

"A large, elongate, dull vittate species allied to and resembling *D. grammicus* Sharp; neither of these fit any of the choices in Fall's key (1923:99) though belonging in the *eximus-corvinus* section on the basis of their rather broadly separated mesocoxae. *D. grammicus* and *titulus* are separable from all species recorded from North America north of Mexico by the densely punctate metatibiae.

Male: Length 5.7mm., width 2.7 mm. Form oblong, subparallel, widest just behind middle of elytra. *Head* and *pronotum* reddish-yellow; head black at base and adjacent to eyes; pronotum black in anterior quarter adjacent to head, narrowly along base, with a broad extension on each side

of median line from base to middle. *Elytra* yellow, each elytron with the suture and 6 vittae black. Sutural black strip enlarged at base and apex; vitta 1 beginning near scutellar enlargement of sutural and vaguely joining its apical broadening; 2nd vitta beginning about on a level with 1st, coalesced ante- and postmedially with 3rd, which extends to base of elytron and is joined postmedially and preapically to 4th; 4th not reaching base; 5th enlarged laterally at elytral base, with large post-humeral and median lateral extensions passing the vague 6th and reaching more than half way to lateral margin. *Undersurface* rufous to piceous, antennae and palpi reddish-yellow.

Head finely evenly punctate, surface between punctures minutely reticulated. Punctuation of *pronotum* coarser and less evenly spaced than that of head, partially masked or obliterated by rugae at base and sides of pronotum, and slightly so adjacent to anterior series of coarse punctures; lateral marginal bead very narrow. *Elytral* punctuation finer than that of pronotum, deeper than that of head; there is a poorly defined stria along the outer margin of vitta 1, another along the inner margin of vitta 3, and along the inner margin of vitta 5, the intervening area being vaguely depressed. Elytra with a few fine, depressed hairs. *Undersurface* shagreened, dull except along parts of median line, metacoxal plates and sides of first few abdominal sternites rugose. *Prosternal* process elongate, parallel-sided, blunt apically, margined laterally, depressed on each side of fine median longitudinal carina which ends anteriorly in an intercoxal prominence. Metacoxal lines diverging anteriorly, enclosed area densely punctate; metatibia densely punctate on outer face except at tip. Metacoxal processes slightly incised at median line, each with a small round tumidity at middle of posterior margin; metacoxal cavities separated by an exposed partition. Apparently 6th abdominal sternite (profile) scooplike, with an angle of nearly 45(degree mark) between anterior margin and apex. *Aedeagus* shallowly, broadly caniculate just before apex on dorsal side (fig.3); parameres stout, strongly chitinized.

Female: Very like the male. Each elytron showing a short diagonal scutellar stria, and having striae 1 and 2 punctate nearly to base; stria 3 and 4 show punctures apically, and there are traces of a premarginal stria. The mesolegs of the allotype have been removed to show that the mesosternal ridge and the tip of the metasternum do not touch."

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PEARSON CORRELATION MATRIX

	TL	TW	PEL	PW	HW
TL	1.000				
TW	0.874	1.000			
PEL	0.931	0.819	1.000		
PW	0.689	0.639	0.620	1.000	
HW	0.837	0.780	0.804	0.682	1.000
PL	0.479	0.374	0.422	0.334	0.355
PM	0.617	0.528	0.506	0.509	0.624
PFL	0.908	0.806	0.841	0.656	0.840
PTL	0.805	0.685	0.746	0.612	0.726
MFL	0.931	0.842	0.869	0.690	0.807
MTL	0.871	0.752	0.802	0.658	0.756
HFL	0.912	0.793	0.848	0.623	0.813
HTL	0.914	0.806	0.863	0.663	0.813
BD	0.810	0.734	0.747	0.531	0.664

	PL	PM	PFL	PTL	MFL
PL	1.000				
PM	0.400	1.000			
PFL	0.395	0.626	1.000		
PTL	0.360	0.534	0.838	1.000	
MFL	0.403	0.607	0.924	0.817	1.000
MTL	0.406	0.590	0.862	0.835	0.891
HFL	0.377	0.553	0.884	0.744	0.898
HTL	0.376	0.578	0.889	0.774	0.900
BD	0.354	0.501	0.744	0.641	0.781

	MTL	HFL	HTL	BD
MTL	1.000			
HFL	0.838	1.000		
HTL	0.835	0.899	1.000	
BD	0.696	0.748	0.740	1.000

NUMBER OF OBSERVATIONS: 173

Table 1. Results of Pearson Correlation Matrix for D. panaminti/D. coelamboides.

Component Loadings for PCA

	1	2	3	4
PW	0.791	0.311	0.100	0.518
PL	0.654	-.743	0.124	0.069
PM	0.801	0.056	0.573	-.163
BD	0.794	0.246	0.377	-.408

Percent of Total Variance Explained

1	2	3	4
58.139	17.828	12.376	11.656

Table 2. Results of Principal Component Analysis on Measures PW, PL, PM, BD.

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(1) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DP	84	-0.703	0.722
DC	89	0.664	0.738

POOLED VARIANCES T = -12.301 DF= 171 PROB = 0.000

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(2) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DP	84	-0.072	1.350
DC	89	0.068	0.476

POOLED VARIANCES T = 0.916 DF= 171 PROB = .361

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(3) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DP	84	-0.222	0.871
DC	89	0.210	1.071

POOLED VARIANCES T = -2.900 DF = 171 PROB = 0.004

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(4) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DP	84	0.124	1.180
DC	89	-0.117	0.783

POOLED VARIANCES T = 1.593 DF = 171 PROB = 0.113

TABLE 3. Results of t-test on principal components grouped by species. Note factors 1 and 3, $p < .025$.

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(1) GROUPED BY SEX

GROUP	N	MEAN	SD
F	82	-0.067	1.049
M	91	0.060	0.955

POOLED VARIANCES T = -0.834 DF= 171 PROB = 0.405

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(2) GROUPED BY SEX

GROUP	N	MEAN	SD
F	82	-0.0108	1.371
M	91	0.097	0.447

POOLED VARIANCES T = -1.352 DF=171 PROB = 0.178

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(3) GROUPED BY SEX

GROUP	N	MEAN	SD
F	82	0.254	1.127
M	91	-0.229	0.810

POOLED VARIANCES T = -1.352 DF = 171 PROB = 0.001

INDEPENDENT SAMPLES OF T-TEST ON FACTOR(4) GROUPED BY SEX

GROUP	N	MEAN	SD
F	82	-0.183	1.320
M	91	0.165	0.534

POOLED VARIANCES T = -2.319 DF = 171 PROB = 0.022

Table 4. Results of t-test on principal components grouped by sex. Note factors 3 and 4 ($p < .025$).

INDEPENDENT SAMPLES T-TEST ON PM/BD GROUPED BY SEX

GROUP	N	MEAN	SD
M	91	0.387	0.032
F	82	0.370	0.063

POOLED VARIANCES T = 2.063 DF = 171 PROB = 0.029

INDEPENDENT SAMPLES T-TEST ON PW/BD GROUPED BY SEX

GROUP	N	MEAN	SD
M	91	1.276	0.078
F	82	1.223	0.232

POOLED VARIANCES T = 2.063 DF = 171 PROB = 0.041

Table 5. Results of t-test on ratio of significant variables for factor 3 and 4.

PEARSON CORRELATION MATRIX

	TL	TW	PEL	PW	HW
TL	1.000				
TW	0.688	1.000			
PEL	0.781	0.479	1.000		
PW	0.627	0.605	0.470	1.000	
HW	0.633	0.501	0.490	0.730	1.000
PL	0.201	0.175	0.174	0.067	0.114
PM	0.370	0.278	0.284	0.551	0.369
PFL	0.445	0.380	0.475	0.188	0.297
PTL	0.326	0.362	0.326	0.399	0.423
MFL	0.580	0.511	0.554	0.500	0.460
MTL	0.214	0.372	0.271	0.354	0.062
HFL	0.599	0.394	0.505	0.581	0.494
HTL	0.621	0.514	0.632	0.498	0.433
BHT	0.631	0.441	0.575	0.472	0.353

	PL	PM	PFL	PTL	MFL
PL	1.000				
PM	-0.104	1.000			
PFL	-0.241	0.296	1.000		
PTL	0.087	0.185	0.194	1.000	
MFL	0.049	0.115	0.527	0.366	1.000
MTL	-0.011	0.227	0.052	0.253	0.204
HFL	0.180	0.370	0.232	0.207	0.517
HTL	0.169	0.198	0.348	0.180	0.554
BHT	0.182	0.455	0.248	0.240	0.261

	MTL	HFL	HTL	BHT
MTL	1.000			
HFL	0.269	1.000		
HTL	0.427	0.598	1.000	
BHT	0.351	0.553	0.569	1.000

NUMBER OF OBSERVATIONS: 60

Table 6. Results of Pearson Correlation Matrix for D. grammicus/D. titulus.

COMPONENT LOADINGS

	1	2	3
TL	0.879	0.028	0.159
TW	0.748	0.026	0.057
PEL	0.793	-0.003	0.232
PW	0.796	0.026	-0.299
HW	0.725	-0.063	0.019
PL	0.167	0.805	0.313
PM	0.503	-0.216	-0.646
PFL	0.506	-0.665	0.267
PTL	0.477	-0.053	-0.027
MFL	0.704	-0.224	0.413
MTL	0.421	0.178	-0.432
HFL	0.734	0.173	-0.048
HTL	0.762	0.152	0.136
BD	0.704	0.226	-0.238

PERCENT OF TOTAL VARIANCE EXPLAINED

44.098	9.513	8.532
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Table 7. Results of Principal Component Analysis for D. grammicus/D. panaminti.

INDEPENDENT SAMPLES T-TEST ON FACTOR(1) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DG	18	-0.467	1.223
DT	42	0.200	0.826

POOLED VARIANCES T = -2.470 DF = 58 PROB = 0.016

INDEPENDENT SAMPLES T-TEST ON FACTOR(2) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DG	18	-0.053	0.635
DT	42	0.023	1.127

POOLED VARIANCES T = -0.268 DF = 58 PROB = 0.789

INDEPENDENT SAMPLES T-TEST ON FACTOR(3) GROUPED BY SPECIES

GROUP	N	MEAN	SD
DG	18	-0.295	1.099
DT	42	0.127	0.940

POOLED VARIANCES T = -1.514 DF = 58 PROB = 0.135

Table 8. Results of t-test on principal components. Note only factor 1 rejects H_0 .

Fig. 1

Fig. 2

Fig. 3

Fig. 4