

## A SYNOPSIS OF THE GENUS *PHALERIA* IN THE UNITED STATES AND BAJA CALIFORNIA (COLEOPTERA: TENEBRIONIDAE)

CHARLES A. TRIPLEHORN AND LARRY E. WATROUS

Department of Entomology, The Ohio State University,  
Columbus, OH 43210

### ABSTRACT

Eight species of *Phaleria* inhabit coastal areas of the United States and Baja California. Four of these, *P. rotundata* LeConte (= *P. limbata* Horn), *P. debilis* LeConte (= *P. insularis* Champion), *P. pilifera* LeConte, and *P. lata* Blaisdell, occur on the Pacific Coast; the other four, *P. testacea* Say (= *P. longula* LeConte), *P. picipes* Say, *P. gracilipes* Casey (= *P. lodingi* Blaisdell), and *P. punctipes* LeConte, occupy the Atlantic Coast. Keys to adults, diagnoses, and distribution maps are presented. Ecology and evolutionary relationships are discussed.

### INTRODUCTION

Members of the genus *Phaleria* are found on ocean beaches in many parts of the world. More than 60 species have been described, and catalogs indicate that they occur on all continents except Australia and the polar regions. They are essentially tropical with a few species extending into temperate areas. Based on the surprisingly wide distribution and variation in color and size of several North American species, we suspect considerable synonymy exists.

Our interests in the genus *Phaleria* include the world fauna. However, most of the specimens available to us have been from North America, and we feel that we understand the fauna of the continental United States and Baja California sufficiently well to present preliminary findings at this time. We anticipate that our studies will continue and that a treatment of the evolutionary history and interesting zoogeographical problems in the genus will eventually be possible.

**Generic diagnosis:** Members of the genus *Phaleria* are small, oval beetles with the head inserted into prothorax as far as the eyes. The epistomal margin is rounded or truncate. The antennae are moderately long, stout, and rarely extend caudad beyond the middle of the pronotum. The eyes are large, transverse, and broadly emarginate anteriorly. The mesosternal groove into which the prosternal process fits is deep and acutely V-shaped. All three pairs of legs are stout, and the tibiae are coarsely and densely spinose, apically expanded (especially the anterior pair which are strongly flattened and fossorial), and have prominent apical spurs. The pronotum has a distinct fovea on each side near the base.

Ten genera belong to the Phaleriini in the World fauna. Three (*Phalerida* Kulzer, *Phaleromela* Reitter, and *Phaleria* Latreille) occur in the Western Hemisphere, and only the latter two have representatives in the Nearctic Region.

New World species of *Phaleromela* include the following (fide Triple-



horn 1961): *P. globosa* (LeConte), *P. picta* (Mannerheim), *P. humeralis* (Laporte), *P. prohumeralis* Triplehorn (= *humeralis* Horn), and *P. variegata* Triplehorn (= *Scaphidema picta* Horn). All except the last species were originally described in *Phaleria*; *P. variegata* was transferred from the *Dia-perini*.

The species of *Phaleromela* differ from those of *Phaleria* in having smaller, rounded eyes with entire anterior margins, less strongly excavate mesosternum, less strongly dilated anterior tibiae, and longer antennae which extend caudad beyond the pronotal base.

Species of *Phaleria* occur on ocean beaches, sometimes in enormous numbers. At least during the day, they hide beneath organic debris deposited at or near the high tide line. When exposed, they burrow rapidly out of sight, and the collector must be prepared to quickly intercept them with a knife blade, trowel, or the hands. Screening the sand under dead objects on the beach should prove successful.

#### MORPHOLOGY

Previous workers used a number of somewhat misleading and ambiguous characters in separating species of *Phaleria*. Ventral characters were almost entirely ignored, probably as a result of the practice of gluing specimens to small cards, thus obscuring the entire ventral surface. We have found some of the most useful and obvious characters to be ventral and have investigated the male genitalia for the first time. The following remarks apply primarily to the 8 species occurring in the United States and Baja California, but, where pertinent, we have discussed extralimital species in anticipation of future work.

**Coloration:** There is not a single species of *Phaleria* we have studied in which coloration is constant. *P. punctipes*, *P. lata*, *P. rotundata*, *P. pilifera*, *P. picipes*, and *P. gracilipes* are usually unpatterned but vary from light testaceous to black. Even in these 6 species, there are exceptions, usually involving individuals with lateral portions of the pronotum and elytra (especially the latter) somewhat lighter than discal portions. Typically, *P. debilis* is yellowish with a discal spot on each elytron, but the spots often are joined at the suture and sometimes are completely absent. *P. testacea* is the most variable of all (see discussion of that species). This, combined with an unusual size variation and wide distribution, is responsible for some of the synonymy we feel certain exists, especially in the West Indies. *P. picipes* is extremely variable in the West Indies but rather constant in continental United States. In our key we have minimized the use of coloration, and we caution future workers against its unreliability.

**Size:** Usually individuals of a single population are fairly uniform in size, but size frequently varies from population to population. Species can be characterized as large (e.g. *P. lata*), medium (e.g. *P. punctipes*), or small (e.g. *P. gracilipes* and *P. debilis*), but enough exceptions have been found that we are hesitant to use size in our key.

**Luster:** All of our species of *Phaleria* have a pattern of cuticular microsculpture which influences the surface luster. *P. pilifera* and *P. rotundata* are always dull in luster, whereas *P. testaceus* is always shiny. We are unable to resolve the problem of how to express degree of shininess or dullness so we have omitted it altogether in our treatment of the genus.



**Eyes:** The size of the eyes is quite constant intraspecifically, yet quite variable interspecifically. This is best expressed as the distance separating the eyes ventrally as compared to the ventral diameter of one eye and how close the eyes approach the submentum. In our species, the eyes are most widely separated in *P. punctipes*, *P. lata*, and *P. rotundata*; they are closest in *P. gracilipes* and *P. debilis*. The other three species are intermediate in regard to this character. This is one of the most useful characters we have found, yet it has never been mentioned by previous workers.

**Thorax:** The shape of the pronotum is interspecifically somewhat variable, but only in *P. lata* have we used it in the key and diagnoses. The base of the pronotum is usually finely but distinctly grooved; in *P. debilis* and *P. gracilipes* the fine basal marginal groove is absent.

In most species of *Phaleria*, the hypomera are glabrous, but in *P. lata*, *P. rotundata*, and *P. pilifera* the hypomera are distinctly setose. All of the Pacific Coast species have a small patch or tuft of long golden setae (usually erect and conspicuous) on the anterior margin of the prosternum (true also of *P. guatemalensis* Champion and *P. dytiscoides* Champion, both from the Pacific Coast of Central America). In the Atlantic Coast species, the prosternum is more or less glabrous (a few short setae at the apex of the prosternal process are sometimes present) except in *P. punctipes* which has scattered setae all along the prosternum from the anterior margin to the apex of the prosternal process. *P. punctipes* is unique in having the prosternal process deflexed between the procoxae; in all other North American species, the process is horizontal and acute apically.

**Elytra:** There are useful taxonomic characters in the elytral interneurs and their intervals, but we have not utilized them in our key. Interneurs of the Neotropical *P. guatemalensis* are composed of large, well separated punctures not set in grooves. At the opposite extreme is *P. neotropicalis* (also Neotropical) in which the interneurs are scarcely traceable against the cuticular microsculpture. None of the species under consideration in this paper approach the situation in *P. guatemalensis*, but both *P. debilis* and *P. gracilipes* have lightly incised, finely punctured interneurs closely approximating those of *P. neotropicalis*.

Marginal setae on the elytra actually arise on the epipleura. They are long, dense, and very conspicuous in dorsal view in *P. rotundata* and *P. pilifera*; short, dense, and not conspicuous in *P. lata*, *P. debilis*, and *P. punctipes*; and absent in the other three species.

**Wings:** Several species, *P. lata*, *P. punctipes*, and *P. rotundata*, have the hind wings reduced. So far, wing length polymorphism within a single species has not been observed. It is interesting that there is a strong correlation between hind wing length, eye size, and overall body form. The 3 species mentioned above also have the smallest eyes, and the most robust bodies.

**Male genitalia:** The male genitalia of all the *Phaleria* we have studied are characterized by a strongly asymmetric basal piece, entirely fused parameres with short and separate anterior processes, and penis rods with the anterior ends free. The most useful interspecific variation occurs in the shape of the fused parameres, the relative lengths of the basal piece to the parameres, and the form of the penis rods. Study of the male genitalia, while not necessary for species identification, has been very helpful in unraveling problems associated with wide variations in color and size. For the



most part, the genitalia appear to be very constant throughout the range of each species. A possible exception to this occurs in *P. gracilipes* (see discussion under that species).

**Sexual dimorphism:** Sexual dimorphism is evident to a remarkable degree in *P. debilis* and *P. guatemalensis*. In the males of both, the basal three tarsomeres of the protarsus are expanded and the basal abdominal sternum has a conspicuous patch of short, dense setae; *P. debilis* has a similar patch on the second abdominal sternum as well. The males of *P. picipes* and *P. gracilipes* have the three tarsomeres of the protarsus expanded but lack patches of setae on abdominal sterna. We are unable to distinguish between the sexes of the other five species from external morphological characters.

**Immature stages:** Except for *P. rotundata*, the immature stages of North American *Phaleria* are undescribed. Moore described the larva (1974: 99) and pupa (1976:173) of *P. rotundata*.

#### EVOLUTIONARY CONSIDERATIONS

Since only a few of the known species of *Phaleria* have been studied, it would be presumptuous to present a detailed phylogeny at this time. However, a few comments on possible evolutionary relationships among the species under consideration are in order. The characters we have found to be significant and useful in our investigations are summarized in Table 1.

*P. punctipes* is by far the most distantly related species, and is the sole North American representative of a distinct lineage, the origin of which is not yet clear. It has several derived character states, the deflexed prosternal process, scattered setae on the prosternum, and broad, elongate, fused parameres of the aedeagus, which are not shared by any other members studied.

The Pacific Coast species, *P. debilis*, *P. pilifera*, *P. rotundata*, and *P. lata*, all have a tuft of setae on the anterior margin of the prosternum, a probable derived character. They are apparently representatives of a lineage quite distinct from the Atlantic Coast species. Possible evolutionary relationships among these species are shown in fig. 40. *P. pilifera* and *P. rotundata*, based on the long and dense setae of the elytral epipleura, are the most closely related. The presence of hypomeral setae groups *P. lata* with *P. pilifera* and *P. rotundata*. The latter relationships are further supported by the close similarity of the male genitalia among these species.

The other species, the Atlantic Coast *P. testacea*, *P. picipes*, and *P. gracilipes*, apparently do not share any derived characters, and may represent elements from disparate lineages. However, the narrowly separated eyes and expanded male protarsi of *P. picipes* and *P. gracilipes* indicate that these may be more closely related to each other than either is to *P. testacea*.

Given the above scenario, several convergences are evident. The most conspicuous are the enlarged eyes, occurring in *P. picipes* and *P. gracilipes* of the Atlantic Coast and in *P. pilifera* and *P. debilis* of the Pacific Coast, and the reduced metathoracic wings of *P. punctipes*, *P. rotundata*, and *P. lata*. As mentioned earlier, these characters along with overall body proportions appear to be highly correlated. These data suggest that there



are at least 2 major divisions available to seashore dwellers. These divisions may be types of behavior, such as methods of dispersal, or they may be types of habitat. Members of several separate lineages have met the requirements of the divisions independently. This is a topic that certainly warrants further study from a behavioral-ecological approach.

#### ACKNOWLEDGMENTS

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- AMNH American Museum of Natural History, New York: Lee H. Herman, Jr.  
 BMNH British Museum (Natural History), London: C. M. F. Von Hayek and M. J. D. Brendell.  
 CNCI Canadian National Collection, Ottawa: E. C. Becker.  
 FMNH Field Museum of Natural History, Chicago: H. S. Dybas.  
 FSCA Florida State Collection of Arthropods, Gainesville: R. E. Woodruff and H. V. Weems, Jr.  
 LACM Los Angeles County Museum, Los Angeles: F. S. Truxal and R. R. Snelling.  
 MCZC Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts: J. F. Lawrence and A. F. Newton, Jr.  
 MSUC Michigan State University, East Lansing: R. L. Fischer.  
 OSUC Ohio State University, Columbus: C. A. Triplehorn  
 UCDC University of California, Davis: R. O. Schuster.  
 UGCA University of Georgia, Athens: W. T. Atyeo.  
 UICM University of Idaho, Moscow: W. F. Barr.  
 USNM United States National Museum, Washington, D.C.: T. J. Spilman.

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#### KEY TO UNITED STATES AND BAJA CALIFORNIA SPECIES OF *Phaleria*

1. Prosternal process deflexed behind coxae, apex obtuse (fig. 1); prosternum with conspicuous setae scattered from anterior margin to base of prosternal process ..... *P. punctipes* LeConte
- 1'. Prosternal process horizontal, apex acute and prominent (fig. 2); prosternal setae inconspicuous or confined to patch or tuft along anterior margin ..... 2
- 2(1'). Prosternum with conspicuous patch or tuft of several to many golden setae at middle of anterior margin (figs. 7-8); epipleural setae projecting laterally and visible from above; Pacific Coast species ..... 3



	1	2	3	4	5	6	7	8	9
<b>debilis</b>	<b>d</b>	<b>a</b>	<b>b</b>	<b>c</b>	<b>a</b>	<b>c</b>	<b>a</b>	<b>b</b>	<b>a</b>
<b>gracilipes</b>	<b>d</b>	<b>a</b>	<b>b</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>b</b>	<b>a</b>
<b>lata</b>	<b>b</b>	<b>a</b>	<b>a</b>	<b>c</b>	<b>b</b>	<b>c</b>	<b>b</b>	<b>a</b>	<b>a</b>
<b>picipes</b>	<b>c</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>b</b>	<b>a</b>
<b>pilifera</b>	<b>c</b>	<b>a</b>	<b>a</b>	<b>d</b>	<b>b</b>	<b>c</b>	<b>a</b>	<b>a</b>	<b>a</b>
<b>punctipes</b>	<b>a</b>	<b>b</b>	<b>a</b>	<b>b</b>	<b>a</b>	<b>b</b>	<b>b</b>	<b>a</b>	<b>a</b>
<b>rotundata</b>	<b>b</b>	<b>a</b>	<b>a</b>	<b>d</b>	<b>b</b>	<b>c</b>	<b>b</b>	<b>a</b>	<b>a</b>
<b>testacea</b>	<b>b</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>a</b>	<b>b</b>

CHARACTER	CHARACTER STATE	
	Primitive	Derived
1. Ventral eye separation:	a, wide, much wider than ventral diameter of one eye;	b, moderate, about equal to or slightly wider than ventral diameter of one eye; c, narrow, less than ventral diameter of one eye, but eye margins distinctly separate from submentum; d, very narrow, eye margins in contact with submentum.
2. Prosternal process:	a, horizontal;	b, deflexed.
3. Pronotal base:	a, with marginal groove;	b, marginal groove absent.
4. Epipleural setae of elytra:	a, absent;	b, short, sparse on apical half; c, short and dense; d, long and dense.
5. Hypomer al setae:	a, absent;	b, present.
6. Prosternal setae:	a, absent;	b, scattered throughout surface; c, forming an anterior tuft.
7. Metathoracic wings:	a, fully developed;	b, reduced.
8. Male protarsi:	a, normal;	b, expanded.
9. Posterior margin of pygidium:	a, broadly rounded;	b, notched.

Table 1. Character state distribution and hypothesized character state polarity for *Phaleria* spp.



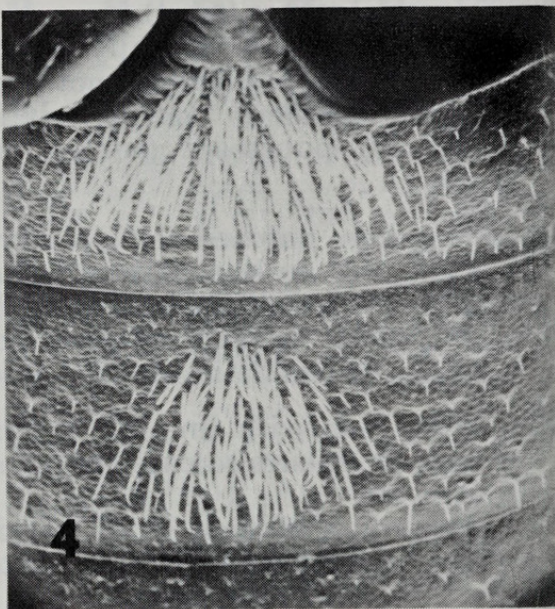
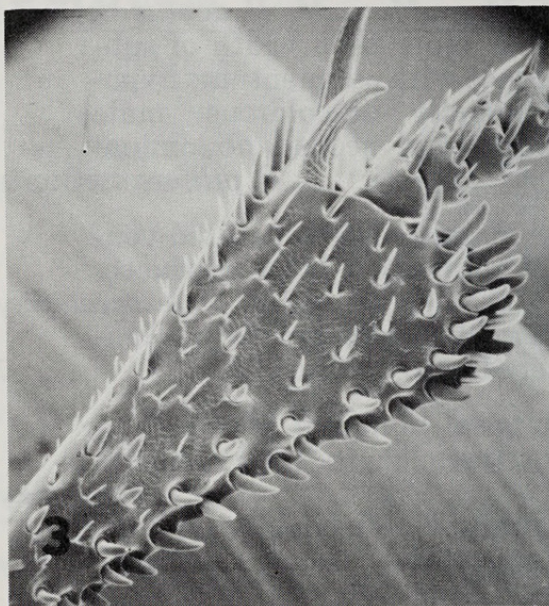
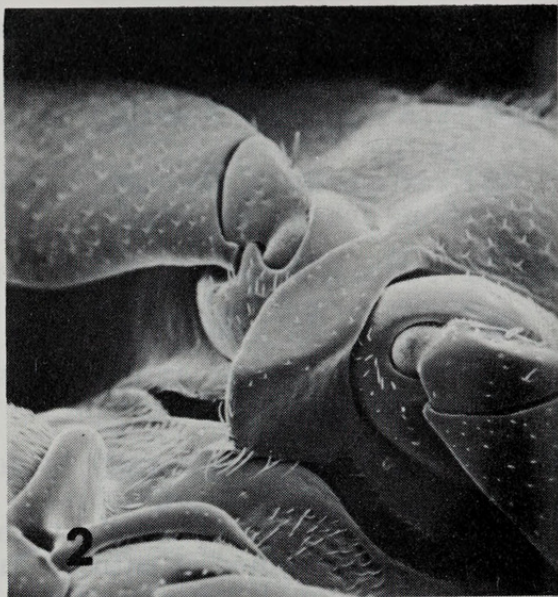
- 2'. Prosternal and epipleural setae inconspicuous; Atlantic Coast species..... 6
- 3(2). Eyes separated ventrally by at least ventral diameter of one eye (fig. 7) ..... 4
- 3'. Eyes separated ventrally by much less than ventral diameter of one eye (fig. 8) ..... 5
- 4(3). Pronotum widest at about middle, narrower at base; basal angles strongly obtuse; length usually greater than 7 mm..... *P. lata* Blaisdell
- 4'. Pronotum widest at base; basal angles right or slightly obtuse; length less than 7 mm ..... *P. rotundata* LeConte
- 5(3'). Eyes separated ventrally by less than width of submentum, inner margins in contact with submentum (fig. 8); hypomera glabrous; elytron usually with black spot on disc (maculae sometimes joined at suture), rarely with more extensive black markings; male with pubescent patches on first and second abdominal sterna (fig. 4)..... *P. debilis* LeConte
- 5'. Eyes separated ventrally by slightly more than width of submentum; inner margins not in contact with submentum; hypomera distinctly setose; elytra usually unicolorous; male without pubescent patches on first and second abdominal sterna ..... *P. pilifera* LeConte
- 6(2'). Pygidium notched along posterior margin; eyes separated ventrally by at least ventral diameter of one eye or distinctly separate from submentum (fig. 5) ..... *P. testacea* Say
- 6'. Pygidium broadly rounded posteriorly; eyes separated ventrally by less than ventral diameter of one eye (fig. 6) ..... 7
- 7(6'). Pronotum with fine but distinct basal marginal groove; elytral interneurs sulcate throughout their length, intervals subconvex ..... *P. picipes* Say
- 7'. Pronotum without basal marginal groove; interneurs not sulcate and intervals flat in basal third ..... *P. gracilipes* Casey

*Phaleria punctipes* LeConte  
(figs. 1, 14, 15, 29, 39)

*Phaleria punctipes* LeConte, 1878:421. Types: Haulover, Florida; in LeConte Collection (MCZC); not examined.

This is the only species of *Phaleria* in the United States in which the prosternal process is deflexed behind the procoxae and the only Atlantic Coast species with conspicuous setae on the prosternum and reduced metathoracic wings. Body proportions are similar to the Pacific Coast *P. rotundata* (stout and strongly convex). Coloration is almost always uniform and ranges from light reddish brown to almost black; sometimes the elytra are reddish and the head and pronotum blackish. The eyes are unusually small, being widely separated both dorsally and ventrally. The interneurs are distinctly sulcate from base to apex of the elytra; the intervals are subconvex and exceedingly minutely punctate. In the series from Jamaica epipleural setae are visible from above, but in all others examined the epipleural setae are minute.





Figs. 1-4, *Phaleria* spp.: 1, *P. punctipes*, prothorax, ventral; 2, *P. testacea*, prothorax, lateroventral; 3, *P. testacea*, front tibia; 4, *P. debilis*, abdominal sterna, male.

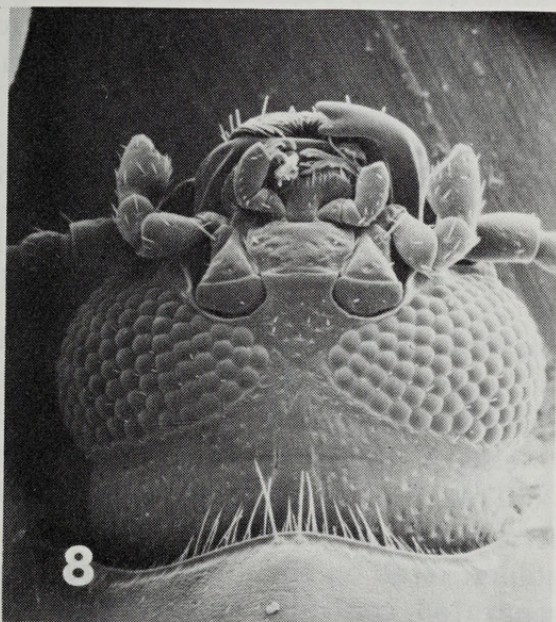
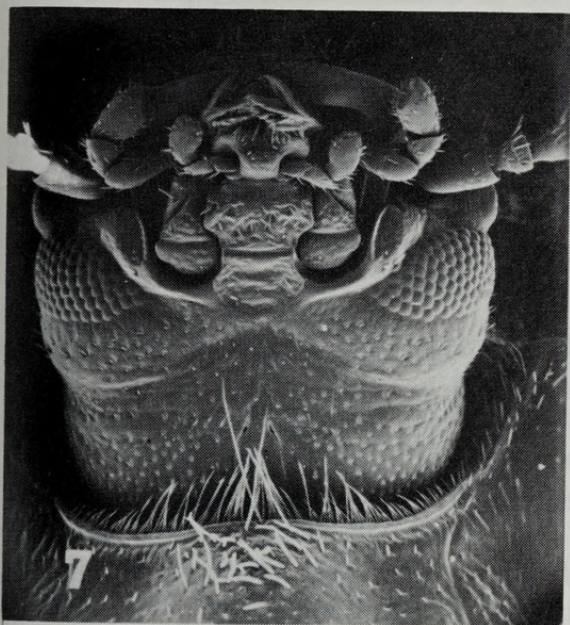
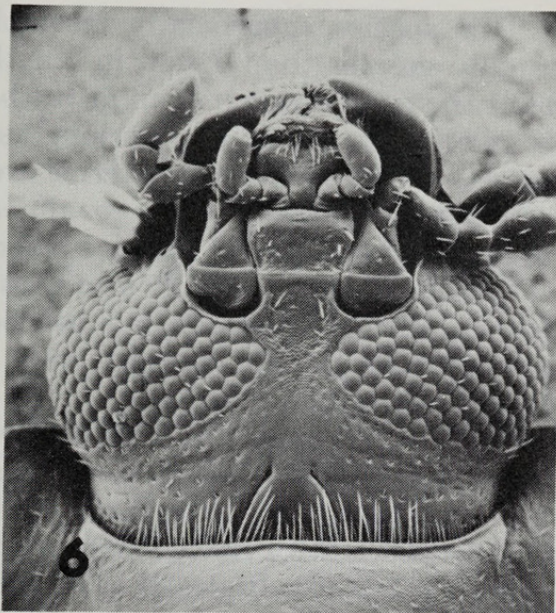
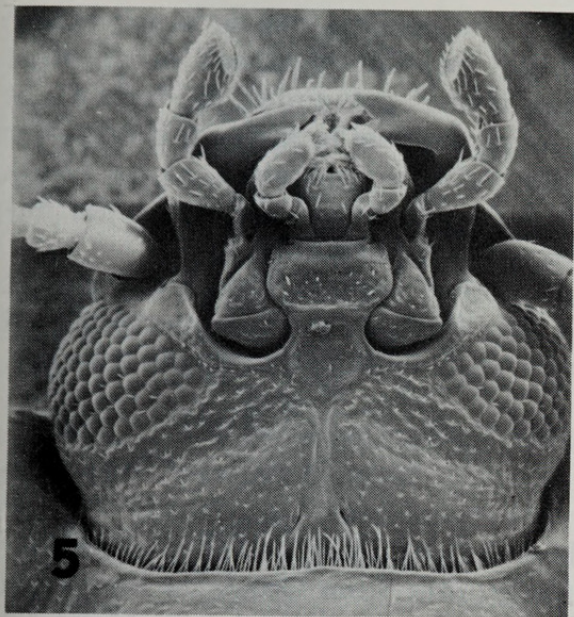
The male genitalia of *P. punctipes* (figs. 14, 15) are among the most distinctive in the genus. The fused parameres are elongate and broad, with a slight constriction at the middle, and the rounded apex is marked by a triangular, translucent area. The penis has a unique internal sclerotized rod and the penis rods are short and swollen at their anterior ends. (Male genitalia examined: 4).

*Measurements*: Length: 5.8-7.2 mm; width: 2.9-4.0 mm.

Specimens have been collected every month of the year except October, November, and January. Ecological data accompanying preserved specimens include: at light, pitfall trap, under seaweed, ocean beach, and in ocean debris.

*Specimens examined*: 265. UNITED STATES: *Florida*. Bahia Honda Key, Biscayne, Capron, Dry Tortugas (Bush Key, Garden Key), Dunedin, Flagler Beach, Fort Lauderdale, Haulover, Jacksonville, Key West, Lake Worth,





Figs. 5-8, *Phaleria* spp.: 5, *P. testacea*, head, ventral; 6, *P. gracilipes*, head, ventral; 7, *P. rotundata*, head, ventral; 8, *P. debilis*, head, ventral.

Lower Matecumbe Key, Ormond Beach, Vero Beach, Sarasota County. VIRGIN ISLANDS: Anegada (Pomato Point, Setting Point), Virgin Gorda (Prickly Pear Island). BAHAMA ISLANDS: Crooked Island, Egg Island, Grand Bahama Island (Freeport), Harbor Island, New Providence, South Bimini, Water Cay. LESSER ANTILLES: Anguilla (Sandy Island), Antigua (Green Island), Barbuda (Cocoa Point, Spanish Point, Oyster Pond). JAMAICA: Duncans. A specimen labelled "Orlando, Florida" (CNCI) is not included in the above listing since its natural occurrence there is unlikely.

*Phaleria lata* Blaisdell  
(figs. 22, 23, 30, 36)

*Phaleria latus* Blaisdell, 1923:276. Types: San Luis Island, Gulf of California; holotype (female) in CASC; not examined.



This species superficially resembles *P. rotundata* but is much larger (usually greater than 7 mm in length) and has the pronotum broadest at about the middle rather than at the base. As in *P. rotundata*, the hind wings are reduced to about half as long as the elytra. Setae along the posterior margins of the abdominal sterna are long, dense, and erect. Color varies from light yellowish brown to almost black; an occasional specimen has the pronotal and elytral margins paler than medial portions.

The male genitalia of *P. lata* (figs. 22, 23) are very similar to those of *P. pilifera* and *P. rotundata*, but can be separated by the more elongate and unconstricted parameres with very narrowly explanate lateral margins. (Male genitalia examined: 4).

*Measurements*: Length: 6.2-9.9 mm; width: 3.5-5.3 mm.

All specimens we have seen were taken between April and July. The only ecological note associated with specimens was "dead turtle" on a series from Puerto Peñasco, Sonora, Mexico. In addition to the type locality (San Luis Island), Blaisdell (1947) listed *P. lata* from Gonzales Bay, Baja California and Puerto Refugio, Angel de la Guarda Island, and Mejia Island, Gulf of California. For some reason it seems to be especially plentiful at Puerto Peñasco, Sonora; four collections were made by different collectors at that location.

*Specimens examined*: 149. MEXICO: Sonora. Cholla Bay, Guaymas, Miramar, Puerto Libertad, Puerto Peñasco. Baja California. San Felipe.

*Phaleria rotundata* LeConte  
(figs. 7, 24, 25, 31, 39)

*Phaleria rotundata* LeConte, 1851:148. Types: San Diego, California; in LeConte Collection (MCZC); not examined.

*Phaleria limbata* Horn, 1870:375 NEW SYNONYMY. Types: San Francisco, California; in Horn Collection (MCZC); not examined.

This is a robust, generally light reddish brown species with long, dense setae bordering both the prothorax and elytra and with a tuft of long, golden setae on the anterior margin of the prosternum. The eyes are widely separated ventrally (fig. 7), and there are distinct setae on the pronotal hypomera. The metathoracic wings are reduced and not capable of sustaining flight. *P. rotundata* is most similar in appearance to *P. lata* but is much smaller (usually less than 7 mm) and has the pronotum widest at the base.

The under surface of the body is occasionally black, and the elytra may be infuscate medially. Rarely the body is entirely blackish. It is to the darker variant with lighter margins that Horn assigned the name *P. limbata*. Moore (1974) described the larva of *P. rotundata* and discussed his observations on the ecology of the species.

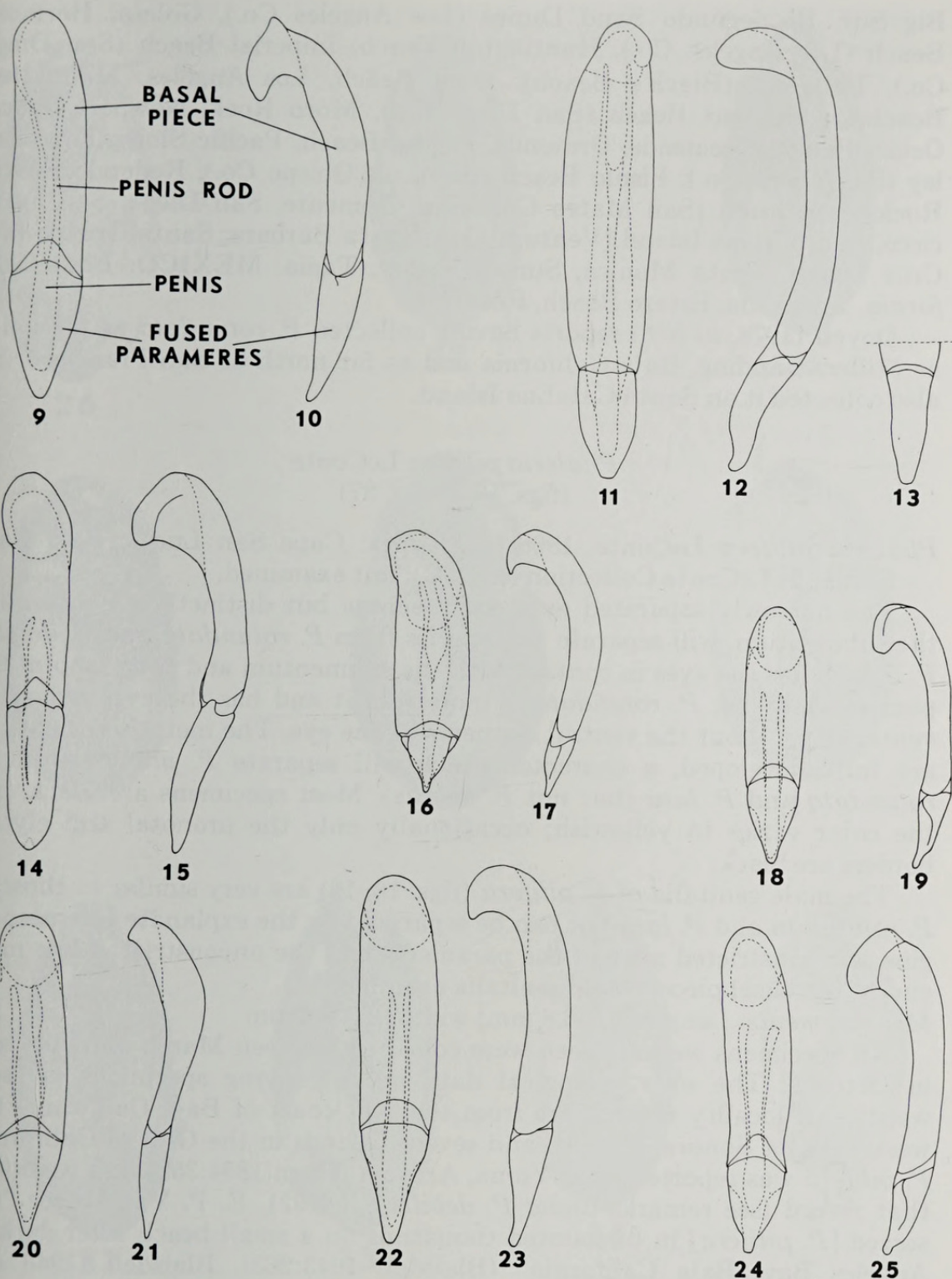
The male genitalia of *P. rotundata* (figs. 24, 25), though similar to *P. lata* and *P. pilifera*, can be separated by the constricted apex and broadly explanate lateral margins of the parameres, and by the slightly constricted side margins of the basal piece. (Male genitalia examined: 4).

*Measurements*: Length: 5.3-6.8 mm; width: 2.8-3.8 mm.

Specimens have been collected in every month except February. All data accompanying specimens indicate that they were collected in or under kelp.

*Specimens examined*: 1069. UNITED STATES: California. Anaheim, Anacapa Island (Ventura Co.), Arch Beach (Orange Co.), Bakersfield, Berkeley,





Figs. 9-25, male genitalia of *Phaleria* spp.: 9-10, *P. testacea* (9, dorsal; 10, lateral); 11-13, *P. gracilipes* (11, dorsal; 12, lateral; 13, dorsal, apex, Alabama specimens); 14-15, *P. punctipes* (14, dorsal; 15, lateral); 16-17, *P. picipes* (16, dorsal; 17, lateral); 18-19, *P. pilifera* (18, dorsal; 19, lateral); 20-21, *P. debilis* (20, dorsal; 21, lateral); 22-23, *P. lata* (22, dorsal; 23, lateral); 24-25, *P. rotundata* (24, dorsal; 25, lateral).



Big Sur, El Segundo Sand Dunes (Los Angeles Co.), Goleta, Hermosa Beach (Los Angeles Co.), Huntington Beach, Imperial Beach (San Diego Co.), La Jolla (Black's Beach), Long Beach, Los Angeles, Manhattan Beach, Monument Beach (San Diego Co.), Moro Rock, Newport Beach, Ocean Beach, Oceanside, Ormonds, Pacific Beach, Pacific Slope, Pine Valley (San Diego Co.), Pismo Beach (San Luis Obispo Co.), Redondo Beach, Rockaway Beach (San Mateo Co.), San Clemente, San Diego, San Francisco, San Nicolas Island (Ventura Co.), Santa Barbara, Santa Cruz, Santa Cruz Island, Santa Monica, Sunset Valley, Tapia. MEXICO: *Baja California*. Ensenada, Estero Beach, Rosarito.

Doyen (1978, *in litt.*) reports having collected *P. rotundata* as far south as Millers Landing, Baja California and as far north as San Francisco. He also collected it on Santa Catalina Island.

*Phaleria pilifera* LeConte  
(figs. 18, 19, 32, 37)

*Phaleria pilifera* LeConte, 1866:125. Types: Cape San Lucas, Baja California; in LeConte Collection (MCZC); not examined.

The narrowly separated eyes, approaching but distinctly not attaining the submentum, will separate this species from *P. rotundata* and *P. debilis*. *P. debilis* has the eyes in contact with the submentum and the pronotal hypomera glabrous; *P. rotundata* is more robust and has the eyes separated ventrally by about the ventral diameter of one eye. The metathoracic wings are fully developed, a character which will separate *P. pilifera* from *P. rotundata* and *P. lata* (but not *P. debilis*). Most specimens are black, but the color varies to yellowish; occasionally only the pronotal and elytral borders are black.

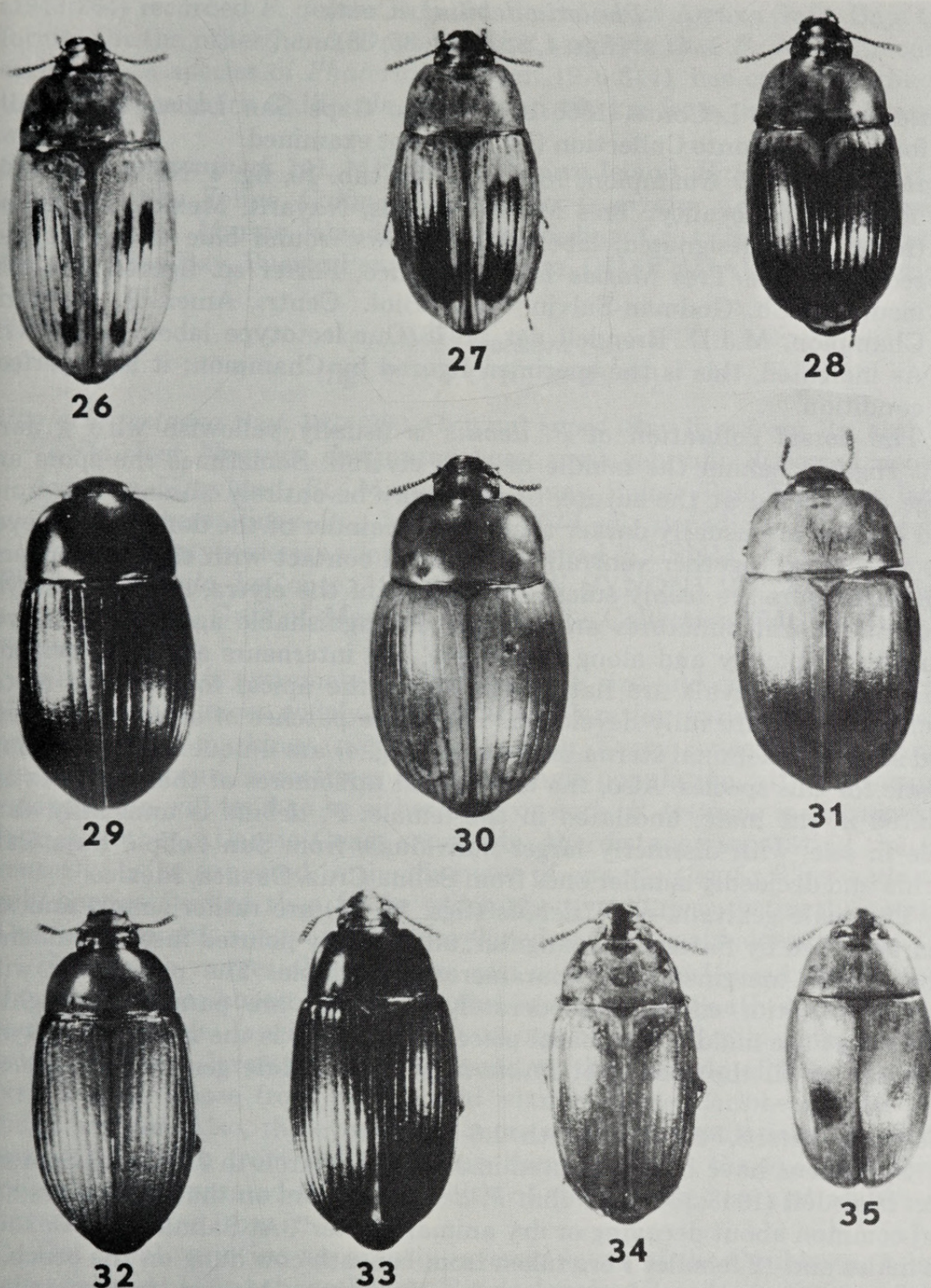
The male genitalia of *P. pilifera* (figs. 18, 19) are very similar to those of *P. rotundata* and *P. lata* but can be separated by the explanate lateral margins and constricted apex of the parameres and the unconstricted side margins of the basal piece. (Male genitalia examined: 7).

*Measurements*: Length: 4.2-6.8 mm; width: 2.5-3.4 mm.

All specimens we have seen were collected between March and July and in October. The only ecological data accompanying specimens is "seaweed". All locality records are from the east coast of Baja California, the west coast of Sonora, Mexico, and several islands in the Gulf of California. *P. pilifera* was reported from Yuma, Arizona (Horn 1894:352), but we doubt that record (see remarks under *P. debilis*). In 1921, E. P. Van Duzee "observed [*P. pilifera*] in uncounted thousands on a small beach after dark at Angeles Bay, Baja California" (Blaisdell 1943:263). Blaisdell (1943 *loc. cit.*) summarized the distribution of *P. pilifera* as follows: *Baja California*: Angeles Bay, Las Animas Bay, Cape San Lucas, La Paz, Concepcion Bay (Coyote Cove), and 12 miles south of Santa Rosalia. *Gulf of California*: Mejia Island, Granite Island, Tiburon Island (Freshwater Bay), Angel de la Guarda Island (Puerto Refugio). *Sonora*: Tepoca Bay.

*Specimens examined*: 606. MEXICO: *Sonora*. Desemboque, Empalme, Kino Bay, La Choya, Puerto Libertad, Puerto Penasco, Tastiota. *Baja California*. Mulege, Puertecitos, San Felipe. *Gulf of California*. Tiburon Island.





Figs. 26-35, habitus of *Phaleria* spp.: 26-28, *P. testacea*; 29, *P. punctipes*; 30, *P. lata*; 31, *P. rotundata*; 32, *P. pilifera*; 33, *P. picipes*; 34, *P. gracilipes*; 35, *P. debilis*.



*Phaleria debilis* LeConte  
(figs. 4, 8, 20, 21, 35, 38)

*Phaleria debilis* LeConte, 1866:126. Types: Cape San Lucas, Baja California; in LeConte Collection (MCZC); not examined.

*Phaleria insularis* Champion, 1886:221, 541, tab. 10, fig. 4. NEW SYNONYMY. Type locality: Tres Marias Islands, Nayarit, Mexico. Lectotype (male) here designated, labelled as follows: round blue disc, syntype/red disc, type/Tres Marias Is., W. Mexico, Forrer/sp. figured/Phaleria insularis Ch./Godman-Salvin Coll. Biol. Centr. Amer./P. insularis Champion, M.J.D. Brendell det., 1978/Our lectotype label; in BMNH. As indicated, this is the specimen figured by Champion; it is in perfect condition.

The dorsal coloration of *P. debilis* is usually yellowish with a dark spot slightly behind the middle of each elytron. Sometimes the spots are large and joined at the suture, or they may be entirely absent. The frons and occiput are usually darker than the remainder of the dorsum. The eyes are very close together ventrally and are in contact with the submentum. The interneurs are feebly sulcate over most of the elytra, and the interval and interneural punctures are scarcely distinguishable against the microsculpture; apically and along the suture, the interneurs are quite evident. The elytral intervals are flat except about the apical fourth. The metathoracic wings are fully developed. The dense patches of setae on the first and second abdominal sterna of the male (fig. 4) are unique and hence diagnostic for this species. Also, the three basal tarsomeres of the protarsus are dilated in the male, undilated in the female. *P. debilis* is unusually variable in size, with distinctly larger individuals from San Felipe, Baja California and decidedly smaller ones from Salina Cruz, Oaxaca, Mexico.

The male genitalia of *P. debilis* (figs. 20, 21) are rather simple and are characterized by flattened, triangular, and sharply pointed fused parameres. The lateral margins of the parameres are simple. The penis rods with swollen anterior ends are moderately long and are parallel to slightly arcuate at the middle. The basal piece of *P. debilis* is the most nearly symmetrical of all the species of *Phaleria* studied. (Male genitalia examined: 5).

*Measurements*: 3.7-6.6 mm; width: 1.8-3.2 mm.

Specimens have been collected in January, March to July, and September. Blaisdell (1943:264) says that *P. debilis* "occurs on the sea beaches and [is] common about decaying or dry animal matter". At Salina Cruz, Oaxaca, 16 males and 12 females were taken from beneath cow dung on the beach. A series of 23 specimens from Acapulco de Juárez, Mexico, intercepted at Brownsville, Texas was found in association with dry coconut shells.

Champion (1886:221) mentioned the closeness of *P. insularis* to *P. debilis*, but his conclusions were based solely on the description of the latter. We studied 3 of the 7 specimens comprising Champion's type series (1 male, 2 females) of *P. insularis* and find them identical to what we consider typical *P. debilis*.

Horn (1894:352) mentions that *P. debilis* occurs at Ft. Yuma [California or Arizona?] but we are inclined to discount that record. It is probable that someone stationed at Ft. Yuma collected the specimens on a trip to the Gulf of California and neglected to pinpoint the collection site. Blaisdell



(1943:264) recorded *P. debilis* from 5 miles north of Arroyo Seco, Baja California. On the other hand, Doyen (*in litt.*) reports that *P. debilis*, recorded earlier as "a species of *Phaleria*" (Doyen 1976:514), has colonized the Salton Sea of southern California, more than 100 km from the nearest oceanic waters.

*Specimens examined*: 141. MEXICO: Socorro Island. *Baja California*. Gonzaga Bay, San Felipe. *Colima*. Manzanillo. *Guerrero*. Acapulco de Juárez. *Nayarit*. Tres Marias Islands. *Oaxaca*. Salina Cruz. *Sinaloa*. Mazatlán. *Sonora*. Kino Bay, Puerto Penasco, Tastiota. GUATEMALA: Champerico.

*Phaleria testacea* Say  
(figs. 2, 3, 5, 9, 10, 26-28, 36)

*Phaleria testacea* Say, 1824:280. Original types (Say lists from Pa. and N.J. to Fla.) lost. Neotype, designated here: male, genitalia dissected; neotype locality, Maryland, St. Marys Co., Piney Point, Tall Timbers; labels, Tall Timbers/Piney Pt., Md., 24-V-27/J. E. Benedict, Jr., Collector/ and our neotype designation label; deposited in USNM.

*Phaleria longula* LeConte, 1866:125. NEW SYNONYMY. Types: Mississippi Island, Gulf of Mexico; in LeConte Collection (MCZC); not examined.

This species is extremely variable in both size and coloration, and it is also one of the most widely distributed. Coloration varies from yellowish-brown without markings to entirely blackish. Every conceivable intermediate pattern occurs, sometimes within a single population, although usually a population will tend to be either light or dark. *P. testacea* is distinguished from all other Atlantic Coast species by the distance separating the eyes ventrally being subequal to the diameter of one eye (fig. 5). This is also the only species studied thus far in which the pygidium is distinctly notched. The metathoracic wings are fully developed and the beetle does fly.

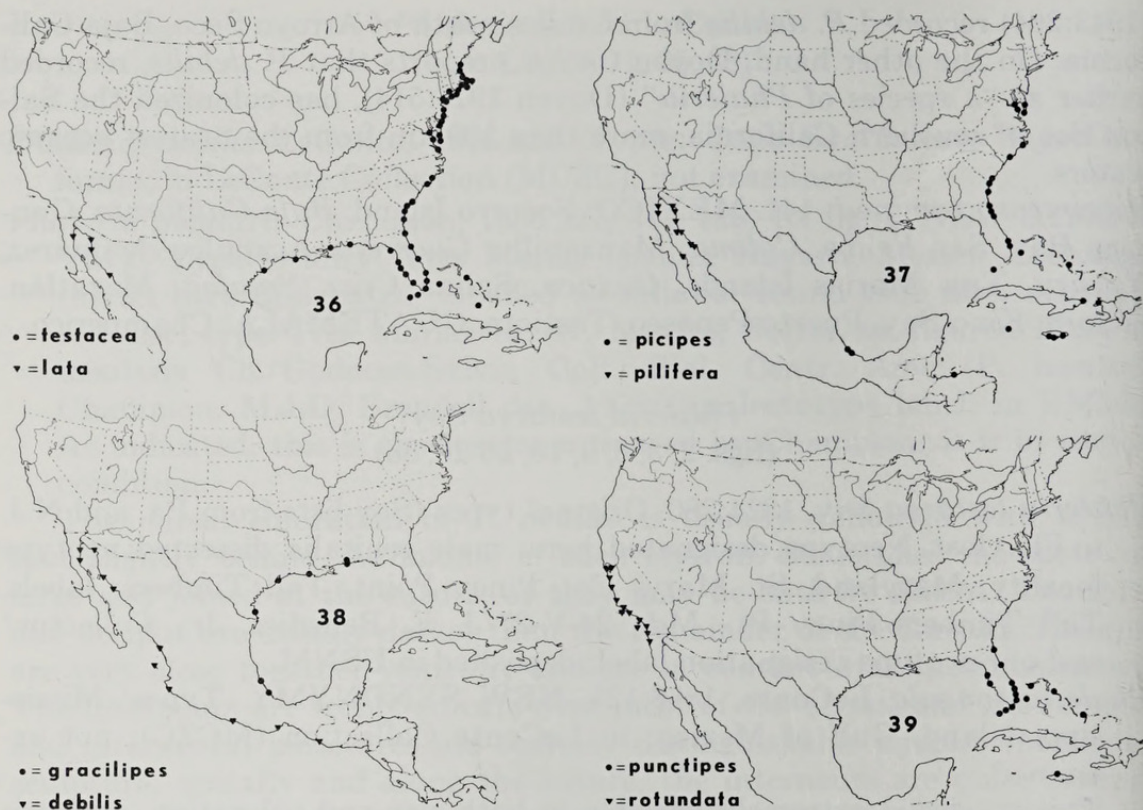
*P. testacea* ranges all along the east coast of the United States, south through the Caribbean, and along the east coast of South America as far south as Rio de Janeiro, Brazil. It varies in size clinally from north to south, with the largest specimens found at the latitude of New York and New Jersey. Those from Florida and islands of the Caribbean tend to be much smaller. Also, the eyes of the more northern populations are farther apart than those from the Caribbean area; however, the eyes are always more widely separated than the width of the submentum and always distinctly separated from it.

The clinal variation apparently reverses south of the Caribbean. A large series taken at Copacabana Beach, Rio de Janeiro, Brazil is indistinguishable from series taken in New York, New Jersey, and Delaware. The smallest individuals we have seen are from Trinidad. Considering the wide distribution and variation in coloration and size, there is probably more synonymy involved than we have discovered thus far.

A unique feature of the male genitalia of *P. testacea* (figs. 9-10) is the divergent and unswollen anterior ends of the penis rods. The fused parameres are rather simple, triangular in outline with the side margins unmodified. (Male genitalia examined: 14).

*Measurements* (Continental United States specimens only): Length: 5.0-7.8 mm; width: 2.4-4.0 mm.





Figs. 36-39, distribution maps of *Phaleria* species.

Specimens have been collected in every month of the year. The following ecological data accompanies preserved specimens: under logs on beach, beach drift, beach sand, ocean beach washup, under seaweed, under dead fish, under dead shark, under dead bird, under porpoise carcass, blacklight trap. *P. testacea* is frequently collected along with *P. picipes*.

*Specimens examined.* 1467. UNITED STATES: *Connecticut.* New Haven, Savin Rock, West Haven. *Delaware.* Cape Henlopen, Fenwick Island, Lewes, Rehoboth Beach. *Florida.* Atlantic Beach, Biscayne Bay, Capron, Cedar Keys, Coronado Beach, Dry Tortugas, Enterprise, Fort Myers, Fort Pierce, Key Largo, Key West, Lake Worth, Miami, New Smyrna, Ormond Beach, Pablo Beach, Palm Beach, Ponte Vedra Beach, Saint Augustine, Saint George Island, Saint Lucie, Sanibel Island, Santa Rosa Island, Sebastian Inlet, Stuart, Tampa Bay, Vero Beach, Gulf Co., Sarasota Co. *Georgia.* Sapelo Island, Savannah Beach, Tybee Island. *Louisiana.* *Maine.* Ogunquit. *Maryland.* Lloyds, North Point, Piney Point, Plum Point, Point Frederick, Point Lookout. *Massachusetts.* Barnstable, Cambridge, Chatham, Chilmark, Duxbury, Elizabeth Island, Humarock, Ipswich, Martha's Vinyard, Manchester, Marion, Mount Tom, Nahant, Nantucket, Naushton Island, Orleans, Provincetown, Somerset, Springfield, Truro, Woods Hole. *Mississippi.* Horn Island. *New Hampshire.* Hampton. *New Jersey.* Anglesea, Atlantic City, Beach Haven, Cape May, Five Mile Beach, Holly Beach, Lavallette, Longport, Ocean City, Peermont, Sea Isle City, Seaside Heights, Surf City, Wildwood. *New York.* Astoria, Babylon, Fishers Island, Fire Island, Long Island, Montauk Point, New York City, Riverhead, Rockaway Beach, Sagamore Hill Nat. Pk., Southhampton, Staten Island. *North*



*Carolina*. Long Beach, Wrightsville Beach. *Rhode Island*. East Greenwich, Newport, Wampanoag, Warwick, Watch Hill. *South Carolina*. Beaufort, Isle of Palms. *Texas*. *Virginia*. Accomac, Cape Henry, Cobb Island, Fort Monroe, Newport News, Virginia Beach, Westmoreland St. Pk. PUERTO RICO: Aguadilla, Boca Vieja, Catano, Cayo Ahogado, Culebra Island, Fajardo, Guamia Bay, Humacao, Mayagüez, Mona Island, Palo Seco, Rio Piedras, San Juan, Santuree. VIRGIN ISLANDS: Anegada, Virgin Gorda (Prickley Pear Island), St. Croix. BAHAMA ISLANDS. Conception Island, Egg Island, Harbor Island, North Bimini Island, South Bimini Island, Ragged Island Group (Nurse Cay). LESSER ANTILLES. Antigua, Barbados, Barbuda, Carriacou, Dominica, Grenada, Guadeloupe (Basse Terre), Montserrat, Mustique, St. Martin, St. Vincent. MEXICO. TRINIDAD. COLOMBIA. CAYENNE. BRAZIL. *Bahia*. Salvador. *Guanabara*. Rio de Janeiro (Copacabana Beach).

The specimens from Trinidad, Colombia, and Cayenne (BMNH) and Mexico (MCZC) have no specific localities on the labels but we are inclined to accept them as authentic. We have seen no specimens with specific localities from Texas and Louisiana, but it is probable that *P. testacea* occurs in these states. On the other hand, we are suspicious of 6 specimens labelled "Duluth, Minnesota" and 2 labelled "Oakland Beach, California" (all in USNM). Our studies indicate that the natural occurrence of *P. testacea* in California and Minnesota is highly unlikely and, if the labels are correct, the specimens were probably introduced. A large series of specimens (261 all in USNM) is labelled: 17 mi. N. Tallahassee, Florida. Being this far inland is very unusual. It is possible they were collected near the coast and mislabelled.

*Phaleria picipes* Say  
(figs. 16, 17, 33, 37)

*Phaleria picipes* Say, 1824:280. Original types (Say gives "Southern States") lost. Neotype, designated here: Male, genitalia dissected; neotype locality, South Carolina, Charleston Co., Folly Beach; labels, South Carolina, Folly Beach, 15 Aug., 1947, O. L. Cartwright/O. L. Cartwright Collection 1962/our neotype designation label; deposited in USNM.

This species closely resembles and is frequently collected along with *P. testacea*. Both are quite variable in size and coloration, and both are widely distributed in the Caribbean area. *P. picipes* may be separated readily from *P. testacea* by the broadly rounded pygidium, the duller luster, and the more narrowly separated eyes in ventral aspect. The head punctures are coarser and denser in *P. picipes* than in *P. testacea*. This character shows a clinal variation, and the difference is much more distinct in the southern Florida, West Indies, and Mexican populations. Males of *P. picipes* have the basal 3 tarsomeres of the protarsus expanded and spongiose-pubescent on plantar surfaces; protarsi in the female are simple. Among the species of *Phaleria* with which we are familiar, only *P. gracilipes*, a Gulf Coast species, and *P. debilis* and *P. guatemalensis* Champion, both Pacific Coast species, share this character with *P. picipes*.

The variation in coloration is unusual. All mainland United States specimens are uniformly colored, ranging from yellowish to black; the northern populations (Virginia to Georgia) tend to be mostly black, and the



southern populations (Florida) are mixed. In the Dry Tortugas, 280 specimens taken on 10 different occasions are all light-yellowish. Most West Indies populations have a mixture of color forms. While some are uniformly colored, many have bold elytral markings in which the ground color is yellowish with large discal maculae joined at the suture; others are dark with only the outer 2 elytral intervals yellowish, a common pattern in *P. dytiscoides* Champion from the Pacific coast of Central America.

Other than coloration and the punctures of the head, the only variation which we have observed is the size. As with *P. testacea*, West Indies specimens tend to be smaller.

*P. picipes* dramatically illustrates that little reliance can be placed upon size and coloration as taxonomic characters in this genus. It is probable that several of the species of *Phaleria* described from the West Indies islands will ultimately prove to be synonyms of *P. picipes*.

The male genitalia of *P. picipes* (figs. 16, 17) are distinctive in having the penis rods broadened and joined near the middle of the penis. The fused parameres are rather short with lateral margins explanate and apex constricted. (Male genitalia examined: 10).

*Measurements*: Length: 3.8-6.9 mm; width: 1.9-3.2 mm.

Specimens have been taken every month of the year except October and January. Ecological data associated with preserved specimens include: under porpoise carcass, under dead shark, beach drift, sifted from beach washup, and blacklight trap.

*Specimens examined*: 976. UNITED STATES: *Florida*. Atlantic Beach, Capron, Coronado Beach, Delray Beach, Dry Tortugas, Fort Lauderdale, Lake Worth, Ormond Beach, Pablo Beach, Palm Beach, Ponte Vedra Beach, Saint Augustine, Sebastian Inlet (Indian River Co.), Stuart, Vero Beach, Vilano Beach. *Georgia*. Tybee Island, Sapelo Island (McIntosh Co.). *Maryland*. Piney Point. *North Carolina*. Long Beach, Carteret County. *South Carolina*. Beaufort, Isle of Palms. *Virginia*. Accomac, Cedar Island, Cobb Island, Folly Beach, Smith's Island. PUERTO RICO: Aguadilla, Isabela, Mona Island, Rio Piedras, San Juan, Santuree, Vieques Island. VIRGIN ISLANDS: St. John's, St. Croix, Virgin Gorda (Prickley Pear Island). BAHAMA ISLANDS: Port Nelson (Rum Cay), South Bimini. JAMAICA: Alligator Pond Beach, Bluefields, Kingston. CUBA: Baracoa. CAYMAN ISLANDS: Grand Cayman (east end), Georgetown. LESSER ANTILLES: Montserrat. HAITI: Bayeaux, Grand Anse, Jean Rabel. MEXICO: *Veracruz*. 5 miles south of Veracruz, 10 miles west of Alvarado, 12 miles northwest of Alvarado. HONDURAS: La Ceiba.

*Phaleria gracilipes* Casey  
(figs. 6, 11-13, 34, 38)

*Phaleria gracilipes* Casey, 1890:484. Holotype: Texas; in Casey Collection (USNM).

*Phaleria lodingi* Blaisdell, 1932:116. NEW SYNONYMY. Types: Mobile, Alabama; in Blaisdell Collection (CASC).

This is the smallest and most slender species of *Phaleria* inhabiting the United States. It also has the largest eyes (fig. 6) of the Atlantic Coast species; ventrally the eyes are separated by less than the width of the submentum with which they are in contact. Coloration is usually uniform (light



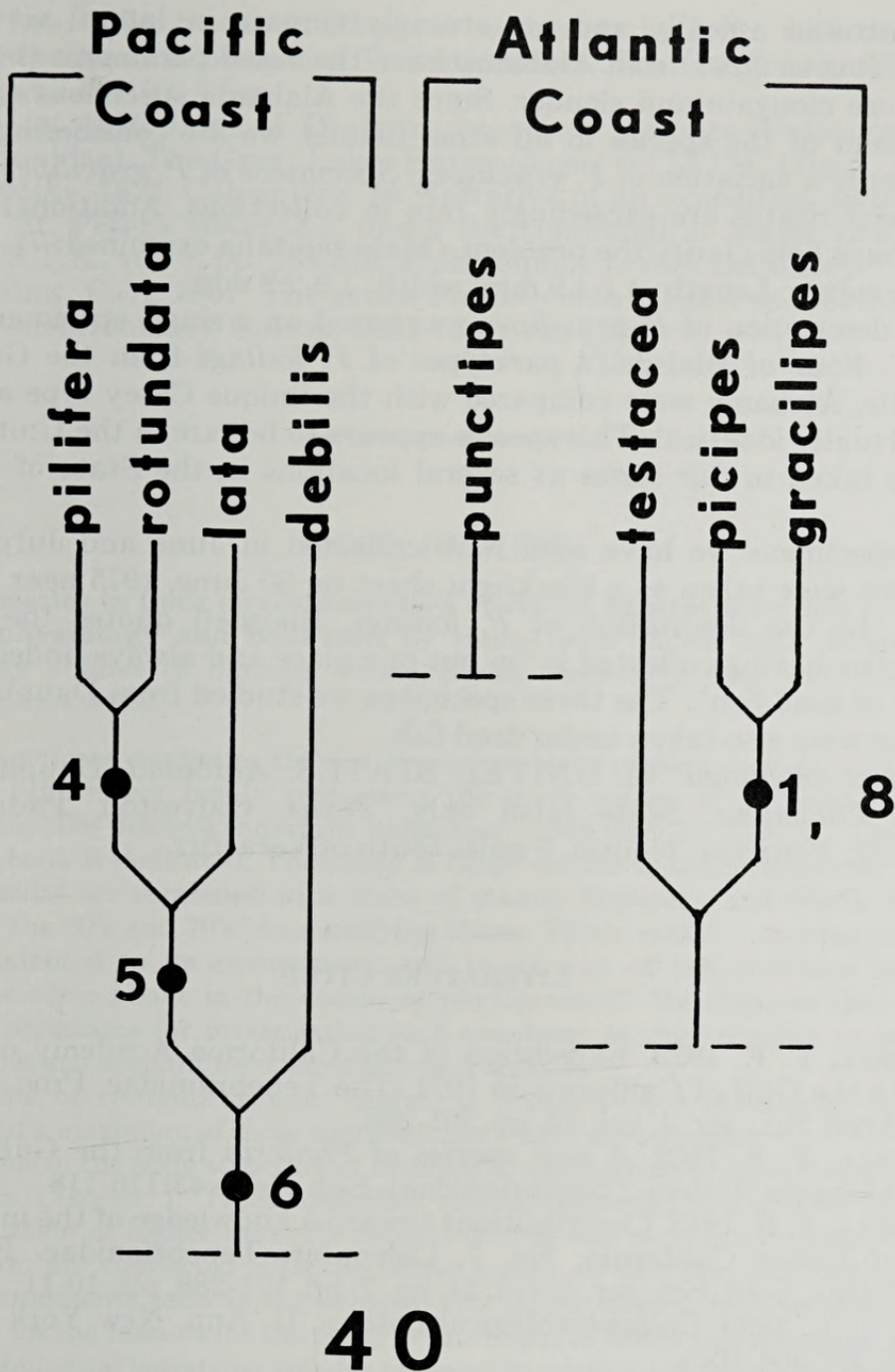


Fig. 40, proposed evolutionary relationships, based on shared derived characters, among *Phaleria* species.

yellowish-brown) with the head frequently darker. The interneurs are not impressed in the basal third of the elytra but are indicated by very fine rows of punctures; apically the interneurs are impressed. Intervals are flat on the basal third and subconvex apically. Punctuation of the head is fine and sparse. The metathoracic wings are fully developed. Males have the basal 3 tarsomeres of the protarsus expanded; protarsi in the female are simple.

The very elongate and flattened basal piece of the male genitalia (figs. 11, 12) is distinctive. The penis rods with unswollen anterior ends are correspondingly elongate and are distinctly joined by membrane for the posterior 2/3 of the penis. The fused parameres are broad basally and triangu-



larly narrowed apically and are strongly sinuate in lateral view. Specimens of *P. gracilipes* from Alabama have the fused parameres (fig. 13) notably more elongate and slender. Since the Alabama specimens agree with our concept of the species in all other details, we are considering this difference only a variation of *P. gracilipes*. Specimens of *P. gracilipes* from the Gulf Coast States are exceedingly rare in collections. Additional material will perhaps help clarify the problem. (Male genitalia examined: 7).

*Measurements*: Length: 4.1-4.9 mm; width: 1.9-2.2 mm.

The description of *P. gracilipes* was based on a single specimen labelled "Texas". Four of Blaisdell's paratypes of *P. lodingi* from the Gulf beach at Mobile, Alabama were compared with the unique Casey type and found to be virtually identical. This species appears to be rare in the United States but was taken in fair series at several locations in the State of Veracruz, Mexico.

All specimens we have seen were collected in June and July. Twenty specimens were taken at a blacklight sheet on 30 June, 1975 near Veracruz, Mexico. In the description of *P. lodingi*, Blaisdell quotes the collector (Löding) as having collected it "in but one place and always under or in the vicinity of dead fish". The three specimens we studied from Dauphin Island, Alabama were also taken under dead fish.

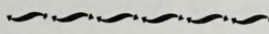
*Specimens examined*: 42. UNITED STATES: *Alabama*. Dauphin Island, Mobile. *Louisiana*. State label only. *Texas*. Galveston, Padre Island. MEXICO: *Veracruz*. Nautla, 5 miles south of Veracruz.

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### BOOK REVIEW

**Carabid beetles in their environments, a study on habitat selection by adaptations in physiology and behavior**, by Hans-Ulrich Thiele. 1977. Zoophysiology and Ecology Volume 10. Springer-Verlag, Berlin, Heidelberg, New York. 152 figures. XVII, 369 pages. \$48.00.

Thiele's volume celebrates the last three decades of carabid ecology. It is a fitting tribute to "the insect family comprising the most species of all" and a splendid corollary to "Die fennoskandischen carabiden" 1945-1949 by Carl H. Lindroth to whom the book is dedicated. The study is based on 585 selected references in which Thiele's results are combined with those of mainly European and North American workers of the 60's and 70's. As a unifying theme Thiele asks "... in what manner is a species adapted to its environment and to its way of life, and how have such adaptations come about in the course of phylogenesis?" He observes that carabids are model organisms for investigating such questions as they number an estimated 40,000 species and account for 4.3% of all insect species.

The table of contents is most useful. It presents clear statements for eleven chapters and a maximum of three subcategories within each chapter.

Variations in the body structure of carabids in adaptations to habitat and niche are discussed in Chapter 1. Thiele describes macromorphological variation as a basis for classification of higher taxa. He recognizes that the most pronounced variations in body form are connected with specialized modes of nutrition and adaptations to special environments such as the arboreal one in the tropics, but that these do not throw light on the reasons for the many forms found in forest and open land habitats. Micromorphological variations are also reviewed in relation to various habitats.

Chapter 2 deals with quantitative investigations on the distribution of carabids in forests and open country habitats of temperate climates. An attractive case is made for the use of pitfall traps. While limitations of the method are recognized, Thiele is right when he says "pitfall traps have done much to clarify our quantitative and qualitative picture of the distribution of carabids in different habitats and plant communities". One interesting point which has emerged from recent findings is that the carabid fauna characteristic of cultivated land probably originated from river banks and sea coasts.

Chapter 3 (94 pages) deals with the connections between carabids and biotic factors in the ecosystem. Thiele questions to what degree biotic factors govern the distribution of carabids in different habitats, and population density, and what are carabid influences on populations of their prey. A superbly detailed review on parasites and predators of carabids is provided. It appears that populations of carabids are not greatly affected by parasites. On the other hand, many types of birds, mammals, frogs and lizards, and predaceous flies and ground spiders are important regulators of carabid population densities.





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