

A NEW SPECIES OF *ODONTOMACHUS* ANT
(HYMENOPTERA: FORMICIDAE) FROM INLAND RIDGES OF FLORIDA,
WITH A KEY TO *ODONTOMACHUS* OF THE UNITED STATES

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ABSTRACT

The ponerine ant *Odontomachus relictus* n. sp. is described from specimens collected in scrub and sandhill habitats on several ancient sand ridges in Florida. It appears to be a relict species from dry periods in the Pleistocene. Workers are similar to the western species *O. clarus* Roger, but males of the two species are strongly divergent. Keys and natural history notes are provided for workers and males of the four *Odontomachus* species known from the U.S. Examination of males might help clarify the taxonomic status of *Odontomachus* of Central and South America.

Key Words: Florida endemics, arenicolous arthropods, *Odontomachus*, ants, Formicidae, Ponerinae

RESUMEN

La hormiga ponerine *Odontomachus relictus* n. sp., es descrita de especímenes recolectados en los hábitat de matorrales y de los bancos de arena en varias lomas de arena antiguas en la Florida. Parece ser una especie reliquia de los periodos secos del Pleistoceno. Los obreros son similares a la especie occidental *O. clarus* Roger, pero los machos de los dos especies son fuertemente divergentes. Se provee las claves y notas de la historia natural sobre las obreras y los machos de las cuatro especies de *Odontomachus* especies conocidas en los Estados Unidos. La examinación de los machos puede ayudar a aclarificar el estatus taxonómico de los *Odontomachus* de centro y de suramerica.

Members of the genus *Odontomachus* are often common and conspicuous insects. They are relatively large for ants (length often around 8 mm), with elongate mandibles whose powerful snapping action is produced by massive muscles accommodated in bulging lobes on the head capsule (Fig. 1A, B). *Odontomachus* has achieved some fame for the speed of its mandibular snap, which occurs in 0.33-1.00 millisecond, the fastest animal movement known (Gronenberg et al. 1993). In spite of these formidable jaws, backed up by a sting strong enough to elicit a definitive reaction in humans, these ants are not particularly fierce, and are usually seen stalking slowly about singly on the surface of leaf litter. As might be expected, examples of such large and obviously interesting ants began to accumulate in collections at an early date, resulting in the naming of numerous species and forms. This proliferation of names was based to a large extent on what seemed to be a good array of useful characters, including pilosity, color, surface sculpture, and the shape of the mandibles and petiole.

Unfortunately, it appears that many of the characters used in diagnoses of *Odontomachus* species show intraspecific variation, resulting in large numbers of synonyms. Bolton's 1995 catalog of For-

micidae includes 161 specific and subspecific names for extant *Odontomachus* species, 60 of which Bolton lists as valid names. Most of the credit for the simplification of nomenclature should go to Brown's 1976 review of the genus. Lineages that include variable species also may include cryptic species, and this seems to be true of *Odontomachus*. In the U.S., *Odontomachus* nomenclature was at its most austere following Brown's 1976 salutary pruning of the genus, resulting in one recognized species in the Southeast, *O. brunneus* (Patton), and one recognized species in the Southwest, *O. clarus* Roger. Deyrup et al. (1985) showed that there were three species in the Southeast: *O. brunneus*, *O. ruginodis* M. R. Smith (probably a relatively recent introduction to the area), and what appeared to be an isolated population of the southwestern *O. clarus*, restricted to arid dunes in central peninsular Florida. New evidence reveals that the southeastern species thought to be *O. clarus* is a different, undescribed species.

The purpose of this paper is to name this new species, to present an identification guide to the four U.S. species, to summarize the known natural history of all four species, to briefly cover the nomenclature of the species, and to indicate a few residual problems.

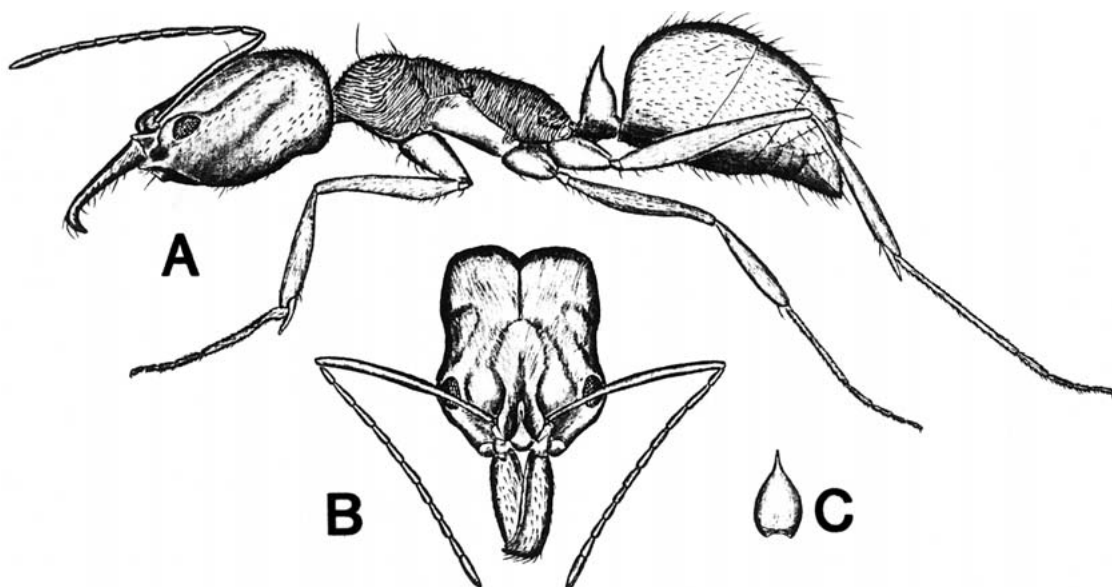


Fig. 1. *Odontomachus relictus*, new species, worker. A. Lateral view. B. Frontal view of head. C: Posterior view of petiole.

CLASSIFICATION AND DIAGNOSIS OF *Odontomachus*

Family Formicidae, subfamily Ponerinae, tribe Odontomachini (Hölldobler & Wilson 1990). *Odontomachus* is a senior synonym of *Pedetes* Dalla Torre, *Champsomyrmex* Emery, and *Myrtoteras* Matsumura (Bolton 1995); these junior synonyms have not been used for more than 25 years, and there is no current confusion about these names.

Diagnosis (modified from Hölldobler and Wilson 1990)

Mandibles slender, elongate, attached near middle of anterior margin of head, abruptly bent inward at apex, widened apices expanded with three teeth arranged in a vertical series; third abdominal segment not differentiated by a constriction from the rest of the abdomen. Nuchal carina (the ridge delimiting the occiput) V-shaped, narrowed toward its median into a mid-dorsal groove; apophyseal lines present as convergent lines from the vertex of the head up to the nuchal carina.

The shape of the nuchal carina and the presence of apophyseal lines distinguish *Odontomachus* from the somewhat similar genus *Anochetus*. A simple character for separating *Odontomachus* from *Anochetus* in the U.S. is the shape of the petiole, ending in a dorsal spine or simple cone in *Odontomachus*, and in a pair of spines or a pair of angles in *Anochetus mayri* Emery, the only representative of its genus known from the U.S. (Deyrup 2002). *Anochetus mayri*, which is native to the West Indies and exotic in Florida, is smaller (4 to 5 mm in length) than the *Odontomachus* species consid-

ered here. *Anochetus kempfi* Brown (West Indies) is within the size range of local *Odontomachus*, but very slender, and with a two-spined petiole.

Odontomachus relictus Deyrup and Cover, new species

Diagnosis of worker (Fig. 1).

Distinguished from other U.S. *Odontomachus* by the following combination of character states: conspicuous striae present on basalar lobe (oval sclerite at dorsal posterior corner of mesopleuron); posterior side of petiole without transverse striae; appressed hair on first gastral tergite sparse, short, spaces between hairs often as wide as the length of hairs.

Description of holotype worker

Features visible in lateral view described from left side. Measurements in mm. Total length (length of head excluding mandibles + length of mesosoma + length of petiole + length of gaster): 7.48; head length: 2.12; width of head at rear margins of eyes: 1.80; width of head at widest part of occipital lobes: 1.62; length of left mandible: 1.20; maximum width of eye: 0.30; maximum width of clypeal area: 0.30; length of mesosoma: 2.67; length of petiole: 0.52; length of gaster: 2.17. Head: fine striae diverging from frontal lobes, covering frontal aspect of head, disappearing before occipital area, covering only the upper quarter of the extraocular furrow; posterior lateral corners, occipital area, underside of head smooth and shining. Mesosoma:

pronotum with roughly circular concentric striae, without longitudinal striae reaching the hind margin; mesonotum and propodeum with transverse striae; striae present on basalar lobe; mesopleuron smooth, shining, with longitudinal striae along dorsal and ventral margins. Petiole: apically spinose; in profile anterior face convex, posterior face bisinuate; posterior face in posterior view smooth and shining, without hairs. Gaster: shining, no surface sculpture except for minute punctures from which hairs emerge; first tergite sparsely covered with short, appressed, pale hairs, spaces between hairs usually as wide as length of hairs; first tergite with sparse, scattered, suberect long hairs, including an uneven subapical row. Color: head, antennae, mesosoma, petiole dark reddish brown, contrasting with blackish-brown gaster; legs dark yellow, contrasting with mesosoma.

Diagnosis of queen

Queens of the four U.S. species were examined. Diagnosis as in worker.

Description of a paratype queen

Measurements in mm. Total length (length of head excluding mandibles + length of mesosoma + length of petiole + length of gaster): 8.37; head length: 2.15; width of head at rear margins of eyes: 1.77; width of head at widest part of occipital lobes: 1.70; length of left mandible: 1.20; maximum width of eye: 0.27; maximum width of clypeal area 0.25; length of mesosoma: 2.75; length of petiole: 0.52; length of gaster: 2.95. Structural character states and color as in worker, except for occurrence of ocelli and expansion of the mesosomal dorsum (pronotum, mesonotum, scutellum) associated with flight; pronotum transversely striate, mesonotum longitudinally striate.

Diagnosis of male

Distinguished from other U.S. *Odontomachus* by the following combination of character states: ocelli very large, wider than the distance between the lateral ocelli and the eyes (Fig. 2A); body color medium brown, antennae yellowish.

Description of a paratype male

Measurements in mm. Total length (length of head excluding mandibles + length of mesosoma + length of petiole + length of gaster): 6.66; head length: 1.07; width of head at widest part, including eyes: 1.45; length of mesosoma: 2.25; length of forewing: 4.95; length of petiole: 0.47; length of gaster: 2.57. Head: in frontal view, eyes longer than the distance between them dorsally; median ocellus wider than the distance between a lateral

ocellus and the margin of the eye; clypeus in profile not strongly protuberant. Mesosoma: pronotum, mesopleural area above and below episternal suture feebly shining, not striate; mesonotum finely striate, transversely on anterior quarter, remainder longitudinally; scutellum convex, shining, lacking a median carina; propodeum without a raised carina, feebly shining, with weak, fine striae in the following patterns: a median series of concentric ovals, posterior portion with transverse bisinuate lines, obliquely longitudinal lines laterally ventral to spiracle; propodeum in profile long and low, without a declivitous posterior portion; gaster shining, tergites without surface sculpture except for fine, hair-bearing punctures, evenly covered with long, fine, sub-appressed hairs.

Type localities and associated information, as appear on specimen labels.—Holotype Worker. FL: Highlands Co., Archbold Biological Station, 15-IV-1996, M. Deyrup, recently burned mature scrub, Red Hill, nest in sand. Paratype dealate queen used for description of queen (designated on label). Same locality, collector as holotype, 18-I-1983, Florida scrub habitat with *Ceratiola ericoides*, E. side of Tract 7. Paratype male used for description of male (designated on label). Same locality, collector as holotype, 8-XI-1990, at window, main building. Paratype workers and queens (all from Florida). The following specimens all have the same locality and collector as the holotype: 18 workers: same data as holotype (nest series with holotype); 2 workers: 30-IX-1982, sandhill area with *Quercus laevis*, SE Tract, at bait; 4 workers: 3-X-1982, in patch of *Hypericum*, road 19E, at bait; 2 workers: 19-IX-1982, mature stand of *Pinus clausa*, SE Tract, trail 10, at bait; 3 workers: 30-XIII-1985, mature sand pine scrub habitat, Red Hill, trail 1; 1 worker: 28-X-1982; 1 worker: 7-VI-1984, sandhill habitat, Tract 19E; 1 dealate queen with associated worker: 13-X-1982, in leaf litter of *Bejaria racemosa*, Tract 7, road 18; 1 worker: 24-XI-1982, in dry leaf litter at base of oak, sandhill habitat, Tract 19; 2 workers: 28-VI-1985, in leaf litter of *Carya floridana*, sandhill habitat, Tract 19E; 1 worker: 6-IV-1983, mature *Pinus clausa* scrub, in pan trap below Townes trap; 1 worker: 5-IX-1985, mature *Pinus clausa* scrub, NE firelane of NE Tract; 1 worker: 14-XI-1985, mature sand pine scrub, Red Hill, SE Tract; 1 worker: 13-VI-1985, sand pine scrub habitat; 1 worker: 17-X-1988; 1 worker: 3-X-1982, in tussock of *Andropogon*; 1 worker: 6-VII-1984, mature sand pine scrub habitat, NE firelane of NE Tract; 1 worker: 25-VII-1984, mature sand pine scrub habitat, NE firelane of NE Tract; 1 worker: 28-VI-1985, Tract 19E, sandhill habitat. Paratype workers and queens not from holotype locality: 3 workers: Highlands Co., Lake Placid, 18-IX-1987, P. Martin, sand pine scrub habitat in former YMCA Camp 2 mi. S. of town on Highway US 27; 1 worker: same locality, collector, habitat as previ-

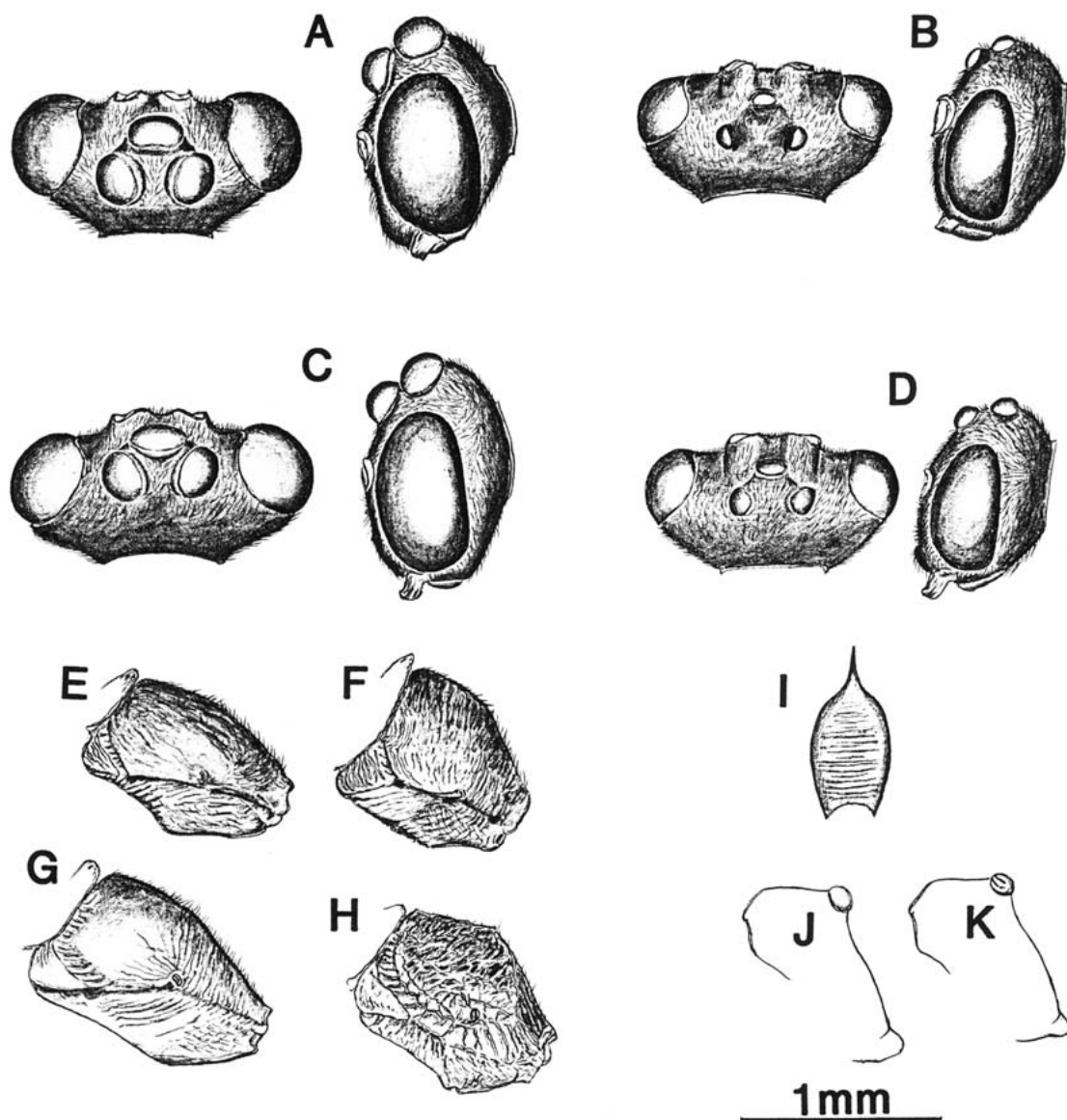


Fig. 2. *Odontomachus* species. A-D: heads of males, occipital and lateral views; A: *relictus*, B: *clarus*, C: *brunneus*, D: *ruginodis*. E-H: propodeal areas of males, lateral views; E: *relictus*, F: *clarus*, G: *brunneus*, H: *ruginodis*. At various times *relictus* (A, E) has been confused with *clarus* (B, F) and *brunneus* (C, G) with *ruginodis* (D, H). I: *ruginodis*, posterior side of petiole of worker. J-K: basalar sclerites (oval structure at upper right corner of mesopleuron) of workers: J: *clarus*, K: *relictus*.

ous, 30-X-1987; 3 workers: same locality, habitat as previous, 27-X-1987, J. Cronin, 1 worker: Highlands Co., Lake Placid, 15-X-1986, M. Deyrup, Holmes Avenue scrub site east of town; 3 workers: Highlands Co., Sebring, 11-IX-1987, P. Martin, former Flamingo Villas Devel., 3.7 mi. SE of Sebring, sand pine scrub; 2 workers: same locality, habitat as previous, 10-XI-1987, J. Cronin; 1 dealate queen with associated worker: same locality, habitat as previous, 17-IX-1990, M. Deyrup; 1 worker: Polk Co., TNC Tiger Creek Preserve, 5-X-

1989, M. Deyrup, recently burned scrub with *Quercus laevis*; 1 worker: Polk Co., Lake Wales, 26-I-1988, P. Martin, Flaming Arrow Boy Scout Camp, east of town, sand pine scrub; 1 dealate queen: same site, habitat as previous, 24-XI-1987, J. Cronin; 12 workers: Orange Co., Walt Disney World, S16, T24S, R27E, 5-VII-1996, Z. Prusak, sand pine/oak scrub zone MW-5 (unburned) #88; 2 workers: Orange Co., Walt Disney World, 22-VII-1996, Z. Prusak, MW-5 Cons. Area, unburned zone, sand pine scrub; 2 dealate queens, 4 work-

ers: Citrus Co., 12 mi. NW of Brooksville, 11-V-2002, M. Deyrup & J. Mosley, Withlacoochee State Forest, Sugar Mill Tract, north of 480, sandhill with oaks; 4 workers: Citrus Co., 5 mi. W. of Inverness, 14-IX-1991, M. Deyrup, sandhill habitat, Withlacoochee State Forest; 2 workers: same locality, collector, habitat as previous, 14-XI-1991; 4 workers: Citrus Co., Withlacoochee State Forest, 14-XI-1991, M. Deyrup, 3.2 km south on forest road that begins 7.2 km west of jct. State Road 44 and County Road 581, open sandhill habitat, sparse ground cover of *Aristida beyrichiana*, scattered mature *Pinus palustris* and *Quercus laevis*; 5 workers: Citrus Co., Pine-Oak Estates, 1-IV-1993, M. Deyrup, sandhill habitat along Rt. 488, 3 mi. NE jct. with Rt. 495. Paratype males. The following males are from the Archbold Biological Station, collected by M. Deyrup in Townes flight traps on trails through mature sand pine scrub; dates as follows: 2: 19-VI-1985; 1: 8-VII-1985; 2: 29-VI-1985; 1: 13-VII-1985; 1: 14-VII-1985; 1: 10-VI-1985; 1: 26-VI-1985; 2: 5-VII-1985; 4: 1-VII-1985; 1: 9-X-1987; 1: 28-XII-1983; 1: 16-VII-1986; 1: 24-VII-1985; 1: 21-VII-1983; 1: 3-VII-1983; 1: 27-VI-1983; 2: 28-VI-1983; 1: 21-VI-1983; 1: 20-XI-1985; 1: 8-VII-1983; 1: 23-VIII-1984. Additional paratype males: 7: Orange Co., Walt Disney World, S16, T24S, R27E, 1-5-VII-1996, Z. Prusak, sand pine/oak scrub zone MW-5 (unburned), Malaise trap; 2: Orange Co., Walt Disney World, 8-13-VIII-1996, Z. Prusak, MW-5 Cons. Area unburned zone, sand pine scrub, Malaise trap.

Deposition of types

Holotype, 3 paratype dealate queens, 32 paratype workers, 12 paratype males: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; 6 paratype workers, 4 paratype males: The Natural History Museum, London; 7 paratype workers, 4 paratype males: Los Angeles County Museum, Los Angeles, California; 10 paratype workers, 4 paratype males: Florida State Collection of Arthropods, Gainesville, Florida; remaining type material in the arthropod collection of the Archbold Biological Station, Lake Placid, Florida.

Etymology

relictus, past participle of *relinquo*: left behind, referring to the distribution of the species on relict patches of Florida scrub and sandhill vegetation on high sand ridges in south-central Florida.

Relationship between *relictus* and other species

Workers of *relictus* and *clarus* are morphologically similar, except for the striate basalar lobe (Fig. 2K) and consistently spinose petiole of *relictus*. Until we compared the males of the two spe-

cies, we had interpreted these differences as small divergences between widely separated populations of a single species, especially since *clarus* shows considerable variation through the Southwest. The differences between males are the only clear evidence at present that *clarus* and *relictus* are distinct. The extraordinarily large eyes and ocelli of *relictus* (Fig. 2A) suggest that there is some feature of *relictus* flight behavior that is different from the flight behavior of *clarus*; any major difference may be likely to confer reproductive isolation. A possibly relevant feature of *relictus* flight behavior is that male activity, as monitored by Malaise traps, seems to be concentrated around moonlit nights (Deyrup et al. 1985). Another major structural difference is the longer, less declivitous propodeum of *relictus*; all four species occurring in the U.S. show conspicuous differences in the shape and sculpture of the propodeal area (Figs. 2E-H).

It is tempting to hypothesize that *relictus* is closely related to *clarus*, representing an eastern offshoot of a western lineage adapted to dry habitats. Some other animals, such as the Florida sand roach (*Arenivaga floridensis* Caudell), the Florida scrub-jay (*Aphelocoma coerulescens*) and the gopher tortoise (*Gopherus polyphemus*) seem to be examples of western lineages in relic desert-like habitats in Florida (Deyrup 1989). These animals could have spread east, along with a rich fauna of now extinct savanna-dwelling vertebrates, along an arid corridor in southern North America during the late Pliocene through mid-Pleistocene (Webb 1990). In Deyrup's 1989 and 1990 papers *relictus*, under the name of *clarus*, is specifically mentioned as an example of such a western lineage. Male *relictus*, however, do not support this hypothesis. They share their large eyes and ocelli, non-carinate scutellum and low propodeum with the other native southeastern species, *brunneus* (Figs. 2C, G). When the taxonomic status and distribution of southeastern *brunneus* is better understood, it may be possible to propose a new hypothesis on the derivation of *relictus*.

All four of the U.S. species of *Odontomachus* are combined with 17 New World species and two Old World species in the *haematodus* species group, distinguished by the reduction of the segments of the labial palps from four to three (Brown 1976).

Habitat and distribution of *relictus*

This species is a subterranean nester, and found only in areas of deep, unconsolidated, silica sand. These areas may be covered with Florida scrub vegetation, consisting of scattered pines, small oaks and other small trees and shrubs. Sometimes there are areas of bare sand, especially in the first few years following a fire. Alternatively, areas where *relictus* occurs may be sandhill vegetation, consisting of scattered pines

above a low layer of grasses and forbs. For descriptions of these habitats, see Myers (1990). Nest entrances are not marked by a mound, but by scattered pellets of sand. Digging into a nest may produce a few workers, sometimes with brood, but no large aggregation of workers.

Odontomachus relictus is known from the Lake Wales Ridge, the southern Brooksville Ridge and the Orlando Ridge. It has not been found in scrub or sandhill habitats on the Atlantic Coastal Ridge, the Northern Brooksville Ridge, or the sandy uplands of northern Florida. The inland south-central sand ridges of the Florida Peninsula are over a million years old, and are known to have many plants and animals found nowhere else (Deyrup 1989, 1990). Some of these species appear to be remnant populations of species that were once more widespread, others are probably true (autochthonous) endemics. Up to the discovery of the distinct status of *O. relictus*, it seemed that this ant was an example of a series of remnant populations; now it appears that this species could just as easily be a true endemic of south-central Florida.

The restricted range and habitat of *O. relictus* might raise questions about its conservation status. About twenty-five years ago, its prospects would have seemed poor. At that time there were only two protected populations, one on the Lake Wales Ridge (Archbold Biological Station), the other on the southern Brooksville Ridge (Withlacoochee State Forest). Upland areas were being converted rapidly to housing and agriculture, and it seemed that few scrub and sandhill areas would remain within the range of *O. relictus*. Since that time, development and habitat destruction have occurred at an unprecedented rate, but the establishment of ecological preserves also has been remarkably fast, especially on the Lake Wales Ridge. This species now appears to be adequately protected, unless it is subjected to some widespread environmental threat that pervades natural areas. *Odontomachus relictus* is a good example of a species that seemed destined for the endangered species list, with all the trouble and expense implied in such listing, but was preemptively protected by more general conservation programs.

SPECIES OF *Odontomachus* IN THE U.S.

The following keys distinguish between the four species known from the U.S. Brief comments on distribution, nomenclature and natural history follow the keys.

Key to Worker and Queen *Odontomachus* of the U.S.

- 1. Hairs on first gastral tergite extremely fine and dense: spaces between hairs less than one-third as wide as the length of hairs (SE U.S., perhaps Neotropics) *brunneus* (Patton)
- 1'. Hairs on first gastral tergite sparse, spaces between hairs at least one half as wide as length of hairs 2
- 2. Posterior face of petiole with conspicuous transverse striae (Fig. 2I) (Florida, W. Indies, perhaps elsewhere in the Neotropics) *ruginodis* M. R. Smith
- 2'. Posterior face of petiole smooth (as in Fig. 1C) 3
- 3. Basalar lobe (oval sclerite at posterior dorsal corner of mesopleuron) conspicuously striate (Fig. 2K) (south-central peninsular Florida) *relictus*, new species
- 3'. Basalar lobe smooth (Fig. 2J) (southwestern U.S., Mexico) *clarus* Roger

Key to Male *Odontomachus* of the U.S.

- 1. Each ocellus at least as wide as space between lateral ocelli and eye (Figs. 2A, C) 2
- 1'. Ocelli much smaller than space between lateral ocelli and eye (Figs. 2B, D) 3
- 2. Head and body pale orange, antennae brown *brunneus*
- 2'. Head and body brown, antennae yellowish *relictus*
- 3. Head and body mostly yellowish, propodeum and sometimes gaster contrasting brown; central area of pronotum smooth and shining *ruginodis*
- 3'. Head and body dark brown; pronotum finely striate *clarus*

Notes on Species

Odontomachus brunneus. This species apparently occurs throughout Florida, although there are no records from the three westernmost coun-

ties. It is also known from southern Georgia and Alabama. We have seen specimens from low coastal areas in Alabama, and there is no obvious reason why it should not occur in coastal Mississippi, Louisiana and Texas, although it is not re-

ported from any of those states. A report of *brunneus* from Cuba (Fontenla 1997) might refer to some other species, as we have seen specimens that would key to *brunneus* from the Dominican Republic, but are probably closer to *O. insularis* Guerin. Its distribution in Central and South America is unclear, since this species was combined with *O. ruginodis* in Brown's revision of the genus (1976). Associating the various *brunneus*-like forms with their males in Central and South America and the West Indies would be an interesting and useful project for local myrmecologists, and might easily yield distributional surprises or new species. Workers can easily be distinguished from other U.S. species by the densely hairy gaster.

Southeastern records of *insularis* in the Formicidae section of the Catalog of the Hymenoptera (D. R. Smith 1979) refer to *brunneus*. Although the catalog appeared several years after Brown's revision, the cut-off date for changes in the Formicidae section was mid-1975. Smith's treatment of North American *Odontomachus* differs from those of Creighton (1950) and M. R. Smith (1951) in elevating to species level three subspecies of *O. haematodus* (Linnaeus). This was backed by no taxonomic references, and certainly was not intended to compete with the earlier, but unavailable, revision by Brown.

Odontomachus brunneus occurs in both well-drained and poorly drained habitats; nests may be in soil or in rotten wood. This species, along with many others, was studied by Van Pelt (1958) at the Welaka Reserve (now Welaka State Forest) in Putnam Co., Florida. Van Pelt found many colonies, which occurred in all the terrestrial habitats in the area, including flatwoods, mesic forest, swamp forest, upland scrub and sandhill. Nests were in various microhabitats, including deep leaf litter, fallen logs, at the bases of trees, and open or sparsely covered sandy areas. At the Archbold Biological Station, *brunneus* occurs in moist habitats, including flatwoods, bayheads, the edges of seasonal ponds, and elevated tussocks or fallen pines within seasonal ponds. It has not been found in the more elevated upland areas of the Station, which are occupied by *relictus*. This distribution gives the impression that there is some competitive displacement based on differential adaptation to moisture conditions, but the evidence remains circumstantial. It may be relevant that in parts of its range devoid of *relictus*, where *brunneus* occurs in dry, upland areas individuals never achieve the large size and dark color seen in some specimens from wet areas. Nobody knows, however, whether the smaller, paler individuals represent stressed individuals in suboptimal conditions, or whether they represent an adaptive phenotypic response in a robust population.

Workers of *brunneus* sometimes emerge to forage on cloudy days, but are generally nocturnal. The formidable jaws of *brunneus* are not used as

assertively as one might expect, and there is fragmentary evidence that *brunneus* is sensitive to chemical defenses. Prey are approached tentatively, and the ant recoils immediately after striking the prey (Brown 1976). There may be a delay before the prey is picked up and carried away; Brown (1976) suggested that these ants react to chemical defenses, which are allowed to dissipate before the prey is retrieved. Alex Wild, while a student at the Archbold Biological Station, twice observed *brunneus* retreating hastily when confronted by aroused workers of *Dorymyrmex bureni* (Trager) (unpublished natural history notes on file at the Archbold Biological Station). *Dorymyrmex bureni* is much smaller than *O. brunneus*, but can release large quantities of defensive chemicals that are pungent to the human nose. Van Pelt (1958) reported accumulations of *brunneus* head capsules in the nests of *Formica archboldi* Smith, and suggested the possibility that *brunneus* is a regular part of the diet of *F. archboldi*. If this is the case, it is more likely that the *brunneus* are subdued by chemical means than by mandible-to-mandible combat.

During this study specimens were examined from the following areas: FL: Alachua, Baker, Bay, Bradford, Brevard, Broward, Citrus, Clay, Collier, Columbia, Dade, De Soto, Dixie, Duval, Franklin, Gadsden, Gilchrist, Glades, Hamilton, Hernando, Highlands, Hillsborough, Indian River, Jackson, Jefferson, Lake, Lee, Leon, Levy, Liberty, Madison, Marion, Martin, Monroe, Nassau, Okeechobee, Orange, Osceola, Palm Beach, Pasco, Polk, Putnam, Sarasota, St. Lucie, Sumter, Taylor, Volusia, Wakulla, Walton Counties; GA: Clinch County; AL: Baldwin, Houston Counties.

Odontomachus clarus. This species is known from northern Mexico and from Texas, New Mexico and Arizona. It is the only *Odontomachus* known from the southwestern U.S. and northern border of Mexico, so specimens may be identified tentatively by their source alone. The similar species *ruginodis* will probably be transported to the southwestern U.S.; *ruginodis* has conspicuous striae on the posterior face of the petiole (Fig. 2I). It is also possible that the species we consider *clarus* includes unrecognized cryptic species. If this is the case, the occurrence of additional species might be detected by finding more than one form of male within the range of *clarus*. We have seen males associated with workers of *clarus* from two widely separated sites: Cochise Co., AZ, and Jeff Davis Co., TX. In our experience, it is difficult to find workers of *clarus* with associated males. Examination of specimens from light traps or flight traps might be a convenient way to establish whether there is more than one western species. Records of *clarus* from the West Indies (Smith 1979) refer to some other species, perhaps *ruginodis*. All references to *clarus* in Florida (Deyrup et al. 1985; Deyrup 1989; Deyrup et al.

1989; Deyrup 1990; Sivinski et al. 1998) should be referred to *relictus*, as discussed above.

The species names *coninodis* Wheeler and *desertorum* Wheeler, listed in the 1979 catalog, were synonymized under *clarus* by Brown (1976). Brown reported that "*coninodis*," which has a blunt petiolar spine, occurs at the higher elevations in Arizona, in isolated, low mountain ranges, surrounded by lower areas occupied by typical *clarus* with an elongate petiolar spine. The distribution of the two forms is unlike that of a normal pair of geographic subspecies, and Brown characterized the short-spined forms as "depauperate ecotypes or ecophenotypes." As in the case (mentioned above) of the smaller, paler *brunneus* found in dry sites, it seems premature to apply the pejorative "depauperate" to a condition that, for all we know, could be a superb adaptive response.

In Arizona this species is found, usually in small numbers, under rocks and grass tussocks, in both dry and mesic sites. In western Texas it shows a preference for more mesic sites and fine soils; nests are usually found under rocks or logs (Cokendolpher & Francke 1990).

During this study specimens were examined from the following sites (we provide more detailed site information for *clarus* than for *brunneus* or *ruginodis* because of evidence of geographic variability in *clarus*). AZ: Cochise Co. (Chiricahua Mts: Cave Creek, Texas, and Idlewild Canyons), Pima Co. (Tucson), Santa Cruz Co. (Patagonia Mts., Pajarito Mts.); TX: Bosque Co. (Meridian), Brewster Co. (Big Bend National Park: Rio Grande Village), Denton Co. (no locality), Jeff Davis Co. (Davis Mts.), Travis Co. (Bull Creek, McNeil); MEXICO: Chihuahua (Riva Palacio, Guerero, Conchos), Coahuilla (25 km E. of Saltillo), Cuernavaca (no locality), Guanajuato (highway 57 km 57), Hidalgo (San Miguel), Jalisco (Guadalupe), Mexico (Pedrigales), Nuevo Leon ((Monterrey), Queretaro (3 mi. W. of Queretaro).

Odontomachus ruginodis. This species occurs sporadically through southern and central Florida, at least as far north as Orlando, and also in the West Indies. Its distribution in South and Central America is unclear because it has been confused with *brunneus*. Its ability to thrive in disturbed habitats should allow it to invade mainland Neotropical areas, if it is not already present. It is probable that this species will be distributed by commerce to disturbed areas in the Southwest. The conspicuous striae on the posterior face of the petiole (Fig. 2I) distinguish workers of this species from the similar *clarus* and *relictus*, but there are additional species with petiolar striae (e.g., *O. bauri* Emery) outside the U.S.

The name *ruginodis* was first applied by Wheeler (1905), and Wheeler was designated as the author of *ruginodis* in Deyrup et al. (1985) and Deyrup et al. (1989). The name *ruginodis*,

however, was first used as a quadrinomial (*Odontomachus haematodus insularis ruginodis*), and therefore is not a valid name under the rules of nomenclature. The first use of *ruginodis* as a trinomial, or subspecies (*Odontomachus haematodus ruginodis*), was by M. R. Smith (1937). Since this is the first valid use of *ruginodis* for this species, M. R. Smith is the author of the name. This, along with hundreds of other tangles of nomenclature, was straightened out in Bolton's 1995 catalog of ants.

In Florida, this species occurs in disturbed areas, including urban and suburban habitats. It occurs along the beaches in the tropical part of the state. It has not yet been found inland in natural habitats. In Puerto Rico it differs from another sympatric species (perhaps *O. bauri*) in its preference for open, sunny areas, especially river bottoms (Smith 1937).

The defensive mandible-snapping behavior of *ruginodis* was studied by Carlin and Gladstein (1989). When a nest is attacked by other ants, the *ruginodis* workers rush out, snapping at anything that seems a threat. Enemy ants may be dismembered or knocked out of the way by the mandibular strikes. If the mandibles hit a solid object, the *ruginodis* may itself be flung into the air for a distance of several centimeters. This does not seem to be an escape mechanism, as the worker, upon landing, immediately charges back into the fray. The nest entrance is usually guarded by a single worker, who stands with cocked mandibles near the entrance. If an intruder approaches within striking distance, the mandibles snap shut, responding to signals from the antennae and long sensory hairs at the bases of the mandibles. The heavy apices of the mandibles do not slice into the intruder, but knock it away a distance of about one to fourteen centimeters. Carlin and Gladstein call this the "bouncer defense."

During this study specimens were examined from the following areas: FL: Brevard, Broward, Charlotte, Collier, Dade, Glades, Hendry, Highlands, Hillsborough, Indian River, Lee, Manatee, Martin, Monroe, Orange, Palm Beach, Pinellas, Orange, Polk, St. Lucie, Volusia Counties; BER-MUDA; BAHAMAS: New Providence, San Salvador, Rum Cay, North Andros Islands; PUERTO RICO: Rio Grande.

Residual Problems

There are still some questions on the taxonomy and distribution of the *Odontomachus* species that occur in the U.S. The distribution of *brunneus* and *ruginodis* is unclear. Does *brunneus* occur in coastal wetlands around the Gulf of Mexico? Is *brunneus* as it appears in the southeastern North America the same species as the *brunneus* populations reported from the West Indies and the mainland Neotropics? Does *ruginodis*

dis occur outside the West Indies and Florida? Another kind of question deals with the morphological divergences between males of different species. Do the kind of differences we have reported relate to differences in ecology and behavior of the species? Will *Odontomachus* males prove useful in distinguishing species throughout the Neotropics? The few males of *insularis* and *bauri* that we have seen show conspicuous species differences, but there could be species complexes that cannot be elucidated by male morphology.

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LITERATURE CITED

- BOLTON, B. 1995. A New General Catalog of the Ants of the World. Harvard University Press, Cambridge, MA. 504 pp.
- BROWN, W. L., JR. 1976. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachini. Section A. Introduction, subtribal characters, genus *Odontomachus*. *Studia Entomologica* 19: 67-171.
- CARLIN, N. F., AND D. S. GLADSTEIN. 1989. The "bouncer" defense of *Odontomachus ruginodis* and other odontomachine ants (Hymenoptera: Formicidae). *Psyche* 96: 1-19.
- COKENDOLPHER, J. C., AND O. F. FRANCKE. 1990. The Ants (Hymenoptera, Formicidae) of Western Texas. Part II. Subfamilies Ecitoninae, Ponerinae, Pseudomyrmecinae, Dolichoderinae, and Formicinae. Museum of Texas Tech University Special Publication 30: 3-76.
- CREIGHTON, W. S. 1950. The Ants of North America. *Bull. Harvard Mus. Compar. Zool.* 104: 1-583.
- DEYRUP, M. 1989. Arthropods endemic to Florida scrub. *Florida Scientist* 52: 254-270.
- DEYRUP, M. 1990. Arthropod footprints in the sands of time. *Florida Entomol.* 73: 529-538.
- DEYRUP, M. 2002. The exotic ant *Anochetus mayri* in Florida (Hymenoptera: Formicidae). *Florida Entomol.* 85: 658-659.
- DEYRUP, M., C. JOHNSON, G. C. WHEELER, AND J. WHEELER. 1989. A preliminary list of the ants of Florida. *Florida Entomol.* 72: 91-101.
- DEYRUP, M., J. TRAGER, AND N. CARLIN. 1985. The genus *Odontomachus* in the southeastern United States (Hymenoptera: Formicidae). *Entomological News* 96: 188-195.
- FONTENLA, J. L. 1997. Lista preliminary de las hormigas de Cuba (Hymenoptera: Formicidae). *Cucujo* 6: 18-21.
- GRONENBERG, W., J. TAUTZ, AND B. HÖLLDOBLER. 1993. Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science* 262: 561-563.
- HÖLLDOBLER, B., AND E. O. WILSON. 1990. The Ants. Harvard University Press, Cambridge, MA. 732 pp.
- MYERS, R. L. 1990. Scrub and high pine, pp.150-193. *In* R. L. Myers and J. J. Ewel [eds.]. *Ecosystems of Florida*. University of Central Florida Press, Orlando. xviii + 765 pp.
- SIVINSKI, J., J. E. LLOYD, S. N. BESHES, L. R. DAVIS, R. G. SIVINSKI, S. R. WING, R. T. SULLIVAN, P. E. CUSHING, AND E. PETERSSON. 1998. A natural history of *Pleotomodes needhami* Green (Coleoptera: Lampyridae): a firefly symbiont of ants. *Coleop. Bull.* 52: 23-30.
- SMITH, D. R. 1979. Formicidae, pp. 1323-1467. *In* K. V. Krombein, P. D. Hurd, Jr., D. R. Smith and B. D. Burks [eds.]. *Catalog of Hymenoptera in North America North of Mexico*. Smithsonian Institution Press, Washington, D. C. 2735 pp.
- SMITH, M. R. 1937. The ants of Puerto Rico. *J. Agric. Univ. Puerto Rico* 20: 819-875.
- SMITH, M. R. 1951. Formicidae, pp. 778-875. *In* C. F. W. Muesebeck and K. V. Krombein (eds.). *Hymenoptera of America North of Mexico*, Synoptic Catalog. Smithsonian Institution Press, Washington, D.C. 1420 pp.
- VAN PELT, A. 1958. The ecology of the ants of the Welaka Reserve, Florida (Hymenoptera: Formicidae). Part II. Annotated list. *American Midland Natur.* 59: 1-57.
- WEBB, S. D. 1990. Historical biogeography, pp.70-100. *In* R. L. Myers and J. J. Ewel [eds.]. *Ecosystems of Florida*. University of Central Florida Press, Orlando, FL. xviii + 765 pp.
- WHEELER, W. M. 1905. The Ants of the Bahamas, with a list of the known West Indian species. *Bull. American Mus. Natur. Hist.* 21: 79-135.