

**STENOTARSUS SUBTILIS ARROW, THE AGGREGATING FUNGUS BEETLE
OF BARRO COLORADO ISLAND NATURE MONUMENT, PANAMA
(COLEOPTERA: ENDOMYCHIDAE)**

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Abstract

Stenotarsus subtilis Arrow (not *S. rotundus* Arrow) is the aggregating endomychid beetle from Barro Colorado Island, Panama, subject of many studies on a diapausing aggregation. Allozyme analysis results (Nei genetic distance = 0.005) supported conclusions from morphological study, revealing the true identity of two diapause groups now known within the Barro Colorado Island Nature Monument. They have an the estimated aggregation density of 2.2 per km², with up to 200,000 individuals in each aggregation. Females predominate in these groups, but sex ratios varied from 1:1 to 1:4. One group has persisted at least 20 years. Bark was depleted of Mg and K on both *Oenocarpus* C. F. P. Martius (Palmae) and *Tetragastris* J. Gaertner (Burseraceae) diapause sites, but did not differ visibly from surrounding bark. Fungi showed no consistent relationship with beetles or sites. Bark and wood substrates of an aggregation did not attract beetles when displaced to other forest areas. We suggest beetles may live more than one year and return to diapause sites after completing the still undocumented mating and reproductive facets of their life cycle. *Stenotarsus rotundus* is synonymized under *S. ovalis* Arrow, **new synonymy**, and a key is given to known species of *Stenotarsus* occurring in Panama.

Adults of *Stenotarsus* Perty were found on Barro Colorado Island (BCI), Panama in an aggregation near the base of a palm tree in 1980 (Cover, this issue). Beetles diapaused there for some 10 months each year, unable to disperse (Wolda and Denlinger 1984). This beetle, previously identified as *Stenotarsus rotundus* Arrow, has been referred to by that name in many publications. Discovery of a second *Stenotarsus* diapause site on the Gigante Peninsula within BCI Nature Monument (BCNM) by the senior author (DWR) in 1993 led to some interesting speculation (Nedved 1996) and prompted another look at beetle identity. After repeated studies of the two beetle aggregations during seven years, including isoenzyme assays and resolution of taxonomic questions, we present new data on the genus. We show that aggregations of *Stenotarsus* are not exclusive to a tree species and we give information on their composition, fungal associates, chemical site characteristics, persistence and formation. An identification key to adult beetles also is provided.

Methods and Materials

Taxonomy. To make identifications we employed H. F. Strohecker's collection of Endomychidae. Strohecker identified many specimens by comparison with type material. Although there are nearly 100 *Stenotarsus* species described from the New World, the Strohecker collection contains only half of them. We quickly discovered that the aggregating beetles of BCNM did not match any beetles identified in Strohecker's personal collection. To avoid a full revision of so many taxa, we decided to search the literature for species from Panama and compare these with the aggregating beetles. After borrowing types of Panamanian species not present in Strohecker's collection, it was clear that beetles of both sites within BCNM matched *S. subtilis* Arrow. Here we present a key to Panamanian *Stenotarsus* and describe additional features of four aggregations that include this and another species. Reference material is deposited in the Fairchild Entomological Collection, University of Panama (FEUP), the Natural History Museum, London (NHML); the Strohecker Endomychidae Collection, Florida State Collection of Arthropods (FSCA); the Smithsonian Tropical Research Institute, Panama (STRI); Ohio State University (OSUC), and P. E. Skelley collection, Gainesville, FL (PESC).

Fungi associated with the aggregating populations were identified only to morphospecies.

Genetics. Our initial study left little doubt that beetles of the two aggregations were of a single species. Nonetheless, the possibility of isolation between aggregating populations on an island and the mainland, and subsequent genetic divergence, was investigated. Genetic characteristics of aggregating *S. subtilis* were evaluated in 1995, twice in 1996 and again in 1998, by sampling several hundred individuals on a given date, then performing horizontal starch gel electrophoresis on a subset of 30–50 beetles from each to assess variation in isoenzymes. This technique is useful for determining whether two taxa are the same species, and is also sensitive to degree of divergence among different populations (Brussard *et al.* 1985; Carman and Packer 1996).

Fifty beetles were compared (25 from each aggregation) using samples taken on October 5, 1995. The preliminary screening included 21 isoenzyme systems, 6 of which proved adequate and scorable (see Table 1). The eight presumptive genetic loci in the six systems included peptidases VLP1 (peptidase valine-leucine), VLP2, LGGP (peptidase leucine-glycine), malate dehydrogenase-NADP (ME), glucose-6-phosphate isomerase (GPI), malate dehydrogenase (MDH1, MDH2), and isocitrate dehydrogenase (ICD1). The isoenzyme data were used to derive a genetic distance coefficient (Nei 1978).

The BCI aggregation was further sampled on 17 January and 14 August, 1996, and again on 27 March, 1998. Samples were run by G. Keller at the STRI protein electrophoresis laboratory in Panama, during September, 1998. Prior to study, beetles were preserved at -70°C . The three samples included 141 beetles, and were run using the same gel and buffer systems used in the initial population comparison. Standard methodology employed gel and enzyme buffer systems taken from Clayton and Tretiak (1972) and Ridgway *et al.* (1970).

Natural History. Many facets in the life cycle of *Stenotarsus* are poorly known. With discovery of the second aggregation, much larger than the one reported on BCI, new avenues of investigation became possible. Position of beetles on the substrate of the second diapause site, a large tree (*ca.* 45 cm diameter) of *Tetragastris panamensis* (Engler) O. Kuntze (Bursaceae) was

Table 1. Allele frequencies in Gigante Peninsula and Barro Colorado Island groups of diapausing *Stenotarsus subtilis* (see Methods).

<i>Locus</i>	<i>Gigante Peninsula</i> <i>N, allele:frequency</i>	<i>Barro Colorado</i>	<i>Barro Colorado</i> (1996–98)
VLP1	25, A: 1.00	25, A: 1.00	
VLP2	25, A: 1.00	25, A: 1.00	
LGGP	25, A: 1.00	25, A: 1.00	
ME	25, A: 1.00	25, A: 1.00	36, A: 0.92 B: 0.08
GPI	25, A: 0.88 B: 0.04 C: 0.04 D: 0.04	25, A: 0.92 B: 0.00 C: 0.08 D: 0.00	
ICD1	24, A: 0.04 B: 0.94 C: 0.02	23, A: 0.06 B: 0.94 C: 0.00	
MDH1	25, A: 0.02 B: 0.00 C: 0.18 D: 0.76 E: 0.04	24, A: 0.00 B: 0.02 C: 0.15 D: 0.73 E: 0.10	80, A: 0.03 B: 0.01 C: 0.06 D: 0.78 E: 0.12
MDH2	15, A: 0.33 B: 0.64 C: 0.03	15, A: 0.08 B: 0.84 C: 0.08	25, A: 0.08 B: 0.55 C: 0.37

noted. Aggregation size was estimated from measurement of total surface area and subsample counts from smaller areas. Certain parts of this and the diapause substrate known on BCI, a small, slender palm tree (*Oenocarpus panamanus* Bailey) clearly were not being used by the beetles, yet the same spots on which beetles had aggregated were again occupied after complete disappearance from the tree. The chemical composition of the bark on the two trees was therefore studied. Samples were taken from bark on which beetles aggregated, and from that adjacent to the aggregation area, where beetles never were seen. The material was dried at *ca.* 60°C, ground to powder with a mortar and pestle, and sent for analysis to the Soil, Water and Plant Testing Laboratory, Colorado State University. Because samples were under 1 g dry weight, limited chemical tests were possible. We considered only pH, electrical conductivity, and the content (milligram equivalents per liter) of Ca, Mg, Na and K.

For fungal screening, further substrate samples were taken on December 8, 1999, both from occupied and unoccupied areas on both diapause site trees. Fungi were grown in laboratory cultures of the beetle and non-beetle samples, then examined with a microscope (courtesy of Enith Rojas, BCI).

Beetle sex ratios in the aggregations were scored using secondary sexual characteristics (see Results, Taxonomy). A total of 12 samples were taken over different times of the year, during 1995, 1997, 1998 and 1999. A standard sample of 50 individuals was assessed, from a larger sample including beetles from different portions of each aggregation.

The *Tetragastris* aggregation tree was blown down during a storm in November of 1998. The aggregation was monitored through this diapause season, dispersal phase, and the following diapause season, until December 8, 1999. In diapause season, beetles occupied a 60 × 15 cm area within the lower

aggregation area on the slowly dying tree. On 8 April, 1999, a portion of the beetles was removed from the aggregation, which then was on the underside of the tree 20 cm above ground. Beetles readily flew at this time, showing they were ready for the annual dispersal (see Tanaka *et al.* 1987). A chain saw was used to slice a 7 cm section of the trunk, passing through the edge of the aggregation area. From this tree trunk slab, two halves were taken: one that had been occupied by the beetles and one that had not. These and approximately 600 beetles were transported to the Pipeline Road within Soberania National Park, on the mainland about 12 km from BCI, and were placed in a semi-sheltered area within old growth forest that resembled that of BCNM where the beetle aggregations were found. Beetles were returned to the tree trunk section they had originally occupied, and the unoccupied section was placed 0.5 m distant.

On 11 April, no beetles were found on either of the displaced substrates. Timing of beetle departure coincided with the first heavy rains of the season, but periodic monitoring up until that date was not performed. As a second experiment, bark of the original aggregation area (*ca.* 50 cm²) was placed on a laboratory balcony on BCI, tied to the railing with nylon rope. These substrate removal experiments were checked in early May, after the dispersal of beetles from the natural BCNM sites, and in early July, after the BCI beetles had again aggregated on the *Oenocarpus* C. F. P. Martius and *Tetragastris* J. Gaertner.

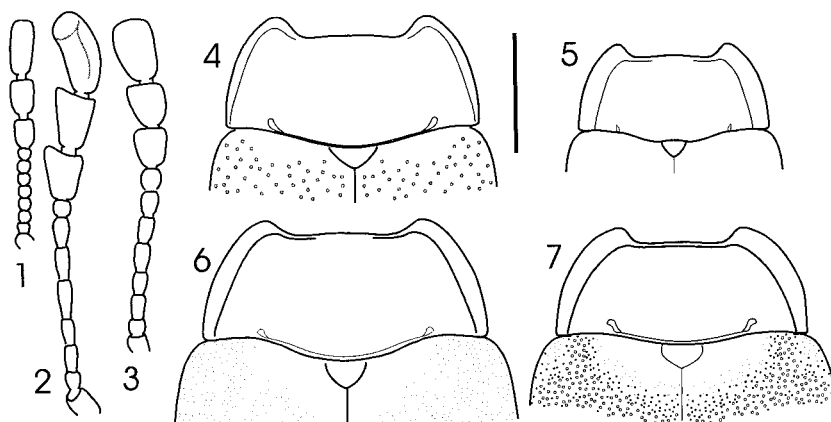
Results

Stenotarsus Perty

Taxonomy. Lawrence and Newton (1995) give the most recent classification of the family, placing *Stenotarsus* in the Epipocinae. *Stenotarsus* has over 250 species occurring primarily in tropical regions throughout the world. The genus is extremely diverse in morphology, which suggests similar diversity in biology. There are no recent revisions to aid identification in the Americas.

Stenotarsus is readily distinguished from other endomychids by the following set of characters—pseudotrimerous tarsi, with tarsomere II lobed and bearing a dense, spongy mat of setae underneath; antennal club 3-segmented, segments not transverse; pronotum with broad, flat lateral bead; body distinctly pubescent, pubescence frequently dense, usually uniformly red-brown; body occasionally with a large black area on each elytron and the pronotum. Strohecker (1953) presents a key to the subfamilies and genera of the World's Endomychidae. Since then, numerous taxonomic reorganizations have occurred. The first description of *Stenotarsus* larvae is in McHugh and Pakaluk (1997) based on two Australian taxa. Larvae of most *Stenotarsus* remain unknown. Published descriptions of adult beetles are brief and generally uninformative, unless one is familiar with the genus. Species identifications are based primarily upon comparison with properly identified material, and revisionary work is needed.

Useful characters exist for identifying species of *Stenotarsus*, for example sexual dimorphism, the shape and color of antennomeres, body size and shape, vestiture color and density, and male genitalia. Species also are distinguishable by the presence or absence of black marks on the pronotum and elytra. Comparison of characters indicates that these marks are somewhat variable within a population, or are clinal (see following Remarks of *Stenotarsus ovalis* Arrow and *S. panamanus* Gorham). Not all species display sexual dimorphism, how-



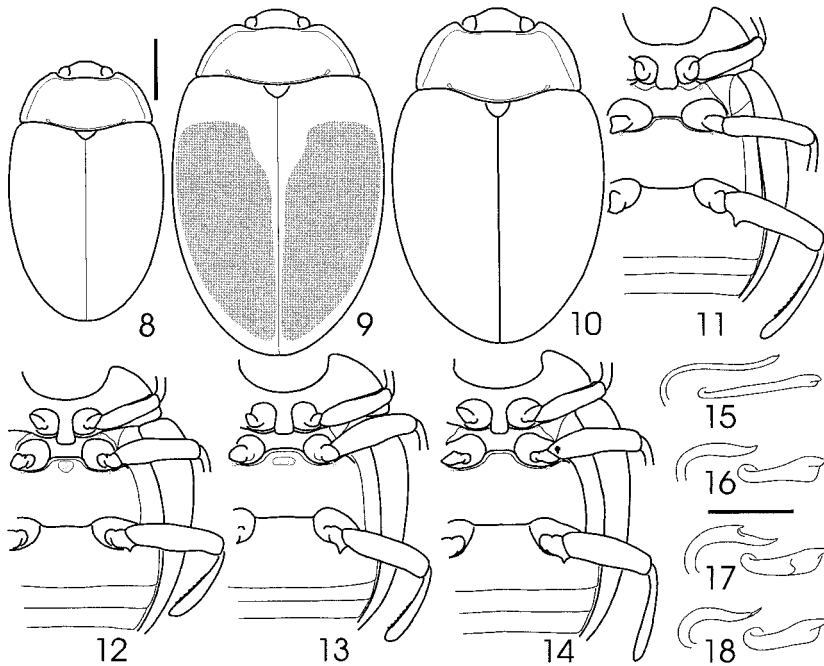
Figs. 1–7. *Stenotarsus* spp.: 1–3) Antenna: 1) *Stenotarsus validicornis*; 2) *S. purpuratus*; 3) *S. subtilis*. 4–7) Pronota and elytral bases: 4) *S. cyanopterus*; 5) *S. lemniscatus*; 6) *S. subtilis*; 7) *S. ovalis*. Scale line = 1 mm.

ever. Males of some species can possess any of the following sexually dimorphic characters: spur on the metatrochanter (Tanaka 1986) or metafemur; metatibia modified, curved, with or without internal tubercles; metasternum with various structures on the anterior edge between the mesocoxae, usually a depression of some definable shape; abdomen sometimes with a dense patch of setae on one or all sternites. In addition, there can be different body and appendage proportions (Nedved and Windsor 1994b). These dimorphisms are present in various combinations and degrees between species, and frequently offer the best characters for identification. Females of many species that lack such characters often are impossible to identify without an associated male.

Many species of *Stenotarsus* occur in Panama. We were unable to identify some of the material available for study, and left these specimens for future work. The following key to eleven Panamanian species includes only those with published records, or specimens identified by Strohecker.

Key to the Known *Stenotarsus* of Panama

- 1) Antennomeres III–VIII not elongate, moniliform; antennal club segments narrow, nearly parallel sided (Fig. 1) *S. validicornis* Gerstaecker
- 1') Some or all of antennomeres III–VIII elongate; antennal club segments not narrowed (Figs. 2, 3) 2
- 2) Antennomere XI elongate and appearing curved (Fig. 2); antenna long, reaching middle of elytra *S. purpuratus* Gerstaecker
- 2') Antennomere XI oval, not elongated or curved (Fig. 3); antenna not as long, reaching only basal 1/3 of elytra 3
- 3) Pronotal lateral margin relatively narrow (Fig. 4), width at hind angle distinctly less than length of antennomere II *S. cyanopterus* Gorham
- 3') Pronotal lateral margin broad for entire length (Figs. 5–7), width at hind angle equal or greater than length of antennomere II 4
- 4) Base of pronotum between pores with margin weak or absent (Fig. 5); pronotal base weakly concave over scutellum ... *S. lemniscatus* Gorham



Figs. 8–18. *Stenotarsus* spp.: 8–10) Dorsal habitus: 8) *Stenotarsus cuprivestis*; 9) *S. panamanus*; 10) *S. subtilis*. 11–14) Ventral view of male: 11) *S. globosus*; 12) *S. obtusus*; 13) *S. ovalis*; 14) *S. subtilis*. 15–18) Aedeagus, ventral and lateral views: 15) *S. panamanus*; 16) *S. obtusus*; 17) *S. ovalis*; 18) *S. subtilis*. Scale line = 1 mm.

- 4') Base of pronotum between pores with strong margin that leads into the pores (Figs. 6, 7); pronotal base convex over scutellum 5
- 5) Elytron with basal punctures in the depression next to the humerus not much larger than those near the scutellum (Fig. 6); disc of elytron with weak foveate punctures *S. subtilis* Arrow
- 5') Elytron with coarse basal punctures in the depression next to the humerus distinctly larger than those near the scutellum (Fig. 7); disc of elytron with notable foveate punctures, often impressed 6
- 6) Body relatively elongate and small, less than 4.5 mm (Fig. 8) *S. cuprivestis* Gorham
- 6') Body oval and larger, generally more than 4.5 mm (Figs. 9, 10) 7
- 7) Body with color pattern (Fig. 9) 8
- 7') Body entirely orange (Fig. 10) 9
- 8) Pronotal pubescence dark purple to black (best viewed in profile); metafemur of male with basal spine (Fig. 11) *S. globosus* Guérin-Ménéville
- 8') Pronotal pubescence golden-yellow; metafemur of male lacking spine *S. panamanus* Gorham and *S. chiriquinus* Arrow
- 9) Male metatrochanter lacking spine; male genitalia long and narrow (Fig. 15) *S. panamanus* Gorham
- 9') Male metatrochanter with spine (Figs. 12–14); male genitalia relatively short and broad (Figs. 16–18) 10

- 10) Male with circular depression on anterior part of metasternum (Fig. 12); male genitalia simple, lacking accessory process (Fig. 16)
 *S. obtusus* Gerstaecker
- 10) Male with transversely elongated depression on anterior part of metasternum (Fig. 13); male genitalia with an accessory process (Fig. 17)
 *S. ovalis* Arrow

Taxonomic notes on Panamanian species

Stenotarsus cuprivestis Gorham (1890:139)

Diagnosis. Length 4.0–4.2 mm; width 2.5–2.8 mm. Body entirely red-orange, elongate (Fig. 8). Named for the color of the vestiture, yet no difference in color from that of many other species was noted. The male available for study is damaged; no sexual dimorphism was found.

Remarks. Some specimens in the type series were from Panama. A male and female from Panama (FSCA) were studied.

Stenotarsus cyanopterus Gorham (1890:133)

Diagnosis. Length 4.5 mm; width 3.0 mm. Body oval, red-orange; each elytron with a central mark of a metallic blue shine; pronotum with the lateral margin narrow (Fig. 4). Sexual dimorphism is unknown.

Remarks. This species was originally described from Panama. Only a female syntype (NHML) was studied. The narrow pronotal margin was commented upon by Arrow (1920), who transferred this species to *Stenotarsus*. Its placement here awaits further studies at the generic level.

Stenotarsus globosus Guérin-Méneville (1857:270)

Diagnosis. Length 5.5–6.1 mm; width 3.5–4.1 mm. Body oval, usually black, with only the elytral margins and suture red, but some specimens mostly red; pronotal setae purple-black; male metafemur with a basal spine, metatibia narrow, with internal row of tubercles (Fig. 11).

Remarks. Based on various comments and discrepancies between localities cited in Gorham (1890), Arrow (1920), Blackwelder (1945), and Strohecker (1953), there is confusion as to the identity of specimens from southern Central America. Blackwelder (1945) states this taxon is in Panama, thus it is included here. Specimens studied were from Mexico and Central America (FSCA).

Stenotarsus lemniscatus Gorham (1890:139)

Diagnosis. Length 3.0–3.8 mm; width 2.0–2.2 mm. Body weakly elongate, red-orange; base of the pronotum without distinct margin (Fig. 5); pronotal base weakly concave over scutellum; no sexual dimorphism observed.

Remarks. Specimens from Panama are present in Strohecker's collection (FSCA).

Stenotarsus obtusus Gerstaecker (1858:310)

Diagnosis. Length 5.0–6.0 mm; width 3.5–4.0 mm. Body red-orange, broadly oval; elytra with distinct coarse punctures near the humerus; male with spine on metatrochanter (Fig. 12), metasternum with a circular depression at anterior margin, hind tibia curved with internal row of tubercles, genitalia simple (Fig. 16), relatively short and broad.

Remarks. Gorham (1890) identified specimens from Panama as this species, based on Gerstaecker's description. We studied material from several South American countries (FSCA). Females were indistinguishable from those of *S. ovalis*, or the red specimens of *S. panamanus*, except by association with a male.

Stenotarsus ovalis Arrow (1920:50)

Stenotarsus rotundus Arrow (1920:52–53) **New Synonymy**

Diagnosis. Length 4.5–5.0 mm; width 3.0–3.5 mm. Body broadly oval, with color pattern or not; elytra with distinct coarse punctures near the humerus (Fig. 7); male with spine on metatrochanter, metasternum with transversely oval depression at anterior margin (Fig. 13), hind tibia curved, with row of internal tubercles, genitalia relatively short and broad, with accessory process (Fig. 17).

Remarks. Arrow's description of *S. ovalis* is based on Gorham's apparent misidentification of *S. orbicularis* Gerstaecker from Guatemala (Gorham 1890). Later in the same paper, Arrow (1920) describes *S. rotundus* from a single Panamanian specimen identified by Gorham as *S. pilatei* Gorham. Strohecker's collection contains his annotated copy of the Genera Insectorum for the Endomychidae (Strohecker 1953). In it, he notes that *S. rotundus* is a synonym of *S. ovalis*, which is a synonym of *S. orbicularis*. Upon studying a male syntype of *S. ovalis* from Guatemala (NHML) and the male holotype of *S. rotundus* from Panama (NHML), no morphological differences were found that would distinguish these nominate species. The only difference observed was that *S. ovalis* has a black mark on each elytron; while *S. rotundus* is entirely red. Such coloration is variable in other species of *Stenotarsus*. Additional specimens studied included Strohecker's solid orange-red specimens of *S. ovalis* from Venezuela (FSCA) and a specimen of *S. rotundus* from Panama, identified by Strohecker (STRI). Strohecker's notes also indicate he studied the type of *S. orbicularis*. Because we did not examine that specimen, no judgement can be made on possible synonymy of *S. ovalis* under *S. orbicularis*. Here we only synonymize *S. rotundus* under *S. ovalis*.

Stenotarsus panamanus (Gorham 1890:138) and *Stenotarsus chiriquinus*
(Arrow 1920:51)

Diagnosis. Length 4.2–5.5mm; width 3.0–4.0 mm. Body oval, usually with a color pattern (Fig. 9) (some solid orange), covered with golden pubescence; male genitalia long and narrow (Fig. 15). No sexual dimorphism noted.

Remarks. *Stenotarsus panamanus* and *S. chiriquinus* originally were described from Panama. The female holotype of *S. chiriquinus* (NHML) and specimens of *S. panamanus* from Panama (FSCA) were studied. No differences were discovered. Without a male to include in comparisons, we are hesitant to synonymize *S. chiriquinus*, which presumably lives at a higher elevation, and also is in the Central American biogeographic region, in contrast to eastern Panama (Kimsey 1992). These species usually have a color pattern. Mixed in with Strohecker's normally colored *S. panamanus* (FSCA) are three solid red specimens from Barro Colorado Island, Panama, which he had identified as "*S. panamanus*?". These specimens, possibly teneral, differ from *S. panamanus* and *S. chiriquinus* only in their lack of the dark body marks. For this reason, *S. panamanus* appears in the key twice.

Stenotarsus purpuratus Gerstaecker (1858:318)

Diagnosis. Length 5.7–7.0 mm; width 4.0–4.8 mm. Body dull orange, elongate; antennae elongated, reaching elytral half; antennomere XI appearing curved (Fig. 2); no notable sexual dimorphism.

Remarks. Specimens studied are from Colombia and Costa Rica (FSCA), thus the species almost certainly occurs in Panama.

Stenotarsus subtilis Arrow (1920:53)

Stenotarsus rotundus Arrow, of authors: Denlinger 1986, 1994, 1996; Nedved 1996; Nedved and Windsor 1994a, b; Tanaka 1986; Tanaka, Denlinger, and Wolda 1987; Tanaka, Wolda, and Denlinger 1987a, b, 1988; Wolda and Denlinger 1984; Yoder, Denlinger, and Wolda 1992.

Stenotarsus “*gigante*” (Nedved 1996:3) **Nomen Nudum**

Diagnosis. Length 4.5–6.0 mm; width 3.5–4.2 mm. Body oval, elytra lacking distinct coarse punctures near humerus (Fig. 6), smoothly and evenly punctate; male with spine on metatrochanter, lacking depression on anterior margin of metasternum (Fig. 14), genitalia relatively short and broad (Fig. 18). Females also recognizable by elytral punctation.

Remarks. Nedved’s (1996) use of the name *S. “gigante”* is not accompanied by a description nor any comments to set the identity of that population. Since we consider the Gigante population to be conspecific with *S. subtilis*, *S. “gigante”* is listed as a *nomen nudum* and placed as a synonym of *S. subtilis*.

Specimens studied include three female syntypes of *S. subtilis* (NHML) from David (near sea level) and V. [Volcan] de Chiriquí, Panama (approximately 1,200 m above sea level), as well as numerous specimens from both the Barro Colorado Island and Gigante Peninsula populations (approximately 100 m above sea level). Specimens from the aggregations collected during 1993–1999 will be deposited in various museums (STRI, NHML, FSCA, PESC, NMNH, OSUC, FEUP).

Stenotarsus validicornis Gerstaecker (1858:331)

Diagnosis. Length 3.5–4.2 mm; width 2.8–3.5 mm. Body stout, red-orange; antennomeres III–VIII short, antennomeres IX–XI elongated and nearly parallel sided (Fig. 1); pronotal lateral edge with a small tooth at middle; no notable sexual dimorphism.

Remarks. According to Arrow (1920:49) the Panama specimens of *Stenotarsus claviger* Gerstaecker (1858) discussed by Gorham (1890) are actually *S. validicornis*. The specimens studied are from several South American countries (FSCA), with one from Panama (PESC).

Genetics

Genetic analysis from the allozyme data confirmed the observation that the Gigante beetles and those previously studied on BCI appeared to belong to the same species. The unbiased estimate of genetic distance given by Nei (1978) was calculated to be 0.005 from the samples taken in October of 1995, based upon a mean sample size of 23–24 beetles per locus. The mean number of alleles per locus was 2.3 for the 25 beetles sampled on BCI and 1.9 from 25 taken on Gigante Peninsula (Table 1). In this genetic survey, three peptidase loci (VLP1, VLP2, LGGP) were monomorphic, as was ME. Nonetheless, the

total percentage of loci found to be polymorphic was 50% for both areas, and subsequent samples of beetles from the BCI site largely conformed to the original observation (see Table 1). However, two alleles originally found in the GPI locus did not reappear, nor did one allele of ICD1. On the other hand, another allele of LGGP was detected, in a single individual, and 1 other allele appeared for ME. Mean heterozygosity for the two groups of beetles was estimated at 0.14 and 0.11 from the BCI and Gigante locations, respectively (by direct counts, rather than Hardy-Weinberg predicted values). These are somewhat above expected levels for open-breeding, diplo-diploid insect populations (Lewontin 1974). Over three years, only a slight change was evident for the BCI group, but this may have been due to sampling error, because sample sizes were low.

Natural History

Two broad areas with irregular patches of beetles were on one side of the trunk of *Tetragastris panamensis*, beginning 20 cm above the ground, and continuing for half a meter, then at approximately 8 m above this, where smaller patches of the beetles occurred along a 2 m portion of the trunk. Both areas on the tree were on the relatively sheltered underside, which leaned 30° from vertical. By the area method described in Methods, beetles were estimated as 100,000 in each area during dry season of 1993 (January), when originally discovered, and also in October of 1995. At the end of this study, December 8, 1999, the aggregation was greatly reduced, occupying only the basal 60 cm of the underside of the tree trunk, then nearly touching the ground, and having an estimated 4,000 beetles. The final site occupied by beetles on *Tetragastris* had not been occupied previously by them, and included the dead tree trunk and a termite nest at the base of the tree and its underside, completely hidden from view.

The size of the aggregation changed during the diapause season and among years, at times occupying as little as one-fifth its fullest area. Beetle aggregations were, however, noticeably multi-layered at time when the aggregations shrank in size, during December of 1994 and 1995. Small clusters of the beetles occasionally were found under a few large rocks near the base of the tree, and on the ground. During the dispersal season, no beetles were found in any bark or rock crevice on the tree or near its base.

Physical site characteristics differed but also shared some notable similarities. The beetle aggregations occupied portions of their respective trees that had low electrical conductivity in one site but relatively high electrical conductivity in another (Table 2). The two areas did not appear different in color or texture, nor were beetles seen biting, scraping or attempting to extract anything from their substrates. At both sites the bark occupied by beetles was substantially depleted of Mg and K (Table 2). No difference was registered for pH of the unoccupied and occupied bark on individual trees, or in the levels of Ca or Na. Substrates that were experimentally relocated, with and without beetles, were not recolonized by July, after the dispersal event that occurred with the first heavy rains in late April.

The fungi that were found on the beetle trees differed between BCI and Gigante, with no species in common. In contrast to Gigante, where substrates occupied by beetles, including a recently established termite nest on the dead *Tetragastris*, had the same fungus as a portion of the trunk unoccupied by beetles, the beetle site on BCI had a fungus not found on the unoccupied

Table 2. Chemical analyses of bark substrates from *Tetragastris panamensis* and *Oenocarpus panamanus* with aggregations of *Stenotarsus subtilis* on Barro Colorado Island Natural Monument, Panama.

Substrate	Chemical* and Indicated Quality Characteristic					
	Ca	Mg	Na	K	pH	EC**
<i>Oenocarpus</i>						
aggregation site	1.64	0.30	1.30	0.40	4.3	1.0
unoccupied site	1.56	1.68	1.49	4.15	4.3	0.3
<i>Tetragastris</i>						
aggregation site	8.34	2.88	2.42	1.01	5.0	0.7
unoccupied site	12.8	5.31	2.66	6.39	5.0	2.2

* Given in milligram equivalents per liter.

** Electrical conductivity in wet sample.

substrate of *Oenocarpus*. However, this fungus was also the most common fungus observed on BCI. Similarly, the fungus associated with the diapause site on Gigante was common in the habitat.

Sex ratios of beetle aggregations were appreciably female-biased (Table 3). In ten samples taken on BCNM, and two of a second species, *S. lateralis* Arrow (1920), collected during dry season in Costa Rica (Table 3), females normally outnumbered males by a factor of two or three. Only twice were 1:1 ratios found. These were from the BCI site in mid-dry season (March) and early wet season (July). For the other periods, including April, May, October and December, BCI had ratios not differing statistically from 1:3 (two samples) or 1:2 (two samples) or 1:4 (one sample), while Gigante displayed ratios of 1:2 in three samples and 2:1 in the final sample (Chi-square test, see Table 3).

Discussion

This work included comparison of two aggregating beetles to decide whether they were distinct entities. When compared to the Barro Colorado Island group,

Table 3. Sex ratios in aggregations of *Stenotarsus* in Panama (PAN) and Costa Rica (CR). Samples collected by D. Roubik, except where noted.

Species	Locality	Date	♂♂:♀♀	Statistical Ratio*
<i>S. subtilis</i>	BCI, PAN	12/10/95	11:39	1:4
<i>S. subtilis</i>	BCI, PAN	10/14/97	14:36	1:3
<i>S. subtilis</i>	BCI, PAN	12/3/98	19:15	1:1
<i>S. subtilis</i>	BCI, PAN	5/19/99	13:37	1:3
<i>S. subtilis</i>	BCI, PAN	7/19/99	26:24	1:1
<i>S. subtilis</i>	BCI, PAN	8/12/99	18:32	1:2
<i>S. subtilis</i>	Gigante PAN	10/10/95	16:34	1:2
<i>S. subtilis</i>	Gigante PAN	4/12/97	14:36	1:2
<i>S. subtilis</i>	Gigante PAN	3/12/98	15:35	1:2
<i>S. subtilis</i>	Gigante PAN	8/12/99	33:17	2:1
<i>S. lateralis</i>	Zarcero, CR	14/3/98	13:21	1:2**
<i>S. lateralis</i>	Escazú, CR	14/3/98	13:37	1:3**

* Statistical ratios were made by comparing the observed frequencies with expected frequencies using a chi-square test.

** Sample collected in cooperation with A. Solís or W. G. Eberhard.

Nedved (1996) states that specimens from Gigante are "... a different species! At first glance they look similar, but the males have a very different shaped aedeagus, and there are other minute differences suggesting we have found another species. Definitely a new one, because J. M. Kingsolver, who has access to Strohecker's collection, failed to determine the species." We have examined genitalia of both and can find no differences. External morphological study also failed to produce differences, even minute ones. Isozyme studies did not reveal significant differences, nor did they suggest a possibility of mixed species aggregations, or notable genetic change over time. While the beetle aggregations may be genetically isolated, they are only separated by five kilometers, and might sustain intersite gene flow. This was certainly the case before 1914, when the artificially made Gatun lake separated BCI from adjacent mainland. To date, the dispersing beetles have not been followed to ascertain their range of activity, nor is it known where they mate or feed. From the observed mean heterozygosity in excess of 11–14%, these beetles appear to be as outbred as *Drosophila* (Lewontin 1974). A genetic distance estimate of 0.005, found between the Gigante and BCI beetle samples, is only a fraction of that found between congeneric species, ordinarily some 6–44%, with a mean for sibling species of 22% (Nei 1978; Brussard *et al.* 1985; Carman and Packer 1996).

Two known aggregations within a defined area of tropical forest, crisscrossed by some 45 km of trails, allow us to estimate the density of such aggregations that may exist. If 10 m to each side of any trail has been effectively scanned for 'beetle trees' by the biologists and naturalists or game wardens passing by, then an area of 0.9 km² has been monitored intensively, and has produced the two aggregations cited here. At this density, there would be 35 aggregations on BCI (15.6 km²). In the forest, if distribution were uniform, the estimated density of the beetle aggregations would be 2.2 per km².

The identity of the aggregating *S. subtilis* is now based on direct comparison with the syntype series. Two known aggregations of another *Stenotarsus*, *S. latipes* Arrow (1920) (STRI, PESC), a species described from Mexico and Guatemala, were shown to DWR and collected in Costa Rica. Entomologists William Eberhard (STRI and University of Costa Rica) and Angel Solis (InBio) had discovered the two aggregations in the early 1980s. Each group was on a substrate that was not a tree—either a horizontal rock face or on damp earth, both near streams. In addition, a large aggregation of *Stenotarsus* was seen at the summit of BCI on the trunk of a *Hura crepitans* Linnaeus (Euphorbiaceae) near the tower clearing. The single female specimen collected by G. Gilbert from this aggregation can not be confidently identified. Denlinger (1996) states that he had learned of other aggregations observed in Central America, presumably those cited above. Even though other species of *Stenotarsus* aggregate, aggregating behavior may have evolved independently in *S. latipes* and *S. subtilis*. Without an explicit phylogeny, evolution of this behavior cannot be traced.

Some organisms aggregate in multi-species masses to wait out unfavorable seasons, and beetles having comparable aggregations, such as erotylids (Goodrich and Skelley 1991; Navarrete-Heredia and Novelo-Gutiérrez 2000) and certain Coccinellidae in the northern temperate zone, may form groups of a single or multiple species (Hodek and Honêk 1996). Endomychid beetles were not previously known to have aggregations. All available specimens collected from both aggregating groups in Panama (including the Gigante specimens sent to J. Kingsolver by O. Nedved) are morphologically identical, which in-

dicates that each aggregation contains only one species. Further, beetles of two aggregations revealed to the authors by W. Eberhard and A. Solis in Costa Rica, each at 1,500 m above sea level in the Meseta Central area, represent a single species.

The sex ratios and substrate characteristics of the beetles suggest arboreal diapause sites may have been modified chemically either by beetles, associated microbes, or by other factors, but they are not for mating *per se*. As much as 10 times the concentration of K and Mg was present in areas adjacent to the beetle aggregations, but upon which beetles apparently never rested. The high proportion of females in aggregations, if not caused by unequal mortality rates of the different sexes, might indicate large changes in sex ratios during the year. However, we believe it is more likely that the beetles disperse from the resting sites to nearby, unidentified, mating areas. The combination of several aggregation sites might therefore produce sex ratios closer to the expected 1:1 ratio. Indeed, dispersing coccinellids, *Semiadalia undecimnotata* (Schneider), similar in size to *S. subtilis*, disperse up to 1.5 km, and have separate aggregation and mating sites (Hodek and Honěk 1996:266). Mating by beetles from different aggregations would be permitted by the estimated density of *S. subtilis* diapause sites and is further suggested by homogeneity of isoenzyme data. No mating pairs have thus far been seen in the vicinity of an aggregation site (Tanaka *et al.* 1987a). Persistence of the aggregations on a particular substrate is, however, striking. The BCI *Oenocarpus* has had aggregations present during most of the year since 1980 (in 1992 there was no large aggregation). The amount of materials removed from the substrate may be small in one season. It is unlikely beetles remove nutrients from the substrate, because such behavior would lead to grazing over the entire bark surface, rather than persistent aggregation on certain areas. Microbes may contribute to ion depletion, but fungi do not seem implicated, from the preliminary results. Similar site persistence is known for Coccinellidae in the temperate zone, with one locality used during winter for at least 60 years (Kuznetsov 1997).

Feeding, oviposition, and mating localities of *Stenotarsus* continue to be elusive. In addition, no larvae have been found at the aggregation sites. Data from the two displacement experiments suggest that the occupied substrates, although highly attractive to beetles when on the substrate tree, have little or no attractive properties in the habitat at large. A living tree, and therefore the associated sap or microbes, are not necessary to sustain a diapause site, as evinced by the aggregation on a dead *Tetragastris* in late 1999. Although evidence is indirect, the rapid repopulation of sites after dispersal suggests that beetles may return to their diapause sites, and that longevity may extend over more than one year. This would not be surprising for a tropical insect that diapauses during most of the year. Beetles that were experimentally displaced with their substrate to a new locality already may have learned orientation cues appropriate to their original site, and thus did not return to an artificial site after dispersal. Previous studies failed to detect return of marked individuals to the BCI *Oenocarpus*. This negative result raises the question of experimental treatment and its effect, as well as beetle orientation and navigational mechanisms. Behavior of beetles marked for recapture studies, or the persistence and effects of the marks themselves, need to be further evaluated. Given our genetic data, and also the sex ratios that vary within a season and between wet and dry seasons, we believe there is possibly intersite dispersal, and the population is outbred. Some beetles may disperse and return to their former

sites, while others either locate conspecifics at new sites, or die at mating or feeding sites.

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