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# Multivariate discrimination among cryptic species of the mite genus *Chaetodactylus* (Acari: Chaetodactylidae) associated with bees of the genus *Lithurgus* (Hymenoptera: Megachilidae) in North America

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**Abstract.** Twenty-seven morphological characters from 111 heteromorphic deutonymphs of the mite genus *Chaetodactylus* Rondani (Acari: Chaetodactylidae) were analyzed. The mites were collected from four species of bees of the genus *Lithurgus* Berthold (Hymenoptera: Megachilidae) in continental North America. Principal component and canonical variates analyses on Darroch and Mosimann shape and size-and-shape variables revealed the presence of three cryptic species. *Chaetodactylus gibbosi* sp. n. (Florida) is geographically isolated from *C. lithurgi* sp. n. distributed in Texas, New Mexico, Arizona, Colorado, and Idaho. Sympatric *C. lithurgi* and *C. abditus* sp. n. (USA: Arizona, Mexico: Socorro Is.) are seasonally isolated in Arizona. *Chaetodactylus gibbosi* is associated with a single bee species, *Lithurgus gibbosus* Smith in Florida. The host range of *C. lithurgi* includes bees flying predominantly in the spring: *L. apicalis* Cresson, *L. littoralis* Cockerell, and western *L. gibbosus*. *Chaetodactylus abditus* sp. n. is associated with *L. planifrons* Friese and *L. echinocacti* Cockerell, flying predominantly in the fall in Arizona. No distinct groups separated by geographic locality or size were detected in any species. A six-variable model developed by the canonical variates analysis and estimated using jackknife resampling and external validation ($n = 100$) is capable of classifying the three species with 100% accuracy. Factors that influenced speciation of cryptic species of *Chaetodactylus* associated with *Lithurgus* are discussed. Based on morphological and geographical data and data on mite associates, the western and eastern populations of the bee *L. gibbosus* are distinct. Therefore, the taxonomic status of *L. gibbosus* s. lat. should be reevaluated.

## Introduction

The astigmatid mite genus *Chaetodactylus* includes four subgenera and 16 species associated with megachilid (Megachilidae: Lithurgini, Osmiini, Megachilini, Anthidiini) and apid (Apidae: Ceratinini) bees (Zachvatkin 1941; Samšiňák 1973; Fain 1981; Kurosa 1987; Fain and Baugnée 1996). The genus is worldwide in distribution, although no records have yet been published from the Australian or Neotropical regions, and the geographic distributions and host relations are poorly understood in most species. At least some *Chaetodactylus* species are cleptopar-

asites, killing the host egg or larva and consuming the provisioned pollen (Krombein 1962; OConnor 1982). Serious damage to managed colonies of *Osmia* species pollinating commercial crops has been reported (Fain 1966; Kurosa 1987; Bosch 1992). In North America, a single species, *Chaetodactylus krombeini* Baker, has been described associated primarily with *Osmia lignaria* Say (Baker 1962). As part of an ongoing survey of bee-associated mites in North America, we have recovered a large number of specimens of *Chaetodactylus* species from a number of species of Megachilidae and Apidae in this region. These collections include a number of previously undescribed species.

From the most recently published key (Fain 1981), it is clear that most characters considered diagnostic for *Chaetodactylus* species are continuous morphometric characters. However, that work and most other prior systematic studies of *Chaetodactylus* have utilized classical taxonomic methods in species separation, using differential morphology and raw measurements. Additionally, prior and subsequent studies have typically omitted sample sizes and evaluation of variation in characters. Samšiňák (1973) and Fain (1981) used raw measurements, while Zachvatkin (1941) and Kurosa (1987) used ratios of dimensions of morphological features to the length of the idiosoma. Complicating matters further, species of *Chaetodactylus* are known to exhibit deutonymphal polymorphism. They produce morphologically regressive or 'inert' deutonymphs in addition to the typical phoretic deutonymphs. In addition, Fain and Pauly (2001) recognized 'small' and 'large' forms within the typically phoretic morphotype that were believed to exhibit biological differences as well. If this distinction is real, the use of raw, size-related characters should be reevaluated.

In this first paper on North American *Chaetodactylus*, we use techniques of multivariate morphometrics to analyze within- and between-sample morphological variability of *Chaetodactylus* collected from different localities and different species in the megachilid genus *Lithurgus*. Factors that might influence speciation in *Chaetodactylus* associated with *Lithurgus* are discussed.

## Material and methods

Mites for this study were collected from museum specimens of the bee subgenus *Lithurgopsis* Fox (Hymenoptera: Megachilidae: *Lithurgus*) from different localities in the southern and northwestern United States and Socorro Is. (Mexico) (Figure 1, see also material under the species descriptions). Five of the seven bee species of the subgenus distributed in continental North America (Snelling 1983, 1986) were sampled. No mites were found on two rare species, *Lithurgus listrotus* Snelling and *Lithurgus bitorulosus* Snelling. The mite specimens were cleared in Nesbitt's fluid and mounted in Hoyer's medium for study (OConnor and Houck 1991). Each host was vouchered with a label: ''Mites removed, B.M. OConnor'', followed by an individual number. Three groups were predefined on the basis of certain metric characters: group 1 ex *Lithurgus littoralis* Cockerell, *L. apicalis* Cresson, and *L. gibbosus* F. Smith from Texas, New Mexico, Arizona, Colorado, and Idaho; group 2

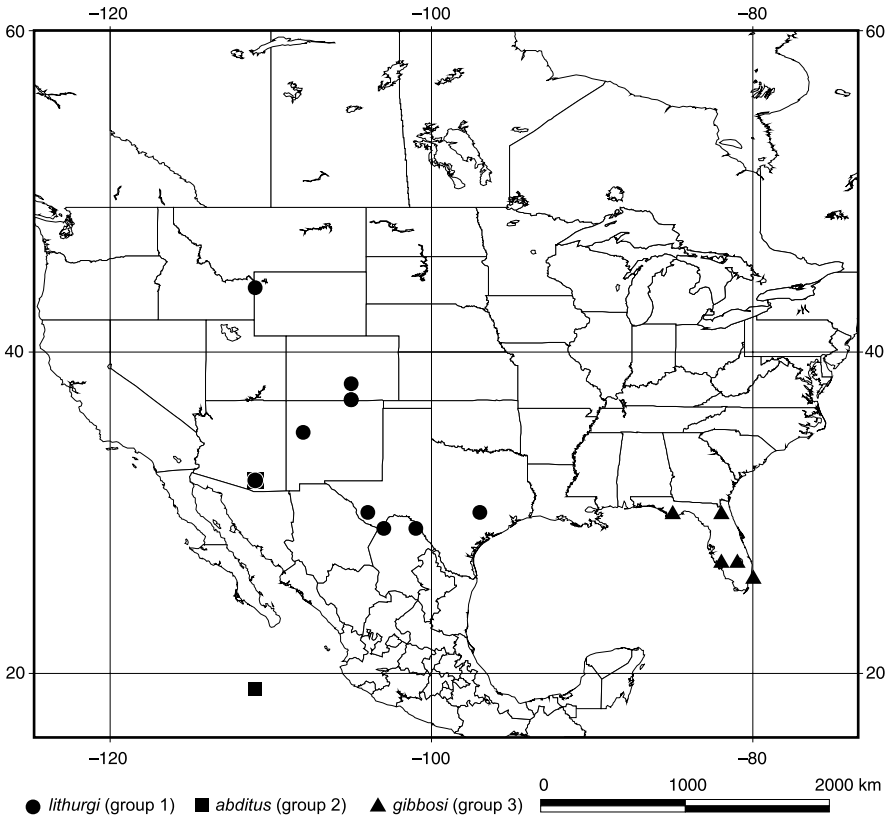


*Figure 1.* Known geographic distributions of three species of the genus *Chaetodactylus* associated with the bee genus *Lithurgus* in North America.

ex *Lithurgus planifrons* Friese and *L. echinocacti* Cockerell from Arizona (USA) and Socorro Is. (Mexico); and group 3 ex *Lithurgus gibbosus* from Florida. We did not include two other undescribed species of *Chaetodactylus* associated with *Lithurgus apicalis* and *Lithurgus antilleorum* Michener in the present paper, because they are clearly distinct and do not require a special morphometric study. These species will be described in a subsequent work.

Thirty-six continuous morphological characters from 111 specimens belonging to the three groups were measured using a Karl Zeiss Axioskop and converted to micrometers. A list of the variables their means and standard deviations is given in Table 1 (64 other standard measurements are also given). Missing data were replaced by values predicted by a linear regression ($X =$ length of idiosoma). Seven variables with more than 5 (9.1%), 3 (10.0%), and 2 (7.7%) missing values for groups 1–3, respectively, were excluded. Two variables (length of hysterosoma and empodium III) were also excluded because they are difficult to accurately measure. The remaining 27 variables (Table 1) were converted to logged Darroch and

*Table 1.* Measurements (range, mean ± SD) of 100 continuous characters of three species of the genus *Chaetodactylus*.

| | Variable | *C. lithurgi* | *C. abditus* | *C. gibbosi* |
|---|---|---|---|---|
| a,b,c | Idiosoma, length | 218–362(304.7 ± 31.19,n = 91) | 243–324(282.3 ± 15.42,n = 66) | 246–331(293.7 ± 20.02,n = 59) |
| | Idiosoma, width | 245–305(269.0 ± 25.76,n = 5) | 217–243(230.4 ± 11.32,n = 5) | 218–306(252.6 ± 24.68,n = 10) |
| a,b,c | Propodosomal shield, length | 59–92(78.2 ± 6.85,n = 91) | 64–90(74.9 ± 4.94,n = 66) | 64–101(81.0 ± 8.23,n = 59) |
| a,b,c | Propodosomal shield, width | 111–183(148.6 ± 13.46,n = 91) | 120–175(142.7 ± 13.12,n = 66) | 121–187(152.0 ± 15.29,n = 59) |
| a | hysterosomal shield, length | 115–191(161.4 ± 17.45,n = 55) | 117–162(137.1 ± 11.62,n = 30) | 125–176(150.1 ± 15.57,n = 25) |
| a,b | Hysterosomal shield, width anterior | 159–257(209.7 ± 19.77,n = 55) | 157–215(189.9 ± 15.21,n = 30) | 172–248(207.1 ± 18.22,n = 26) |
| a,b,c | Hysterosomal shield, width at $f_2$ level | 76–148(117.9 ± 14.69,n = 91) | 87–112(100.2 ± 5.64,n = 66) | 89–136(113.5 ± 10.91,n = 59) |
| | length of free palpomeres | 8–12(10.4 ± 1.50,n = 5) | 8–11(9.6 ± 1.16,n = 5) | 9–12(10.9 ± 0.95,n = 10) |
| | Width of free palpomeres (base) | 5–8(6.8 ± 1.13,n = 5) | 5–8(6.7 ± 1.18,n = 5) | 6–8(7.4 ± 0.67,n = 10) |
| | Gnathosomal solenidion | 14–18(16.2 ± 1.62,n = 5) | 16–21(17.7 ± 2.05,n = 5) | 16–19(17.2 ± 1.01,n = 10) |
| | Sternum | 47–55(50.5 ± 2.78,n = 5) | 41–55(47.6 ± 4.99,n = 5) | 41–58(50.2 ± 6,n = 10) |
| | Apodeme II | 55–84(70.4 ± 6.07,n = 55) | 59–72(64.9 ± 4.43,n = 10) | 62–82(72.0 ± 5.87,n = 26) |
| a,b | Apodeme III | 41–67(58.4 ± 6.18,n = 55) | 45–59(52.8 ± 3.34,n = 30) | 46–65(55.9 ± 4.55,n = 26) |
| | Apodeme IV | 57–64(61.0 ± 3.04,n = 5) | 52–59(55.1 ± 2.50,n = 5) | 52–66(59.4 ± 4.09,n = 10) |
| | Posterior apodeme IV | 25–28(26.7 ± 1.60,n = 5) | 19–21(20.1 ± 0.85,n = 5) | 12–31(21.6 ± 5.25,n = 10) |
| | *vi* | 11–14(13.0 ± 1.13,n = 5) | 11–14(12.2 ± 1.26,n = 5) | 9–14(11.5 ± 1.78,n = 10) |
| a,b,c | *si* | 24–51(37.1 ± 6.21,n = 90) | 29–55(39.6 ± 4.67,n = 65) | 18–47(28.1 ± 5.18,n = 58) |
| | *se* | 50–62(55.4 ± 5.68,n = 5) | 48–55(50.3 ± 3.28,n = 5) | 41–59(51.9 ± 5.24,n = 9) |
| a,b,c | $c_1$ | 15–30(21.1 ± 3.75,n = 88) | 13–22(17.3 ± 1.79,n = 63) | 9–15(11.7 ± 1.31,n = 55) |
| | $c_2$ | 49–57(53.8 ± 3.30,n = 5) | 45–51(48.2 ± 2.41,n = 5) | 43–55(49.5 ± 3.33,n = 9) |
| | $c_3$ | 36–44(39.9 ± 2.98,n = 5) | 34–38(35.7 ± 1.38,n = 5) | 33–44(39.3 ± 4.19,n = 10) |
| | $c_p$ | 53–62(58.7 ± 3.68,n = 5) | 47–59(52.6 ± 4.75,n = 5) | 45–62(53.4 ± 4.94,n = 10) |
| a,b,c | $d_1$ | 16–32(23.4 ± 3.45,n = 88) | 20–33(26.2 ± 2.84,n = 65) | 10–18(14.2 ± 1.81,n = 58) |
| | $d_2$ | 40–47(44.2 ± 2.76,n = 5) | 33–43(37.8 ± 3.92,n = 5) | 37–46(40.5 ± 2.77,n = 10) |
| a,b,c | $e_1$ | 13–29(21.3 ± 3.28,n = 88) | 18–32(23.7 ± 2.93,n = 66) | 9–18(13.4 ± 1.98,n = 59) |
| | $e_2$ | 33–45(38.7 ± 4.55,n = 5) | 32–38(35.3 ± 2.43,n = 5) | 30–48(37.1 ± 5.09,n = 10) |
| | $f_2$ | 29–37(33.8 ± 3.65,n = 5) | 27–34(30.5 ± 3,n = 5) | 28–38(32.0 ± 3.47,n = 9) |
| a,b,c | $h_1$ | 11–29(21.3 ± 3.29,n = 89) | 16–28(21.3 ± 2.69,n = 66) | 11–19(14.9 ± 1.83,n = 59) |

*Table 1.* continued.

| | Variable | *C. lithurgi* | *C. abditus* | *C. gibbosi* |
|---|---|---|---|---|
| a,b,c | $h_2$ | 17–39(27.5 ± 4.44,n = 90) | 10–28(18.0 ± 3.69,n = 66) | 17–31(24.2 ± 3.28,n = 59) |
| | $h_3$ | 17–21(18.9 ± 1.40,n = 5) | 16–20(18.4 ± 1.97,n = 5) | 16–23(18.1 ± 2.27,n = 10) |
| | *1a* | 60–72(64.2 ± 5.19,n = 4) | 54–58(56.6 ± 1.86,n = 4) | 52–64(59.7 ± 4.41,n = 6) |
| a,b | *3a* | 13–22(16.5 ± 1.66,n = 52) | 13–19(15.8 ± 1.53,n = 29) | 16–21(17.2 ± 1.30,n = 26) |
| | *3b* | 34–38(35.3 ± 1.48,n = 5) | 33–44(38.7 ± 4.76,n = 5) | 32–47(39.2 ± 3.97,n = 10) |
| a,b,c | *4a* | 23–37(28.9 ± 3.01,n = 88) | 27–42(33.4 ± 3.34,n = 58) | 21–34(27.0 ± 2.85,n = 58) |
| a | *g* | 8–13(9.8 ± 1.34,n = 49) | 6–12(9.0 ± 1.26,n = 28) | 8–15(11.0 ± 1.78,n = 26) |
| a,b,c | Length of attachment organ | 47–61(54.5 ± 3.21,n = 91) | 42–56(49.8 ± 2.96,n = 66) | 47–62(53.9 ± 3.23,n = 59) |
| | Width of attachment organ | 56–62(58.7 ± 2.83,n = 5) | 53–62(56.1 ± 3.69,n = 5) | 55–59(56.4 ± 1.80,n = 10) |
| | Anterior sucker ($ad_3$) | 9–10(9.6 ± 0.61,n = 5) | 9–11(9.8 ± 0.61,n = 5) | 9–11(9.7 ± 0.71,n = 10) |
| a,b | Median sucker ($ad_1 + 2$) | 18–23(20.7 ± 1.26,n = 55) | 16–22(18.7 ± 1.34,n = 30) | 18–23(20.1 ± 1.28,n = 26) |
| | Anterior lateral conoid ($ps_2$) | 4–6(5.6 ± 1.13,n = 5) | 4–6(5.1 ± 0.78,n = 5) | 5–6(5.5 ± 0.68,n = 10) |
| | Posterior lateral conoid ($ps_1$) | 4–7(5.9 ± 0.98,n = 5) | 5–6(5.5 ± 0.78,n = 5) | 4–7(5.9 ± 0.76,n = 10) |
| | Anterior cuticular conoid | 2–4(3.2 ± 0.52,n = 5) | 3–5(3.8 ± 0.77,n = 5) | 3–5(3.8 ± 0.75,n = 10) |
| | *ih* | 5–6(5.5 ± 0.62,n = 5) | 3–5(4.6 ± 0.78,n = 5) | 3–6(4.8 ± 1.05,n = 10) |
| | Leg I | 131–139(134.8 ± 3.46,n = 5) | 122–134(125.9 ± 4.86,n = 5) | 117–140(126.7 ± 8.16,n = 10) |
| | Tarsus I | 36–41(38.7 ± 2.11,n = 5) | 34–41(37.6 ± 2.37,n = 5) | 31–41(35.8 ± 3.81,n = 9) |
| | Empodium I | 22–32(26.2 ± 4.74,n = 5) | 27–30(28.5 ± 1.31,n = 5) | 23–37(29.1 ± 5.12,n = 10) |
| a | ω1 I | 19–36(22.6 ± 2.73,n = 54) | 21–27(23.2 ± 1.24,n = 29) | 16–21(18.8 ± 1.57,n = 19) |
| | ω2 I | 9–17(12.2 ± 1.98,n = 47) | 11–14(12.6 ± 0.91,n = 11) | 8–12(9.5 ± 1.07,n = 15) |
| a,b | ω3 I | 32–47(38.4 ± 3.24,n = 55) | 34–47(38.1 ± 3.32,n = 29) | 31–39(34.7 ± 2.37,n = 25) |
| | Famulus I | 3–7(5.0 ± 0.73,n = 42) | 3–6(4.4 ± 0.80,n = 10) | 3–7(4.7 ± 1,n = 21) |
| a,b,c | *f* I | 44–70(58.0 ± 5.70,n = 84) | 45–67(54.8 ± 5.19,n = 64) | 48–69(59.0 ± 5.15,n = 52) |
| a | *e* I | 62–95(77.7 ± 8.03,n = 54) | 62–89(73.7 ± 6.30,n = 27) | 69–92(80.0 ± 6.47,n = 23) |
| | *ra* I | 20–28(24.1 ± 2.18,n = 46) | 20–27(22.4 ± 1.90,n = 9) | 21–27(24.3 ± 1.87,n = 20) |
| | *la* I | 23–29(26.4 ± 2.23,n = 5) | 24–27(25.4 ± 0.89,n = 5) | 22–28(25.1 ± 2.40,n = 9) |
| a | *wa* I | 30–44(36.1 ± 3.42,n = 52) | 29–41(34.9 ± 2.78,n = 30) | 31–37(34.1 ± 2.27,n = 23) |
| | *gT* I | 31–34(32.0 ± 1.10,n = 5) | 23–33(26.7 ± 3.59,n = 5) | 26–33(29.0 ± 2.70,n = 9) |
| | *hT* I | 23–29(26.3 ± 2.68,n = 5) | 20–28(23.7 ± 2.84,n = 5) | 20–28(22.7 ± 2.93,n = 9) |

*Table 1.* continued.

| | Variable | *C. lithurgi* | *C. abditus* | *C. gibbosi* |
|---|---|---|---|---|
| | ϕ I | 45(n = 1) | n.m. | 50(n = 1) |
| | *mG* I | 37–44(39.0 ± 3.31,n = 4) | 28–36(32.4 ± 3.48,n = 5) | 29–39(34.5 ± 3.38,n = 10) |
| | *cG* I | 55–66(59.7 ± 4.32,n = 5) | 47–55(50.5 ± 3.09,n = 5) | 47–62(55.5 ± 5.39,n = 10) |
| a | σ I | 11–21(15.9 ± 1.76,n = 50) | 16–21(17.8 ± 1.38,n = 27) | 13–19(15.7 ± 1.48,n = 21) |
| a,b | *vF* I | 41–60(51.1 ± 5.28,n = 55) | 45–63(53.6 ± 4.13,n = 29) | 41–53(47.3 ± 2.81,n = 24) |
| | *pR* I | 62–70(65.9 ± 4.10,n = 4) | 50–64(58.1 ± 6.42,n = 4) | 51–69(58.9 ± 6.33,n = 7) |
| | Leg II | 127–136(131.7 ± 3.09,n = 5) | 118–134(127.0 ± 8.24,n = 5) | 114–144(126.6 ± 10.22,n = 10) |
| | Tarsus II | 37–41(38.7 ± 1.62,n = 5) | 35–39(37.5 ± 1.87,n = 5) | 31–41(36.6 ± 3.04,n = 9) |
| | Empodium | 23–31(29.0 ± 3.37,n = 5) | 26–31(28.2 ± 1.95,n = 5) | 22–34(28.2 ± 4.19,n = 10) |
| a | ω1 II | 20–28(24.7 ± 2.03,n = 50) | 23–28(25.4 ± 1.44,n = 26) | 19–25(22.0 ± 2.01,n = 24) |
| a,b,c | *f* II | 45–66(57.2 ± 5.53,n = 88) | 45–66(54.4 ± 4.54,n = 63) | 45–69(58.5 ± 4.94,n = 57) |
| a,b | *e* II | 65–94(78.4 ± 8.31,n = 53) | 61–81(72.6 ± 5.31,n = 28) | 69–87(78.6 ± 4.65,n = 25) |
| | *ra* II | 22–27(25.4 ± 2.07,n = 5) | 22–26(24.0 ± 1.73,n = 4) | 20–28(25.5 ± 2.85,n = 8) |
| | *la* II | 24–28(25.7 ± 1.68,n = 4) | 20–27(23.4 ± 2.47,n = 5) | 20–34(25.8 ± 4.08,n = 9) |
| | *wa* II | 28–38(32.3 ± 4.43,n = 5) | 32–34(33.1 ± 0.89,n = 5) | 29–37(33.2 ± 3.01,n = 10) |
| | *gT* II | 23–28(25.3 ± 2.25,n = 5) | 20–25(22.1 ± 2.51,n = 3) | 16–27(21.9 ± 3.74,n = 7) |
| a,b,c | *hT* II | 16–29(21.5 ± 2.55,n = 89) | 19–29(24.2 ± 1.85,n = 64) | 16–24(20.0 ± 1.99,n = 59) |
| | ϕ II | 41–51(46.4 ± 7.17,n = 2) | 59,(n = 1) | 51–52(51.9 ± 0.55,n = 2) |
| | *mG* II | 41–47(42.8 ± 2.83,n = 5) | 32–38(36.0 ± 2.64,n = 5) | 32–46(40.2 ± 4.81,n = 10) |
| | *cG* II | 11–12(11.4 ± 0.70,n = 5) | 10–12(11.2 ± 1.02,n = 5) | 10–15(12.2 ± 1.70,n = 10) |
| | σ II | 10–12(10.8 ± 0.92,n = 4) | 9–13(11.4 ± 1.30,n = 5) | 9–11(10.4 ± 1.02,n = 8) |
| a,b,c | *vF* II | 34–52(43.4 ± 4.57,n = 91) | 39–59(48.5 ± 3.74,n = 66) | 30–48(39.9 ± 3.71,n = 58) |
| | *pR* II | 62–78(67.5 ± 6.38,n = 5) | 51–78(61.4 ± 11.59,n = 4) | 52–70(61.1 ± 7.25,n = 7) |
| | leg III | 95–110(103.5 ± 5.65,n = 5) | 95–111(103.0 ± 7.66,n = 5) | 92–108(100.9 ± 5.49,n = 10) |
| | Tarsus III | 25–42(33.9 ± 4,n = 53) | 28–37(32.0 ± 2.57,n = 10) | 23–37(30.8 ± 3.40,n = 26) |
| a | Empodium III | 17–31(23.3 ± 3.37,n = 55) | 16–27(20.9 ± 3.48,n = 30) | 17–33(25.9 ± 3.26,n = 26) |
| | *d* III | 112–165(140.0 ± 11.45,n = 41) | 129–144(135.7 ± 6.18,n = 8) | 112–150(129.4 ± 9.92,n = 17) |
| | *e* III | 50–59(54.3 ± 4.60,n = 5) | 48–56(52.9 ± 3.72,n = 5) | 51–62(56.5 ± 4.45,n = 8) |
| | *f* III | 36–59(48.8 ± 5.09,n = 52) | 41–48(43.5 ± 2.49,n = 10) | 44–59(49.7 ± 3.87,n = 24) |

*Table 1.* continued.

| | Variable | *C. lithurgi* | *C. abditus* | *C. gibbosi* |
|---|---|---|---|---|
| | *s* III | 25–28(26.3 ± 1.61,n = 4) | 25–31(26.8 ± 2.79,n = 5) | 25–31(27.7 ± 1.89,n = 8) |
| | *kT* III | 20–26(22.9 ± 2.03,n = 5) | 18–23(21.2 ± 2.02,n = 5) | 12–24(19.9 ± 4.61,n = 10) |
| a | ϕ III | 16–27(20.9 ± 2.57,n = 50) | 17–28(23.1 ± 2.44,n = 27) | 16–22(18.6 ± 1.65,n = 20) |
| | *nG* III | 23–35(28.8 ± 2.95,n = 55) | 27–31(28.1 ± 1.61,n = 10) | 22–33(27.0 ± 2.98,n = 26) |
| a,b | *cR* III | 27–43(34.0 ± 3.05,n = 53) | 31–47(35.8 ± 3.85,n = 27) | 27–34(31.4 ± 2.47,n = 24) |
| | Leg IV | 62–69(64.6 ± 2.37,n = 5) | 58–67(63.0 ± 3.57,n = 5) | 59–69(64.4 ± 2.92,n = 10) |
| a,b | Tarsus IV | 14–25(20.6 ± 2.46,n = 55) | 18–23(21.0 ± 1.41,n = 30) | 16–21(18.9 ± 1.09,n = 26) |
| | *d* IV | 315–343(327.3 ± 11.27,n = 5) | 265–329(287.4 ± 26.78,n = 5) | 264–388(306.0 ± 44.01,n = 6) |
| a,b | *e* IV | 4–11(7.0 ± 1.60,n = 52) | 3–8(6.1 ± 1.29,n = 27) | 4–9(7.6 ± 1.53,n = 26) |
| | *f* IV | 5–9(7.3 ± 1.42,n = 5) | 6–8(6.7 ± 0.70,n = 5) | 5–11(8.2 ± 1.74,n = 8) |
| | ω IV | 6–16(10.5 ± 3.83,n = 5) | 9–12(10.2 ± 1.36,n = 5) | 8–19(11.3 ± 4.05,n = 8) |
| | r IV | 5–11(7.8 ± 2.14,n = 5) | 9–13(10.7 ± 1.37,n = 5) | 5–9(7.6 ± 1.90,n = 7) |
| | ϕ IV | 8–14(10.9 ± 1.27,n = 23) | 9–15(12.3 ± 2.26,n = 6) | 8–12(9.8 ± 0.99,n = 12) |
| a,b | *vF* IV | 28–33(31.0 ± 1.78,n = 5) | 22–31(26.0 ± 2.31,n = 28) | 22–33(27.3 ± 2.92,n = 25) |

a – 36-variable dataset; b – 27-variable dataset; c – 16-variable dataset; n.m. – non-measurable.

Mosimann shape variables (Darroch and Mosimann 1985; see details and discussion in Jungers et al. 1995) for subsequent analyses.

*Principal component analysis.* PCAs were conducted on variance–covariance matrices of log raw data (i.e., size-and-shape) and log shape variables to determinate the extent to which overall differences among individuals can be attributed to a combination of size and shape versus shape only (Darroch and Mosimann 1985). Logarithmic transformation (base *e*) was done to avoid assuming that the variances are the same for all variables. PCA on shape variables was used to interpret the pattern of variation in the three putative groups.

*Canonical variates analysis.* CVAs were conducted to select the smallest set of variables that has the highest precision in classification (variable selection) and to develop a classification rule for discrimination of the morphs. Prior probabilities for the groups were assumed equal.

*Variable selection.* If fewer original predictors may be used in the classification rule without compromising classification accuracy, it would be less costly in obtaining data on the predictors for the purpose of classifying new specimens. We used the potency index (Hair et al. 1998) as the criterion for assessing contribution of the predictor variables to group discrimination. The variable with the smallest potency index was dropped from the model, and for the remaining variables a new variance–covariance matrix was constructed and subjected to a new CVA. This method was used for both size and size-and-shape variables. Because there was no difference between hit rates of CVA based on shape and size-and-shape data, for the log raw data, we also used the best-subset and stepwise methods of variable selection (Huberty 1994). The two analyses cannot handle shape data because every removal of a variable requires size-correction of the remaining variables. Equally best models were evaluated using Akaike (1973) Information Criterion (AIC). Some variables were highly intercorrelated, nevertheless all of them passed the tolerance test.

*Validation of results.* Canonical variates were derived from the original data using the jackknife method to assess the classification accuracy rate (Huberty 1994; Lance et al. 2000). Because the sample size is relatively small and the number of predictors is comparatively large, we did not divide the cases into analysis (training, calibration) and holdout samples. An additional sample of the three putative species was employed as the holdout sample to estimate the external validity of canonical functions derived from the reduced subsets of variables. The holdout sample includes 31 specimens of putative *C. lithurgi* (group 1), 36 specimens of *L. abditus* (group 2), and 33 specimens of *C. gibbosi* (group 3).

All morphometric analyses were done with the program SPSS ver. 10.0.7a for Macintosh (SPSS Inc., Chicago, IL).

In the descriptions and analyses, idiosomal chaetotaxy follows Griffiths et al. (1990). The leg chaeto- and solenidiotaxy follow Griffiths (1970). All measurements are in micrometers (μm). Statistical data are presented as range, mean ± standard deviation.

The following abbreviations are used for institutions where mite specimens or bee hosts examined in this study are held or have been deposited: CAS – California Academy of Sciences, San Francisco. CUIC – Cornell University Insect Collection, Ithaca, New York; FSCA – Florida State Collection of Arthropods, Gainsville; IRSNB – Institut royal des Sciences naturelles, Brussels, Belgium; HNHM – Hungarian Natural History Museum, Budapest, Hungary; KU – University of Kansas Natural History Museum, Lawrence, Kansas; LACM – The Natural History Museum of Los Angeles County, Los Angeles, California; MSU – Department of Entomology, Michigan State University, East Lansing, Michigan; UNAM – Universidad Nacional Autónoma de México, México City; UMMZ – Museum of Zoology, University of Michigan, Ann Arbor, Michigan; USDA – USDA Bee Biology and Systematics Laboratory, Logan, Utah; USNM – U.S. National Museum of Natural History, Washington, DC (mite collection maintained at USDA Systematic Entomology Laboratory, Beltsville, Maryland).

## Results

### *Principal component analysis*

The main purpose of this analysis was to explore pattern of variation among the samples and estimate the influence of size on group separation. Principal components derived from log size-and-shape and log shape variables are summarized in Table 2 and Figure 2. The analyses on size-and-shape variables produced four components accounting for 80.5% of the total variance (Table 2). The first principal component (44.7% of the total variance) has 13 (48.1%) positive loadings that are high or moderately high, indicating that this component is influenced by size. However, it does not support the existence of separate 'large' and 'small' deutonymphs (Fain and Pauly 2001) as distinct morphs. Five variables ($d_1$, $e_1$, *si*, $h_1$, $c_1$, *vF* II, *vF* I, and tarsus IV) have high coefficients (>0.6). Two loadings are negative and small. This component separates group 3 from group 2. The second component (21.4% of the total variance) also separates these groups, but there is a small overlap (Figure 2A). It contrasts some measurements of dorsal shields and $h_2$ with several dorsal and ventral setae (Table 2). A combination of PC1 and PC2 allows separation of groups 1–3, with a small overlap between groups 1–2 (Figure 2B). None of the subsequent components itself serves to separate the groups, although PC1 versus PC4 separates group 3 from group $1 + 2$ and PC2 versus PC4 separates group 2 from group $1 + 3$.

The analyses on shape variables resulted in three components accounting for 72.5% of the total variance (Table 2). Compared to the size-and-shape analyses, the total variance reduced from 0.593 to 0.435. The difference represents an isometric vector that was explicitly removed (26.7% of the total variance) in the shape analysis. However, respective loadings on PC1 in both analyses are highly negatively correlated ($r = -0.940$, $p < 0.01$), indicating that shape is not independent of scale. PC1 (43.2% of the total variance) is a clear contrast of several dorsal setae and several measurements of dorsal shields and attachment organ (Table 2). PC1

*Table 2.* Principal components extracted by the $111 \times 24$ size-and-shape and shape analyses. High absolute loadings ($\geq 0.6$) are underlined.

| | Size-and-shape | | | | Shape | | |
|---|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC4 | PC1 | PC2 | PC3 |
| Idiosoma, length | 0.325 | 0.716 | −0.155 | 0.328 | 0.659 | −0.109 | 0.297 |
| Propodosomal shield, length | 0.000 | 0.627 | –0.032 | 0.469 | 0.736 | 0.199 | 0.160 |
| Propodosomal shield, width | 0.159 | 0.692 | −0.017 | 0.498 | 0.742 | 0.116 | 0.162 |
| Hysterosomal shield, width anterior | 0.258 | 0.711 | −0.205 | 0.342 | 0.645 | −0.119 | 0.336 |
| Hysterosomal shield, width at $f_2$ level | 0.315 | 0.805 | −0.106 | 0.131 | 0.571 | −0.465 | 0.129 |
| Apodeme III | 0.401 | 0.621 | −0.225 | 0.287 | 0.458 | −0.161 | 0.378 |
| *si* | 0.890 | −0.024 | 0.092 | 0.163 | −0.787 | −0.012 | −0.089 |
| $c_1$ | 0.876 | 0.183 | −0.093 | −0.338 | −0.706 | −0.604 | −0.045 |
| $d_1$ | 0.929 | −0.276 | 0.011 | −0.030 | −0.956 | 0.021 | −0.021 |
| $e_1$ | 0.929 | −0.207 | 0.096 | −0.023 | −0.926 | −0.001 | −0.125 |
| $h_1$ | 0.883 | 0.049 | 0.017 | −0.042 | −0.751 | −0.227 | −0.065 |
| $h_2$ | 0.103 | 0.886 | −0.222 | −0.245 | 0.507 | −0.787 | 0.096 |
| *3a* | −0.016 | 0.408 | −0.037 | 0.403 | 0.580 | 0.297 | 0.161 |
| *4a* | 0.524 | −0.298 | 0.093 | 0.373 | −0.239 | 0.655 | 0.076 |
| Length of attachment organ | 0.080 | 0.726 | −0.090 | 0.209 | 0.748 | 0.039 | 0.152 |
| Median sucker ($ad_1 + 2$) | 0.279 | 0.701 | −0.145 | 0.229 | 0.676 | −0.027 | 0.237 |
| ω3 I | 0.511 | 0.045 | 0.054 | 0.097 | 0.000 | 0.336 | 0.029 |
| *f* I | 0.182 | 0.663 | −0.114 | 0.310 | 0.642 | −0.019 | 0.212 |
| *vF* I | 0.622 | −0.118 | 0.116 | 0.325 | −0.227 | 0.552 | 0.024 |
| *f* II | 0.095 | 0.637 | −0.268 | 0.340 | 0.668 | 0.039 | 0.364 |
| *e* II | 0.219 | 0.585 | −0.125 | 0.316 | 0.574 | 0.054 | 0.231 |
| *hT* II | 0.545 | −0.159 | 0.181 | 0.477 | −0.201 | 0.643 | −0.008 |
| *vF* II | 0.684 | −0.224 | 0.134 | 0.415 | −0.361 | 0.673 | 0.035 |
| *cR* III | 0.567 | −0.027 | 0.030 | 0.451 | −0.108 | 0.572 | 0.157 |
| Tarsus IV | 0.621 | 0.150 | 0.118 | 0.302 | −0.115 | 0.322 | −0.024 |
| *e* IV | −0.081 | 0.476 | 0.868 | −0.105 | 0.471 | −0.014 | −0.881 |
| *vF* IV | 0.264 | 0.463 | 0.103 | 0.291 | 0.436 | 0.143 | −0.019 |
| Variance explained (%) | 44.7 | 20.7 | 8.7 | 6.3 | 44.4 | 16.4 | 11.7 |

allows for complete separation of groups 1 and $2 + 3$. PC2 partially separates groups 2 and 3 and completely separates groups 1–2. A combination of PC1 and PC2 completely separates all three groups.

Comparison of size-and-shape versus shape scatterplots on Figure 2 reveals that both log raw and shape variables can be used for group discrimination, although the latter is more preferable. Raw measurements themselves or ratios cannot be used for discrimination of any group. No distinct clusters distinguished by geographic locality or host were detected within the three groups by the shape and size-and-shape PCAs.

The PCAs mentioned above corroborate our a priori assessment that the three predefined groups represent separate entities that differ from each other in multivariate space. The gap between the three is much larger when the size component is

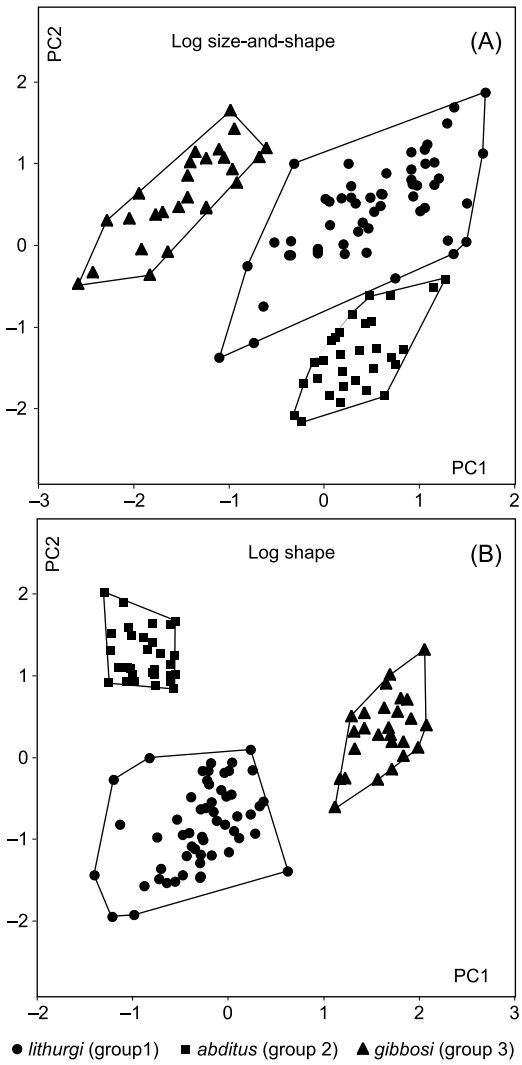


*Figure 2.* Scatterplot of scores of principal component 1 versus 2 derived from the 111 × 27 PCAs on log size-and-shape (A) and shape variables (B).

removed (Figure 2B), indicating that the differences are probably influenced by genetic variation and the groups, therefore, are three different species that we describe below as:

*Chaetodactylus lithurgi* sp. n. (group 1)
*C. abditus* sp. n. (group 2)
*C. gibbosi* sp. n. (group 3).

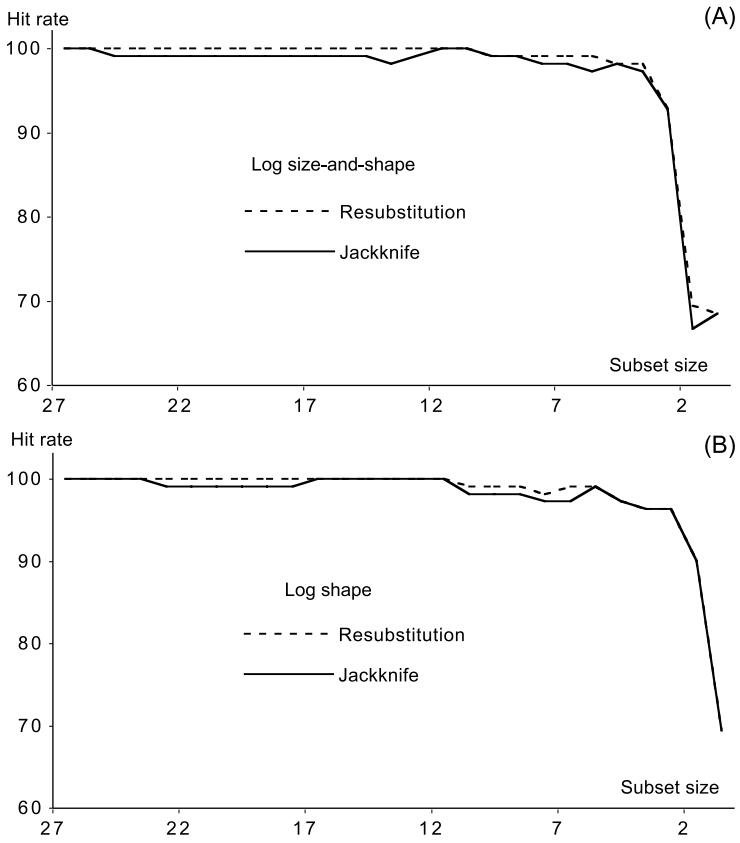


*Figure 3.* Variable selection based on the potency index; dataset includes log size-and-shape (A) and shape (B) variables.

Differences between them will be described by a Canonical Variates Analysis, another multivariate technique focusing on prediction and description of group membership.

### *Variable selection*

The results from the previous PCA suggest that some variables contribute a little to group separation (Table 2) justifying employmet of variable selection. Variable selection based on the potency index (Figure 3) suggests that the original dataset can be reduced up to 11 (size-and-shape) or 12 (shape) variables, without loss of information content. The smaller subsets (3–4 variables) still give an acceptable level of classification accuracy (Figure 3). A stepwise CVA analysis reduced the original 27 log raw variables to a 14-variable subset capable of classifying all originally grouped specimens in both resubstitution and jackknife resampling.

*Table 3.* Six-variable subsets with the highest hit rate found by best subset analysis on the 111 × 16 log size-and-shape dataset.

| No. | Subset | Classification accuracy (%) | | | AIC | *p* |
|---|---|---|---|---|---|---|
| | | Analysis | Jackknife | Holdout ($n$=100) | | |
| 1 | Hysterosomal shield width at $f_2$ level, $c_1$, $h_2$, $f$ I, $hT$ II, $vF$ II | 100 | 100 | 100 | 114.61 | 0.00 |
| 2 | Hysterosomal shield width at $f_2$ level, $c_1$, $d_1$, $h_2$, $4a$, $f$ I | 100 | 100 | 100 | 119.88 | 0.00 |
| 3 | length of idiosoma, hysterosomal shield width at $f_2$ level, $c_1$, $h_2$, $hT$ II, $vF$ II | 100 | 100 | 100 | 118.20 | 0.00 |
| 4 | Hysterosomal shield width at $f_2$ level, $c_1$, $d_1$, $h_2$, $hT$ II, $vF$ II | 100 | 100 | 100 | 108.95 | 0.00 |

AIC – Akaike Information Criterion; *p* – probability.

Results from the best subset method suggest that the two former methods, and especially stepwise CVA, failed to find the most optimal subsets of predictors. Twenty-nine subsets of size 5 and 100% classification accuracy in analysis and jackknife resampling were found. The size of the best subsets indicates that nearly 80% of the original variables are redundant.

Since the above conclusions are formulated on the estimated hit rate, we extended the validation process through use of additional sampling to test the external validity of the results. The additional sample was measured from 100 specimens and includes 16 variables, a combination of the size-and-shape and shape subsets selected on the basis of the potency index. The best subset methods produced four subsets of size six that have maximal classification accuracy (100%) in both jackknife and external cross-validation (Table 3).

The size of the best subsets increases compared to the analyses based on the estimated classification accuracy, indicating a small positive bias of the jackknife approach (see above). Akaike statistics suggests that subset 4 is the most optimal model within the six-variable subset level (Table 3), also, compared to the others, this subset includes all variables that are very easy to measure. We selected this subset as the final classification model that will be described in detail below.

### *The classification model*

CVA was conducted on the reduced subset of six log size-and-shape variables (Table 3, model 4) measured from 111 specimens; 100 additional specimens were used as the holdout sample. The first canoncal function accounts for 75.4% of the variance explained by the two functions. The total amount of the variance explained by this function is 91.0%. The second function explains 76.6% of the remaining variance (9.0%). The total variance explained by both functions is 97.9%. All pairs of groups show statistically significant differences ($p < 0.001$), denoting that the

*Table 4.* Loadings, unstandardized coefficients and constants derived from CVA on the $111 \times 6$ log size-and-shape dataset. Variables ordered by absolute size of correlation within function.

| Variable | Loadings | | Unstandardized coefficients | |
|---|---|---|---|---|
| | CV1 | CV2 | CV1 | CV2 |
| $d_1$ | 0.481 | 0.479 | 6.371 | 2.205 |
| *vF* II | 0.244 | 0.004 | 1.099 | −6.686 |
| *hT* II | 0.214 | −0.029 | 5.488 | −2.539 |
| $c_1$ | 0.209 | 0.771 | 2.338 | 5.609 |
| $h_2$ | −0.344 | 0.538 | −4.973 | 3.241 |
| Hysterosomal shield, width at $f_2$ level | −0.180 | 0.310 | −9.365 | −1.294 |
| Constant | | | 12.511 | 6.259 |

canonical functions created separation not only in an overall sense, but for each group as well. Box's test showed that covariance matrices of the three groups are not equal, violating the assumptions of CVA. However many researchers (e.g., Hair et al. 1998) believe that CVA can be robust even when this assumption is violated.

The predictive accuracy level of the functions was assessed using the following three criteria (Hair et al. 1998). The maximum chance criterion value, 68.75% (proportion of cases in the largest group multiplied by 1.25), is substantially smaller than the percentages of correctly classified specimens estimated by internal, jackknife, and holdout sampling (100% for all). The value of the proportional chance criterion, $37.3*1.25 = 46.7\%$, is smaller than the value of the maximum chance criterion, therefore the latter is the measure to outperform. Press' $Q$ statistic values, 222.0 (analysis) and 200.0 (holdout), both exceed the critical value 6.63 at 0.01 significance level. By all three criteria, we would interpret our model as having accuracy above that expected by chance.

Unstandardized coefficients, constant terms, loadings of the two functions are given in Table 4. CV-1 completely separates *C. abditus* and *C. gibbosi* and partially separates *C. lithurgi* from two other groups. CV-2 partially separates *C. lithurgi* from *C. abditus* + *C. gibbosi*. The strongest contributions to CV-1 were provided by variables: $d_1$, *vF* II, and *hT* II; and to CV-2 by $c_1$, $h_2$, and width of hysterosomal shield at $f_2$ level (Table 4). A combination of CV-1 and CV-2 allows for complete separation of the three groups (Figure 4).

## Discussion

Canonical variates and principal component analyses of both size-and-shape and shape variables confirmed the existence of three putative morphospecies: *C. lithurgi*, *C. abditus*, and *C. gibbosi*. The latter species can be distinguished by a bivariate variable, the ratio of the length of propodosomal shield to the length of the seta $d_1$. Thus, this species fits the concept of morphospecies used by most tradi-

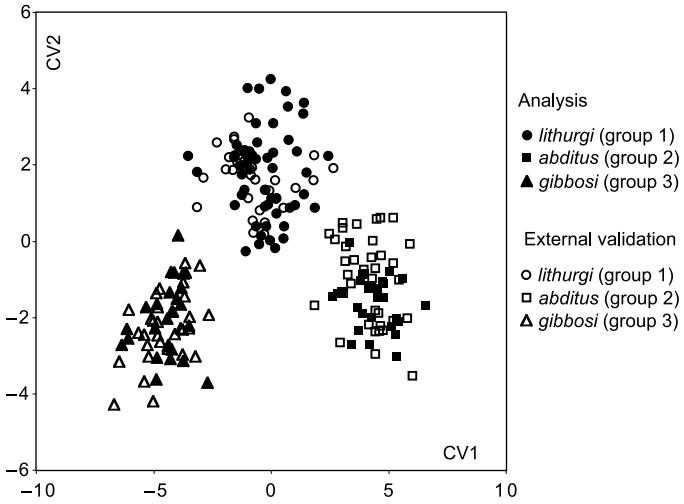


*Figure 4.* Plot of canonical variate 1 versus 2 derived from the $111 \times 6$ size-and-shape analysis. CVs were validated using an additional sample ($n = 100$).

tional taxonomists. In contrast, *C. lithurgi* and *C. abditus* can only be separated by methods of multivariate morphometrics. A model developed in this paper (Table 4) can classify them using two composite variables calculated from six morphometric variables and two constants (Table 4). Thus, a problem exists of how to interpret these 'subtle' differences, whether they are due to genetic variation or non-genetic host-related or seasonal variation. Because the differences between the two putative species involve shape-related variance, we believe that they, or at least most of them, are influenced by the existence of genetic variation. This conclusion is also supported by the existence of a large gap in multivariate space and the fact that there is no overlap in the host ranges, which might indicate reproductive isolation between the species. The differences cannot be influenced by seasonal, non-genetic variation, since there are several fall records of *C. lithurgi* which normally occur in the spring. It should be noted that geographic differences within any of the three mite species were not detected despite the broad ranges of some of them. The host effect, however, cannot be completely ruled out because the two species occur on different hosts. *Chaetodactylus lithurgi* and *C. abditus*, therefore, can be considered as separate species having different biological properties and subtle but stable morphological differences.

Substantial shape differences can occur in one species associated with different hosts, for example, in the rice brown planthopper *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). Rearing experiments showed that these differences are induced primarily by environmental factors, such as relative food qualities of the different varieties of the host plant (Claridge and Gillham 1992). On the other hand, some reproductively isolated cryptic species show very little morphological differentiation (Umphrey 1996; Burks and Heraty 2002). Our study, therefore is only

one approach in the attempt to find discontinuities between populations that might provide evidence for reproductive/genetic isolation. Additional data (e.g., gene sequences, rearing experiments) will be required to test whether the mite populations are genetically distinct

As mentioned above, *C. gibbosi* and *C. lithurgi* are probably geographically isolated. This statement was based on the collection data and requires further discussion as both mite species share a common host species, *L. gibbosus*.

If the range of the bee is contiguous, gene flow is possible between the two mite populations. But there are two reasons to believe the opposite. *L. gibbosus* s. lat. has been collected in Florida, Georgia, North Carolina, Texas, Oklahoma, and Kansas, and the eastern and western populations are distinctly different from each other (Snelling 1983). Males from Florida and Georgia have an abrupt and quite prominent median labial elevation (Snelling 1983, Figure 12). The median elevation in males from Texas is less pronounced (Snelling 1983, Figure 13). These observations indicate that the western and eastern bee populations are also geographically isolated and probably represent two cryptic species, as was demonstrated for the mites. The taxonomic status of *L. gibbosus* s. lat., thus, should be reevaluated.

*Chaetodactylus abditus* and *C. lithurgi* are sibling species occurring on different, partially sympatric hosts. *Chaetodactylus lithurgi* is associated with bees flying predominantly in the spring: *L. apicalis*, *L. littoralis*, and western *L. gibbosus*. *Chaetodactylus abditus* occurs exclusively on fall flying *L. echinocacti* and *L. planifrons* in the northern part of their range. *Lithurgus echinocacti* is distributed from New Mexico to southern California in the United States and in northwest Mexico, south to Nayarit. The range of *L. planifrons* extends from southern Arizona to Costa Rica (Snelling 1983). Unfortunately, Snelling (1983) did not give phenological information for the species. Collection data on the bees we examined in different museums suggest that *L. planifrons* occurs in the fall in Arizona and in May–early June on Soccoro Islands. We hypothesize that at least three factors might influence the separation of *C. lithurgi* and *C. abditus*: (1) Temporal isolation in the northern part of the range of *L. planifrons* and *L. echinocacti*; (2) Geographic isolation in the southern part of the range of *L. planifrons* or in the northern part of the ranges of *L. apicalis* and *L. littoralis*; and (3) Habitat isolation associated with the host preference. These hypothesis can only be tested using more sensitive methods on a wider range of material. However, one may conclude that the former and the last hypotheses are less plausible because gene flow is naturally possible between populations of *Chaetodactylus* from different sympatric hosts. Bees of the genus *Lithurgus* excavate their own borrows in rotten wood (Michener 2000). They also can construct cells in old borrows and use nest debris from old borrows (Parker and Potter 1973), facilitating mite exchange between different bee species or between different generations of the same bee species. *Chaetodactylus* is well-adapted to such behavior by forming highly regressive, non-phoretic deutonymphs that can survive for a long time without the presence of the host.

Finally, ‘large’ and ‘small’ phoretic deutonymphs were reported for *Chaetodactylus ludwigi* (Trouessart) as well as for other species of *Chaetodactylus* and ‘related genera’ by Fain and Pauly (2001). The authors speculated that large and

sclerotized specimens are 'mature' and able to molt to tritonymphs. Our analyses did not identify any distinct group by size in any species. Fain and Pauly's interpretation, therefore, may not be entirely justified.

*Species accounts*

Chaetodactylus lithurgi *sp. n.*

*Diagnosis (phoretic deutonymphs).* Belongs to the nominal subgenus as diagnosed by Fain (1981) and OConnor (1993). Similar to *C. ludwigi* (Trouessart), the only described species of *Chaetodactylus* associated with *Lithurgus*. The differences between the two species are as follows (character states of *C. ludwigi* are in parenthesis): solenidion of free palpomeres longer than palpomeres (approximately equal); distance between free palpomeres not exceeding 1/3 width of palpomeres (exceeding this distance); *la* I–II setiform (foliate); attachment organ width shorter than distance between *4a* (longer); anterior cuticular sucker weakly developed, not overlapping cupule *ih* (well-developed, overlapping); *w* and *f* IV shorter than tarsus IV (longer); long leg or dorsal setae, *cG* I, *si*, *se*, *si*, $c_2$, $c_p$, and often $e_2$ and $f_2$, weakly but distinctly pectinate (smooth); $h_1$ approximately equal to $e_1$ (distinctly shorter).

The following key* can help to distinguish *C. lithurgi* from two other cryptic *Chaetodactylus* described in this paper. Comparison based on canonical variates requires that six variables (Table 4) be measured. Conversion to micrometers or any other standard units is not necessary. Each value is converted to natural logarithms and multiplied by appropriate set of corresponding unstandardized coefficients (Table 4). These products and the constant (Table 4) are added to give the canonical variate value. Computer based identification using the same approach is available at http://insects.ummz.lsa.umich.edu/beemites/Morphometrics/Chaetodactylus_Lithurgus.htm

(1) Ratio length of propodosomal shield/length of seta $d_1$ 4.7–7.3 ($5.8 \pm 0.70$). CV1 and 2 fall within *gibbosi* group on Figure 4. Associated with *L. gibbosus* in Florida (USA) ..... *C. gibbosi* sp. n.
– Ratio length of propodosomal shield/length of seta $d_1$ 2.4–4.4 ($3.2 \pm 0.43$). CV1 and 2 do not fall within *gibbosi* group on Figure 4 ..... 2.
(2) CV1 and 2 fall within *lithurgi* group on Figure 4. Associated with *L. apicalis*, *L. littoralis*, and *L. gibbosus*. Texas, New Mexico, Arizona, Colorado, Idaho (USA) ..... *C. lithurgi* sp. n.
– CV1 and 2 fall within *abditus* group on Figure 4. Associated with *L. planifrons* and *L. echinocacti*. Arizona (USA), Socorro Is. (Mexico) ... *C. abditus* sp. n.

*There are at least two other new species. We did not include them in the present paper, because they are distinct and do not require a special morphometric study.

*Phoretic deutonymph (Table 1).* Distance between free palpomeres usually shorter than 1/3 their width. Two longitudinal sclerites on rostral projection; sclerites distinctly not reaching level of *se*. Propodosomal shield with transverse cellular pattern; hysterosomal shield with pattern transverse anteriorly and longitudinal posteriorly. Dorsal setae of medium length (Table 1), flattened. Setae $c_1$ placed on hysterosomal shield. Longest setae (*se*, *si*, $c_2$, $c_p$, and often $e_2$ and $f_2$) with weakly developed, but distinct pectination on tips. Setae $h_1$ approximately equal to $e_1$. Ventral setae *1a*, *3a*, and *3b* filiform; *3a* much shorter than *1a* and *3b*. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II weakly sclerotized, about 1/3 length of lateral edge of sternal shield. Anterior and posterior apodemes IV disjunct. Attachment organ width shorter than distance between *4a*. Conoids $ps_1$ and $ps_2$ posterior to central sucker, almost on same transverse level ($ps_2$ slightly anterior). Cupules *ih* placed on sclerotized margin of attachment organ, usually close to anterior cuticular sucker. Latter small, not overlapping *ih*. Central sucker ($ad_1 + ad_2$) weakly sclerotized. Ventral setae *pR* I–II, *vF* II, *mG* II, *1a*, and $h_3$ distinctly shorter than combined length of femur, tibia and genu I. Genual seta *cG* I pectinate, enlarged; *cG* II filiform, smooth, seta *mG* I slightly pectinate; *mG* II longer than *mG* I but not more than twice its length. Tarsal setae *la* I–II filiform, setae *wa* I–II slightly widened at base, attenuated. Seta *s* III apical, setae *e* and *f* IV subequal, both short, much shorter than tarsus IV length, setae *r* and *w* IV shorter than tarsus, not protruding or slightly protruding beyond apex of tarsus IV. Non-phoretic deutonymphs, adults and other feeding stages unknown.

*Abnormalities.* *C. lithurgi* s. str.: one ϕ IV elongated (17) and widened (03-0127-001#66); two solenidia (σ) on one genu I (03-0127-001#68); one $c_1$ missing, its alveolus located anterior to hysterosomal shield (95-0323-021#48); one $c_1$ placed on unsclerotized cuticle, anterior to hysterosomal shield (95-0323-021#50, 96-0510-011#07); one $e_1$ duplicated (96-0510-009#36); one $h_1$ duplicated (95-0323-021#49); one $h_1$ very small, microseta (8), ω1 on one tarsus I longer than on another (35 and 25) (96-0510-009#35).

*Type material.* Holotype: DN – U.S.A.: New Mexico, Colfax Co., Cimarron Canyon, ex *L. apicalis* (propodeum/metepisternum), 12 June 1956, R. & K. Dreisbach, MSU (BMOC 95-0323-021). Paratypes: 14 + 5 + 5 + 4 DN (propodeum/metepisternum + propodeum + wingbase + hindleg), other data as for holotype; 7 DN – same host and collection data (propodeum), MSU (BMOC 95-0323-020); 2 + 1 DN – New Mexico, Cibola Co., El Malpais National Monument, North Pasture, T7N R10W S30 NOPA, ex *L. apicalis* (pronotum + 1st metasomal tergite), 26 August 1991, D.C. Lightfoot, USDA (BMOC 96-0510-008); 1 DN – Arizona, Pima Co., Tucson, ex *L. apicalis* (1st metasomal tergite), on *Opuntia* (Caryophyllales: Cactaceae), 28 May 1953, G.D. Butler, USDA (BMOC 96-0510-007); 15 DN – Arizona, Santa Cruz Co., Santa Rita Mountains, ex *L. apicalis* (propodeum), 5 September 1937, W. Benedict, KU (BMOC 96-0916-191); 3 + 1 DN – Colorado, Fremont Co., Cañon City, ex *L. apicalis* (1st metasomal tergite, propodeum, midfemur + pronotum), 3 July 1949, L.D. Beamer, KU (BMOC 96-

0916-192); 14 DN – Idaho, Fremont Co., St. Anthony Sand Dunes, ex *L. apicalis* (ventral metasoma), 29 June 1977, W.F. Barr, USDA (BMOC 96-0510-009); 7 + 5 DN – Texas, Brewster Co., Big Bend National Park, Oak Canyon, 1400–1520 m, ex *L. littoralis* (between hind coxae + propodeum), on *Prosopis juliflora* (Sw.) DC. (Fabales: Fabaceae), 11 April 1986, T. Griswold, USDA (BMOC 96-0510-011); 6 + 5 DN – Texas, Lee Co., Giddings, ex *L. gibbosus* (forewing base + propodeum), on *Opuntia*, 10 May 1953, L.D. Beamer, KU (BMOC 96-0916-199); 5 DN – Texas, Lee Co., Giddings, ex *L. gibbosus* on *Opuntia* (around wing bases), 12 May 1953, R.H. Beamer KU (BMOC 96-0916-200); Texas, Maverick Co., Quemado, ex *L. littoralis* (proboscidial fossa) on *Opuntia*, 11 April 1950, Michener, Rozen, Beamer & Stephen, KU (BMOC 96-0916-204).

*Etymology.* The name of the new species is derived form the name of the host genus, *Lithurgus*, and is a noun in the genitive case.

*Distribution.* USA (Texas, New Mexico, Arizona, Colorado, Idaho).

*Hosts.* *Lithurgus apicalis*, *L. littoralis*, and *L. gibbosus*.

*Type deposition.* Holotype: MSU. Paratypes: MSU, KU, USNM, UMMZ, IRSNB, HNHM.

Chaetodactylus abditus *sp. n.*
*Diagnosis.* Closely related to *C. lithurgi* sp. n. and *C. gibbosi* but differs by means of several variables (Table 4). Two canonical variates calculated from these variables allow for complete separation from the above mentioned species (see Diagnosis of *C. lithurgi* and Tables 1 and 4).

*Phoretic deutonymph.* (Table 1, Figures 5 and 6). Distance between free palpomeres usually shorter than 1/3 their width. Two longitudinal sclerites on rostral projection; sclerites distinctly not reaching level of *se*. Propodosomal shield with transverse cellular pattern; hysterosomal shield with pattern transverse anteriorly and longitudinal posteriorly. Dorsal setae of medium length (Table 1), flattened. Setae $c_1$ placed on hysterosomal shield. Longest setae (*se*, *si*, $c_2$, $c_p$, and often $e_2$ and $f_2$) with weakly developed, but distinct pectination on tips. Setae $h_1$ approximately equal to $e_1$. Ventral setae *1a*, *3a*, and *3b* filiform; *3a* much shorter than *1a* and *3b*. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II weakly sclerotized, about 1/3 length of lateral edge of sternal shield. Anterior and posterior apodemes IV disjunct. Attachment organ width shorter than distance between *4a*. Conoids $ps_1$ and $ps_2$ posterior to central sucker, almost on same transverse level ($ps_2$ slightly anterior). Cupules *ih* placed on sclerotized margin of attachment organ, usually close to anterior cuticular sucker. Latter small, not overlapping *ih*. Central sucker ($ad_1 + ad_2$) weakly sclerotized. Ventral setae *pR* I–II, *vF* II, *mG* II, *1a*, and $h_3$ distinctly shorter than combined length of femur, tibia and genu I. Genual seta *cG* I pectinate, enlarged; *cG* II filiform, smooth, seta *mG* I slightly pectinate; *mG* II

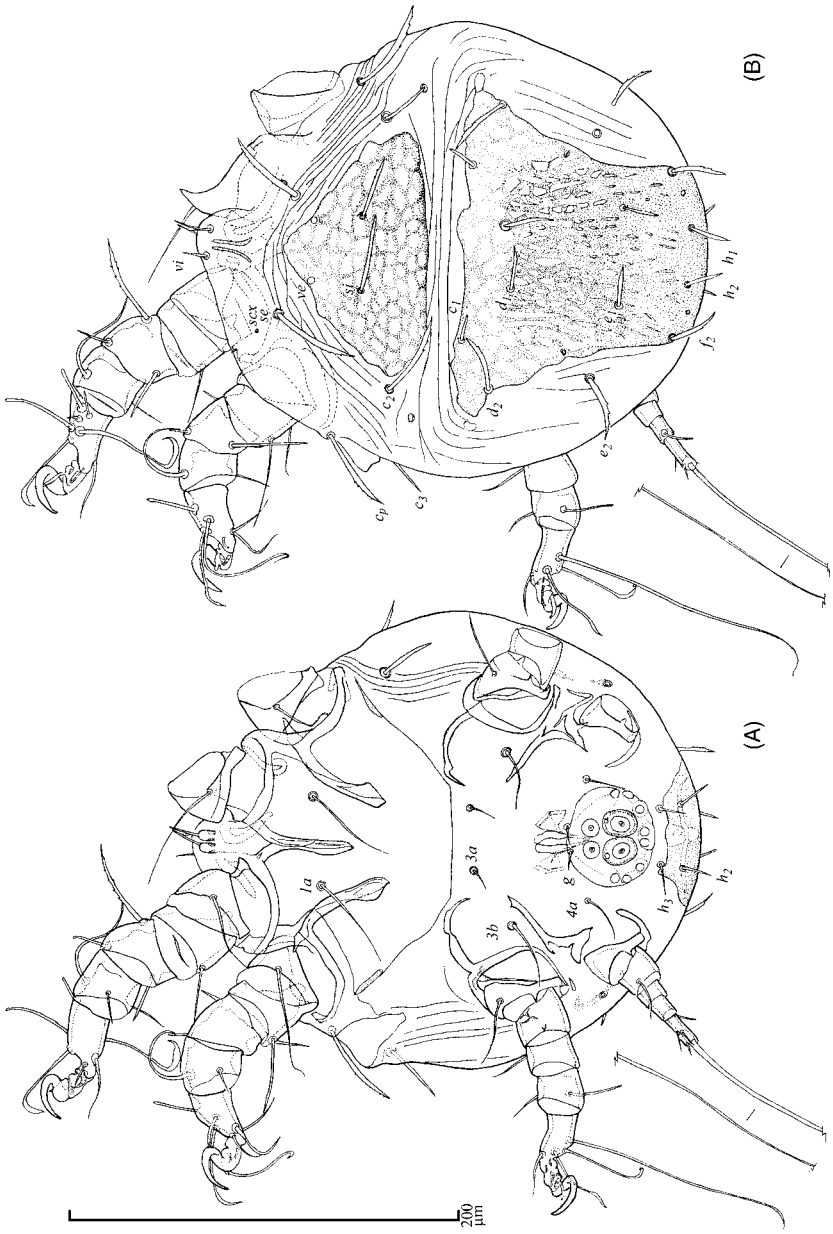


*Figure 5.* *Chaetodactylus abditus* sp. n., holotype: ventral view (A); dorsal view (B).

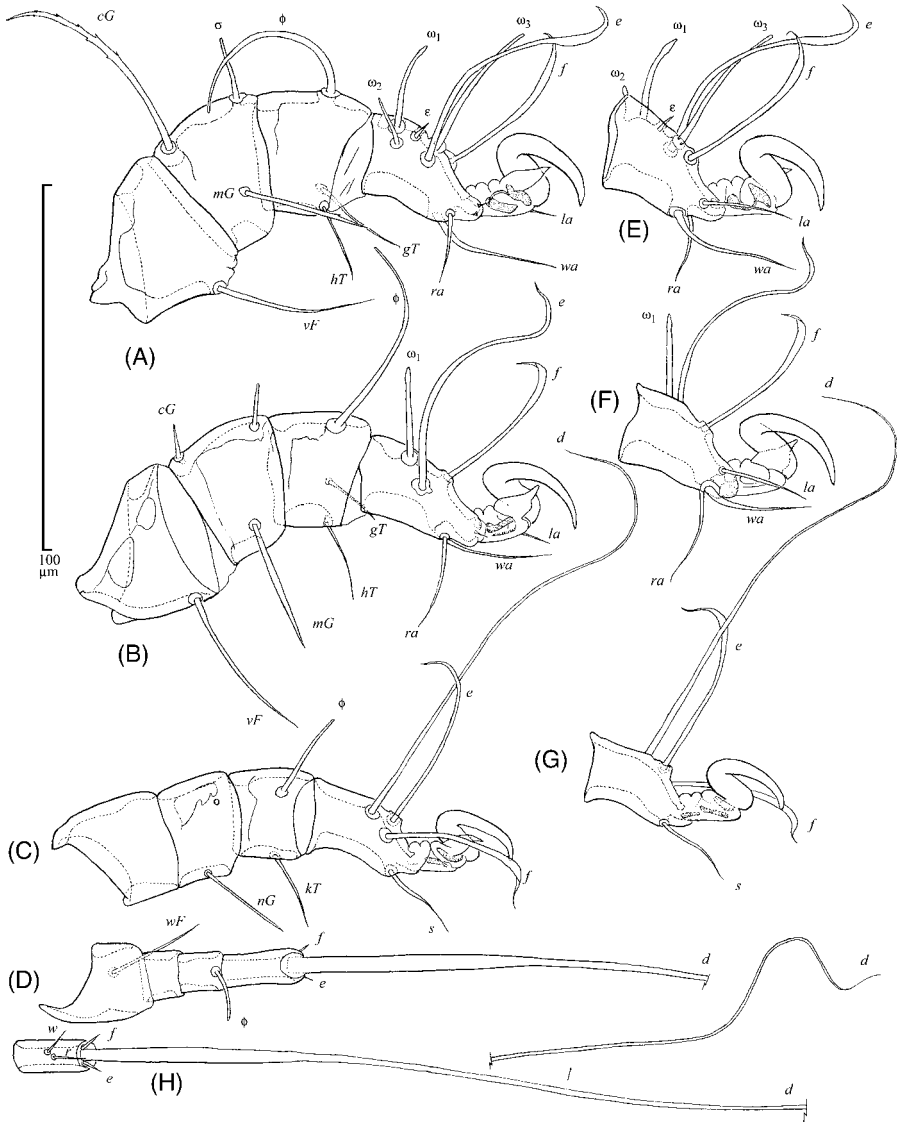


*Figure 6.* *Chaetodactylus abditus* sp. n.: legs I–IV (A–D, respectively); tarsi I–IV (E–H, respectively).

slightly longer than *mG* I. Tarsal setae *la* I–II filiform, setae *wa* I–II slightly widened at base, attenuated. Seta *s* III apical, setae *e* and *f* IV subequal, both short, much shorter than tarsus IV length, setae *r* and *w* IV shorter than tarsus, not protruding or slightly protruding beyond apex of tarsus IV.

Non-phoretic deutonymphs, adults and other feeding stages unknown.

*Abnormalities.* Base of *wa* I wide, as wide as diameter of ω3 (96-0510-012#56).

*Type material.* Holotype: USA: Arizona, Pima Co., Continental, ex *L. planifrons* (ventral thorax), 8 September 1978, Knowlton & Hanson, USDA (BMOC 96-0510-012). Paratypes: 5 + 3 + 1 DN – USA: same host and collection data (lateral thorax + ventral thorax + 1st metasomal tergite), USDA (BMOC 96-0510-012); 34 DN – USA: Arizona, Pima Co., near Continental, elevation 1019 m., 10 am, 31°49.49′N 110°55.58′W, ex female of *L. echinocacti* (mostly pronotum) on *Ferocactus* (Caryophyllales: Cactaceae), 3 September 2003, P. Klimov, UMMZ (BMOC 03-0903-001); 5 DN – Mexico: Colima, Revillagigedo Arch., Socorro Is., ex *L. planifrons* (pronotum and posterior head), 1–5 May 1955, McDonald & Blodget, LACM (BMOC 03-0127-001); 3 DN – same locality, Station 5, Elevation 900 ft. (274.3 m), ex *L. planifrons* (thorax, including propodeum), 8 June 1977, C. Hogue & A. Evans (Steele Exped.), LACM (BMOC 03-0127-002); 5 DN – same host and collection data (metepisternum), LACM (BMOC 03-0127-003); 8 + 3 + 15 HDN – same locality, Bahia Braithwaite, ex *L. planifrons* (propodeum + mesepisternum + ventral mesosoma), 7 May 1925, H.H. Keifer, CAS (BMOC 03-0604-003).

*Etymology.* The name of the new species is a Latin participle (abditus = concealed, secret) referring to its similarity to related species.

*Distribution.* USA (Arizona), Mexico (Socorro Is.).

*Hosts.* *Lithurgus planifrons*, *L. echinocacti*.

*Type deposition.* Holotype: USNM. Paratypes: USNM, CAS, UNAM, UMMZ, IRSNB, HNHM.

Chaetodactylus gibbosi *sp. n.*
*Diagnosis.* Similar to *C. lithurgi* sp. n and *C. abditus* sp. n. Mainly differs from them by shorter dorsal setae (Tables 1 and 4). See also diagnosis of *Ch. lithurgi* above.

*Phoretic deutonymph (Table 1, Figure 7).* Distance between free palpomeres usually shorter than 1/2–1/3 their width. Two longitudinal sclerites on rostral projection; sclerites distinctly not reaching level of *se*. Propodosomal shield with transverse cellular pattern; hysterosomal shield with pattern transverse anteriorly and longitudinal posteriorly. Dorsal setae of medium length, some short (Table 1), flattened. Setae $c_1$ placed on hysterosomal shield. Longest setae (*se*, *si*, $c_2$, $c_p$, and often $e_2$ and $f_2$) with weakly developed, but distinct pectination on tips. Setae $h_1$ approximately equal to $e_1$. Ventral setae *1a*, *3a*, and *3b* filiform; *3a* much shorter than *1a* and *3b*. Sternal apodeme not bifurcated posteriorly. Posterior apodeme II weakly sclerotized, about 1/3 length of lateral edge of sternal shield, sometimes splitted. Anterior and posterior apodemes IV disjunct. Attachment organ width shorter than

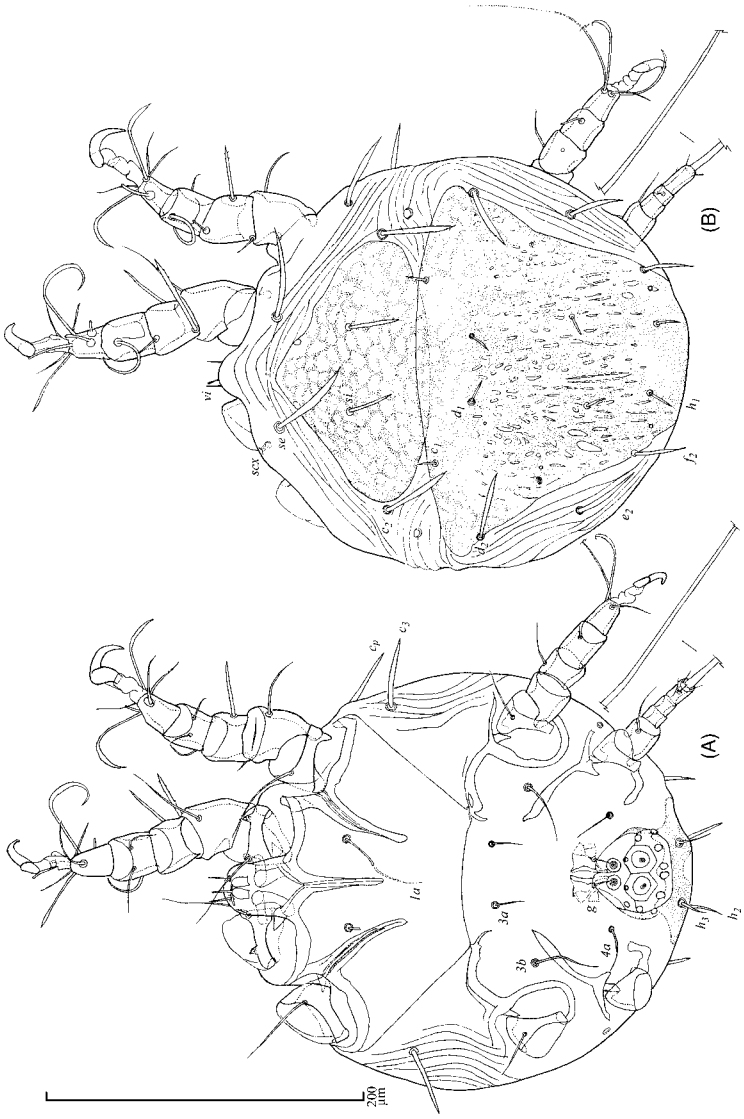


*Figure 7.* *Chaetodactylus gibbosi* sp. n., holotype: ventral view (A); dorsal view (B).

distance between *4a*. Conoids $ps_1$ and $ps_2$ posterior to central sucker, almost on same transverse level ($ps_2$ slightly anterior). Cupules *ih* placed on sclerotized margin of attachment organ, usually close to anterior cuticular sucker. Latter small, usually not overlapping *ih*. Central sucker ($ad_1 + ad_2$) weakly sclerotized. Ventral setae *pR* I–II, *vF* II, *mG* II, *1a*, and $h_3$ distinctly shorter than combined length of femur, tibia and genu I. Genual seta *cG* I pectinate, enlarged; *cG* II filiform, smooth, seta *mG* I slightly pectinate; *mG* II slightly longer than *mG* I. Tarsal setae *la* I–II filiform, setae *wa* I–II slightly widened at base, attenuated. Seta *s* III apical, setae *e* and *f* IV subequal, both short, much shorter than tarsus IV length, setae *r* and *w* IV shorter than tarsus, not protruding or slightly protruding beyond apex of tarsus IV.

Non-phoretic deutonymphs, adults and other feeding stages unknown.

*Abnormalities.* *ih* and anterior cuticular sucker touching each other (96-0510-010#08, 96 0510 010#09); pattern on anterior part of hysterosomal shield consists of short narrow strips, similar to those on posterior part but oriented transversely (96-0510-010#16-19).

*Type material.* Holotype: DN – USA: Florida, Liberty Co., T 2 N R7W, ex *L. gibbosus* (pronotum), 3 May 1924, T.H. Hubbell, UMMZ (BMOC 02-1205-006). Paratypes: 3 + 6 DN – (pronotum + ventral metasoma), same host and collection data; 3 DN – Florida, Alachua Co., Gainesville, ex *L. gibbosus* (pronotum, hind femur, metasoma), 20 May 1929, ''V. K. B. #113'', UMMZ (BMOC 02-1205-007); 5 + 11 + 20 DN – Florida, Miami-Dade Co., Coral Gables, ex *L. gibbosus* (propodeum + 1st metasomal tergite + pronotum), ''19'', no collector, USDA (BMOC 96-0510-010); 10 DN – Florida, Highlands Co., Highlands Hammock State Park, ex *Lithurgus* sp. (propodeum), 4 April 1974, G.C. Eickwort, CUIC (BMOC 95-0422-103); 14 DN – Florida, Highlands Co., Archbold Biological Station, ex *Lithurgus* sp. (metepisternum, posterior coxae III), 20 April 1969, L.L. Pechuman, CUIC (BMOC 95-0422-107).

*Etymology.* The name of the new species is derived from the name of the host species, *gibbosus*, in the genitive case.

*Distribution.* USA (Florida).

*Hosts.* *Lithurgus gibbosus*.

*Type deposition.* Holotype: UMMZ. Paratypes: UMMZ, USNM, CUIC, IRSNB, HNHM, FSCA.

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