

**REVIEW OF FOSSIL *PRENOLEPIS* GENUS-GROUP SPECIES
(HYMENOPTERA: FORMICIDAE)**

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Abstract.—The fossil record of the *Prenolepis* genus-group is comprehensively reviewed for the first time. Five fossil species are presently known from this clade: *Nylanderia vetula*, **sp. nov.** (Dominican amber); *Nylanderia pygmaea*, **comb. nov.**, *Prenolepis henschei* and *Pseudolasius boreus* (Baltic and other contemporaneous amber deposits); and *Protrechina carpenteri* (Arkansas amber). With the reclassification of *Nylanderia pygmaea*, it is now clear that the major lineages of the *Prenolepis* genus-group existed by at least the Eocene.

Key Words: Formicinae, *Nylanderia*, *Protrechina*, *Pseudolasius*, fossils

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The *Prenolepis* genus-group of ants has been recently defined by LaPolla et al. (2010), and represents a large clade of formicine ants (Formicidae: Formicinae) of over 200 described extant species. Members of this genus-group span the globe, with *Nylanderia* possessing both the widest distribution and the highest species diversity. The genera display a range of interesting life history strategies. Many species in the genus-group are generalist omnivores, and these species in particular often form conspicuous components of a local ant fauna. *Nylanderia* has several species that are known invasive species and *Paratrechina longicornis* (Latreille 1802) is one of the worst pantropical invasive species known. While most *Prenolepis* genus-group species are epigaeic, there are examples of hypo-

gaeic species in most genera, with many, if not most, *Pseudolasius* putatively hypogaeic in habit. Nomadic fungivory has been documented in at least one species of *Euprenolepis* (Witte and Maschwitz 2008, LaPolla 2009).

The fossil record for the *Prenolepis* genus-group is sparse relative to extant species diversity and abundance, although one fossil species, *Prenolepis henschei* Mayr 1868, is well represented in Baltic and other northern European amber deposits, comprising upwards of 6% of the total fossil ant specimens in samples. At present the *Prenolepis* genus-group is only represented from 3 amber deposits (Arkansas, Baltic and other contemporaneous amber deposits, and Dominican), although given the extant worldwide distribution and the fact that we now know the clade existed since at least the Eocene, additional

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fossil species discoveries might be expected from more fossil deposits in the future. The fossil record of the *Preneolepis* genus-group is here comprehensively reviewed for the first time with a synthesis of the known fossil species and with the hope it encourages future discoveries of additional fossil species.

MATERIALS AND METHODS

Specimens examined for this study are deposited in the following institutions:

AMNH: American Museum of Natural History, New York, NY, USA (Baltic and Dominican amber)

AWC: Personal collection of A. Wiszniewski, Warsaw, Poland (Rovno amber)

BMNH: Natural History Museum, London, United Kingdom (Baltic amber)

CGC: Personal collection of Carsten Gröhn, Glinde, Germany (Baltic amber)

GZG.BST: Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen, Germany (Baltic amber). Part of this collection was formerly owned by the Geological Institute of Königsberg and described by W. M. Wheeler (1915) and contains some of Wheeler's types. In the listings of examined material under each species we indicate both the new numbers (preceded by GZG.BST) and the old numbers from the Königsberg collection (in parentheses).

GZG.BST (MKC): personal collection of Manfred Kutscher, Sassnitz, Rugen, Germany, deposited at Geowissenschaftliches Zentrum, University of Göttingen (Bitterfeldian amber)

HM: Humboldt Museum, Berlin, Germany (HM) (Bitterfeldian amber)

MZ: Museum Ziemi PAN, Warsaw, Poland (Baltic amber)

MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (Dominican amber)

NHMW: Naturhistorische Museum in Wien, Austria; G. Mayr types (Baltic amber)

PIN: Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (Baltic amber)

SIZK: Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine (Rovno amber)

ZMUC: Zoological Museum of University of Copenhagen, Copenhagen, Denmark (Scandinavian and Baltic ambers)

Morphological terminology for measurements and indices employed throughout are defined below.

EL (Eye Length): maximum length of compound eye in full-face view.

FWL (Forewing Length): length of forewing from base to furthest distal point.

GL (Gaster Length): the length of the gaster in lateral view from the anterior-most point of first gastral segment (third abdominal segment) to the posterior-most point.

HL (Head Length): the midline distance from the anterior clypeal margin to a line drawn across the posterior margin of the head.

HW (Head Width): the maximum width of the head in full-face view (not including eyes).

PrFL (Profemur Length): the length of the profemur from its margin with the coxa anteriorly to its margin with the tibia posteriorly.

PrTL (Protibia Length): the length of the protibia from its margin with the

femur proximally to its margin with the tarsus distally.

MPL (Maxillary Palp Length): lengths of individual segments of the maxillary palp measured from margin to margin of each segment.

SL (Scape Length): the maximum length of the antennal scape excluding the condyle.

TL (Total Length): HL+WL+GL

WL (Weber's Length): in lateral view, the distance from the posteriormost border of the metapleural lobe to the anteriormost border of the pronotum, excluding the neck.

RESULTS AND DISCUSSION

Systematic Paleontology.—Hymenoptera: Formicidae: Formicinae: *Prenolepis* genus-group (*sensu* LaPolla et al. 2010)

List of Fossil Species

Nylanderia pygmaea (Mayr, 1868),
comb. nov.—Baltic and other contemporaneous amber

Nylanderia vetula, **sp. nov.**—Dominican amber

Prenolepis henschei Mayr 1868—Baltic and other contemporaneous amber

Protrechina carpenteri Wilson 1985—Arkansas amber

Pseudolasius boreus Wheeler, W.M. 1915—Baltic and other contemporaneous amber

Nylanderia pygmaea (Mayr, 1868),
comb. nov.
(Figs. 1–2)

Worker.—*Measurements* (n=2): HM # 7/260: TL=1.5–1.6, HL=0.53, SL=0.43, EL=0.13, WL=0.57; HM # 14/255: HW=0.36, SL=0.45, WL=0.47.

Overall body color brown, with a shining cuticle. Head slightly longer

than wide, with rounded posterior corners and straight or weakly concave posterior margin; scattered erect setae along posterior margin; scape surpasses posterior margin by the length of the first two funicular segments. Mesosoma compact; pronotum with 2 pairs of erect setae; mesonotum with a pair of erect setae; metanotal area distinct; dorsal face of propodeum gently convex, with longer declivitous face. Gaster with scattered erect setae.

Male.—*Measurements* (n=8). GZG.BST.03966: TL=1.8, HL=0.40, SL=0.33, EL=0.17, FWL=1.6, WL=0.73; CGC # 3318: WL=0.625; CGC # 774: SL=0.45; FWL=1.75, WL=0.775; CGC # 670: FWL=1.7, WL=0.7; CGC # 844: WL=0.625; GZG.BST (MKC) # 27.036: TL=1.7, SL=0.33, FWL=1.8, WL=0.62; GZG.BST (MKC) # 27.036: TL=1.9, HL=0.41, SL=0.32, EL=0.17, WL=0.66; GZG.BST (MKC) # 27.195: FWL=1.6.

Gyne.—*Measurements* (n=3). GZG.BST.04294: TL=3.3, WL=1.08; GZG.BST.04321: TL=3.05, HL=1.27, SL=0.6, FWL=2.85, WL=0.66; GZG.BST.04561: BL~2.5, WL=1.0

Type material.—Mayr described this species from 20 males and 2 gynes, however only one syntype male was located in the collections: NHMW 1984/31/140 (location of remaining syntypes unknown).

Material examined.—Baltic amber: Male determined by W.M. Wheeler as *Prenolepis pygmaea*: GZG.BST # 04098 (α 143, K5803) (male); Determined by W.M. Wheeler as *Prenolepis henschei*: GZG.BST ## 04294 (G2936) (gyne), 04295 (G2934) (male), 04298 (K4522) (male), 04301 (G2916) (2 males), 04321 (B5318) (gyne), 04346 (B5190) (male), 04353 (G2907) (male), 04369 (B19034) (gyne), 04561 (G2928) (gyne); Determined by W.M. Wheeler as *Prenolepis* sp.: GZG.BST ## 04322

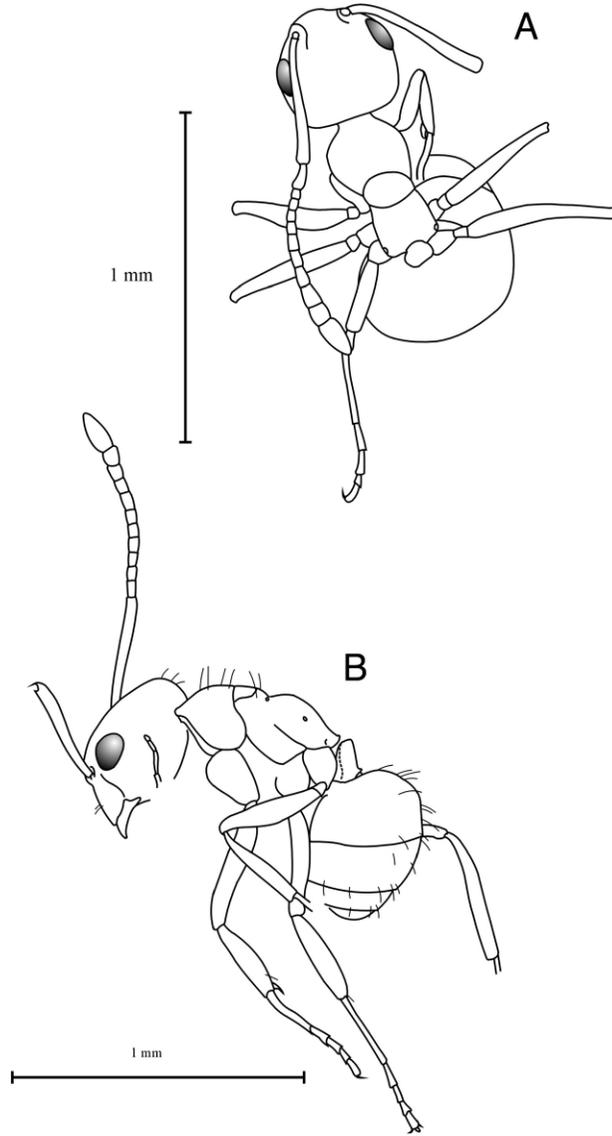


Fig. 1. *Nylanderia pygmaea* workers from two pieces of Bitterfeldian amber. A) worker in dorsal view (Humboldt Museum no. 14/255) (note: pilosity is not depicted); B) worker in lateral view (Humboldt Museum no. 7/260).

(G4634) (3 males), 04336 (G4633) (male); Other specimens: GZG.BST (K5803) (2 males), 04080 (K5261) (male), 04091 (G5296) (2 males), ## 03852 (K1080) (male), 03854 (K1044) (male), 03966 (α 182, K2661) (male), 04009 (K4521) (male), 04037 (K7729) (2 males), 04050 (K7543) (male), 04053 (K5801) (male), 04055 (K5281) (male), 04063 (K7525) (3 males), 04068 (K5270) (male), 04078 (K5803) (2 males), 04080 (K5261) (male), 04091 (G5296) (2 males), 04100 (α 187, K5756) (gyne); PIN ## 964/295 (male), 964/449 (male); MZ ## 1889/13 (male), 1945/1 (male), 2189/58 (male), 7219 (male), 8367 (male), 8542 (male), 8734 (male), 8949 (male), 9244 (male), 10378 (male), 13657 (male), 14145 (12

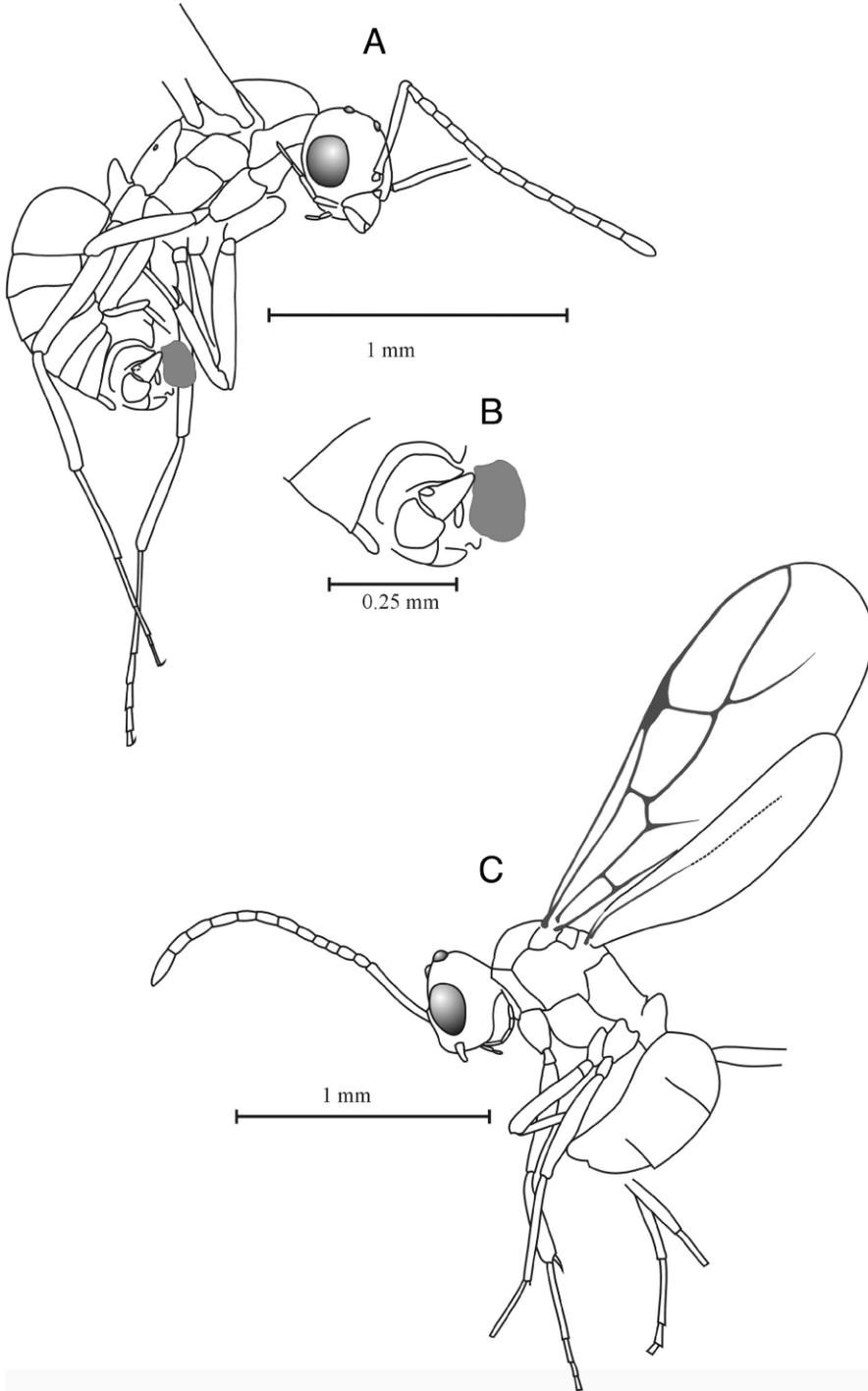


Fig. 2. *Nylanderia pygmaea* male from Bitterfeldian amber (M. Kutscher collection; A & B are specimen no. GZG.BST.27.039; C is specimen GZG.BST.27.036). A) male in lateral view; B) close-up of male genitalia; C) male in lateral view. Note pilosity is not depicted in any of the illustrations.

males), 14606 (male), 16348 (male), 16512 (male), 16768 (male), 17196 (male), 18741 (male), 19137 (3 males), 19143 (male); CGC ## 670 (male), 774 (male), 844 (male), 3318 (male), 3322 (3 males); BMNH ## PI.II.1089 (male), PI.II.1090 (male), PI.II.1096 (male), PI.II.1109 (male), PI.II.1111 (male and gyne), PI.II.1115 (male); ZIN ## DD-4.08 (male), DD-4.11 (male).

Bitterfeldian amber: HM ## 7/230 (male), 7/260 (worker), 10/221 (male), 11/263 (male), 11/283 (male), 11/384 (male), 12/213 (worker), 14/255 (worker); GZC.BST (MKC) ## 27.011 (gyne), 27.016 (6 males), 27,020 (male), 27.022 (male), 27.026 (male), 27.034 (male), 27,036 (male), 27.039 (male), 27.040 (5 males), 27.042 (male), 27.043 (gyne), 27.195 (male), 27.196 (male), 27.197 (male).

Rovno amber: SIZK ## D-2082 (male), K-563 (male), K-566 (3 males), K-1498 (2 males), K-2508 (male), K-2509 (male), K-2511 (male), K-2512 (male), K-3505 (male), K-4211 (2 males), K-4213 (male), K-4214 (male), K-4215 (male), K-4251 (gyne), K-5448 (male).

Scandinavian amber (males): ZMUC ## 267 (A. K. Andersen, 28.03.1968), 268 (A. K. Andersen, 28.03.1968), 269 (A. K. Andersen, 28.03.1968), 270 (G. V. Henningsen, 17.05.1963), 271 (G. V. Henningsen, 01.05.1967), 272 (G. V. Henningsen, 22.05.1959), 273 (G. V. Henningsen, 01.05.1967), 274 (G. V. Henningsen, 14.11.1959), 283 (A.K.Andersen, 28.03.1968).

Notes.—We transfer this species to *Nylanderia* based on the number of mandibular teeth (6), mesosomal shape (no constriction behind pronotum), and the pattern of mesosomal setae all of which match the generic definition of *Nylanderia* (LaPolla et al. 2010). Additionally, the basic shape of the male parameres conforms to many extant *Nylanderia* species, and certainly dif-

fers from *Prenolepis* male paramere shape. With this transfer, *N. pygmaea* becomes the oldest definitive *Nylanderia* species known from the fossil record. It is interesting to note that there are no extant native *Nylanderia* species known from Europe.

In Baltic amber this species represents between 0.3–3.6% of individuals found as amber inclusions, 3.6% in Scandinavian amber, 3.7% in Rovno amber, and 1.3% in Bitterfeldian amber. However, the vast majority of inclusions are reproductives, with workers only rarely encountered. This may suggest that workers of this species did not commonly forage on tree trunks, as is probably the case with *Pr. henschei* workers (see below). The majority of extant *Nylanderia* species display leaf litter and ground dwelling foraging patterns, and infrequently visit tree trunks. The high number of reproductives as inclusions may suggest that they climbed up tree trunks before their mating flight or that they landed on tree trunks during mating.

Nylanderia vetula, sp. nov.

(Fig. 3)

Worker.—*Measurements* (n=1): MPL: segment 6: 0.125; segment 5: 0.104; segment 4: 0.120; segment 3: 0.128; SL: 0.513; WL: 0.662; PrCL: 0.253; PrCW: 0.175; PrFL: 0.581; PrTL: 0.412

Overall body color brown, with an apparently shining cuticle. Head with pubescence across surface, especially dense in medial region; scattered erect setae present, especially along posterior margin, medial region, and clypeus; scapes with short pubescence; scapes surpass posterior margin by the length of the first 2.5 funicular segments. Mesosoma compact, with pronotum rising at about 45°; pronotum with two

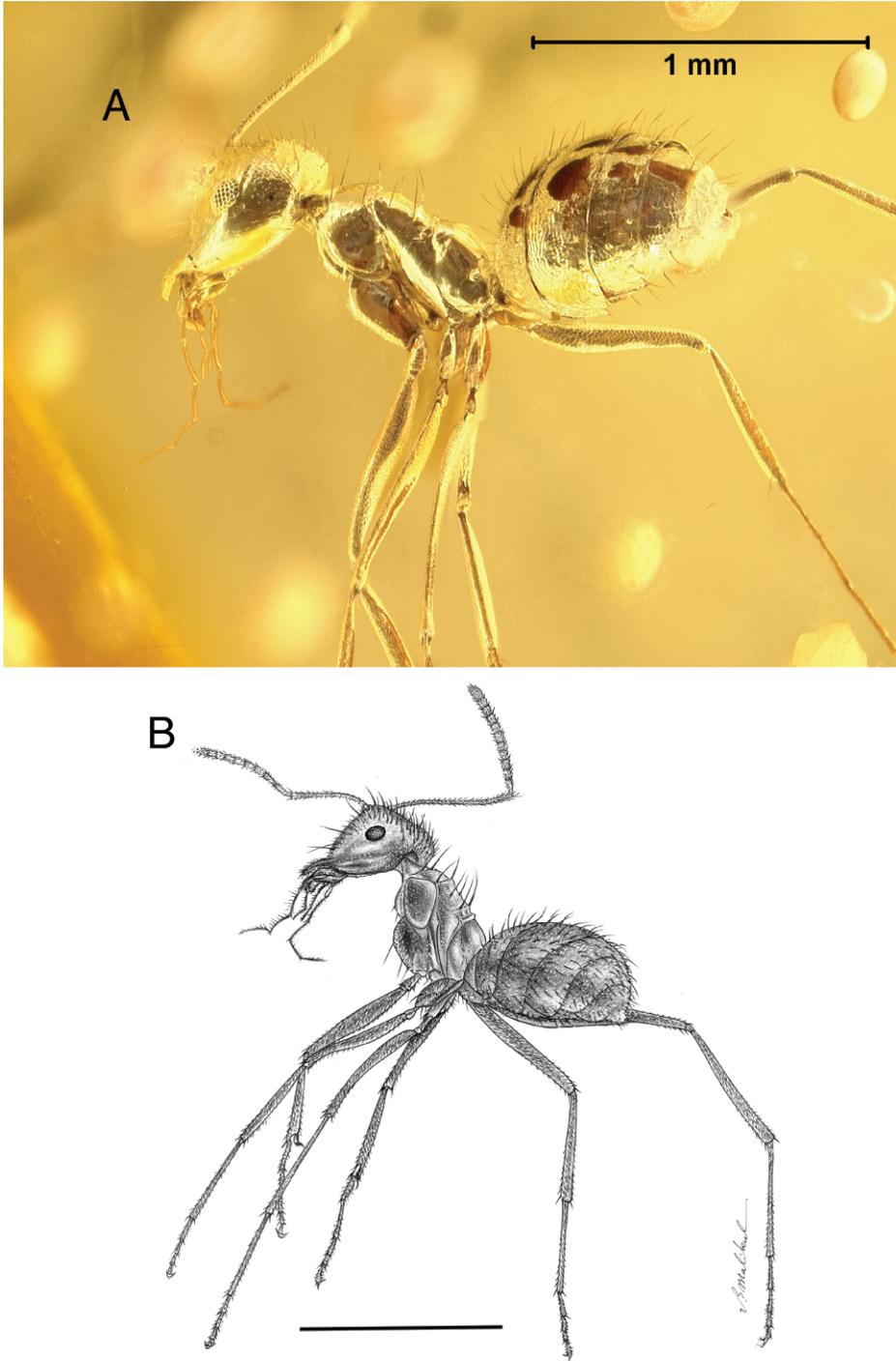


Fig. 3. Holotype worker of *Nylanderia vetula* (AMNH no. DR-10-193) from Dominican amber (A & B).

rows of paired erect setae of the same height; mesonotum with two rows of paired erect setae of the same height as longer pronotal setae; metanotal area distinct, with prominent mesonotal spiracles. Propodeum slightly distorted, but it appears the dorsal face is gently rounded with a declivitous face of about the same length. Coxae with scattered erect setae, especially along anterior margins; remainder of leg segments without erect setae, but with a layer of appressed to slightly decumbent pubescence. Gaster with scattered erect setae of about the same height as erect setae on the mesosoma; shorter layer of decumbent pubescence underneath erect setae.

Holotype.—Worker specimen from a piece of Dominican amber, deposited in AMNH (AMNH no. DR-10-193).

Etymology.—The specific epithet, *vetula*, is Latin for little old woman.

Notes.—Several dozen pieces of Dominican amber known to contain ants were examined in both the AMNH and MCZ collections for *Nylanderia* specimens, but only a single piece was found with a single *Nylanderia* inclusion. This apparent paucity of *Nylanderia* in Dominican amber is surprising, because extant *Nylanderia* are frequently encountered in most habitats around the world. For instance, Ward (2000) found that *Nylanderia* (called *Paratrechina* in that paper) was the fifth most frequently encountered ant genus in leaf litter samples from around the world. However, part of the explanation certainly lies in the fact that most *Nylanderia* species are either ground or leaf litter dwelling and seldom climb into trees, where being trapped in resin is much more likely. Although *N. pygmaea* can represent up to 3.6% of all ant specimens collected in some Baltic amber deposits, the vast majority of these specimens are reproductives (males and females). This

would lead us to suspect that reproductives of *N. vetula* are likely to exist in Dominican amber and reproductive specimens will hopefully be discovered in the future.

The lack of erect setae on the scapes of *N. vetula* is similar to what is observed in the extant *N. parvula* from North America, which always lacks erect setae on the scapes (scapes lacking erect setae is also occasionally observed in two other North American species: *phantasma* and *wojciki*) (Trager 1984). The pattern of erect mesosomal setae is also similar in all of the above-mentioned species. In *N. parvula* erect setae are found, although sparsely, on the femora and tibiae, whereas *N. vetula* appears to lack them. This could be due to abrasion during capture in the resin or the fossilization process, but all six legs are clearly visible in the amber and none of them possess erect setae. The lack of erect setae on the legs is unusual among *Nylanderia* species and is similar to what is observed in species of the paleotropical genus *Parapatrechina*. This species however is definitively *Nylanderia* based on the presence of six mandibular teeth, the rounded dorsal face of the propodeum, and the lack of a pair of erect setae on the propodeum.

The lack of erect setae on the scapes of *N. vetula* might suggest that this species is closely related to North American *Nylanderia*, which form a well supported clade (LaPolla et al. 2010), and where several species either have no erect setae on the scapes (*N. parvula*) or they possess very few erect setae on the scapes.

Prenolepis henschei Mayr, 1868
Figs. 4–5

Worker.—*Measurements* (n=13). GZG.BST.04296: TL=2.3, HW=0.55, SL=0.67, WL=0.73; GZG.BST.04300:

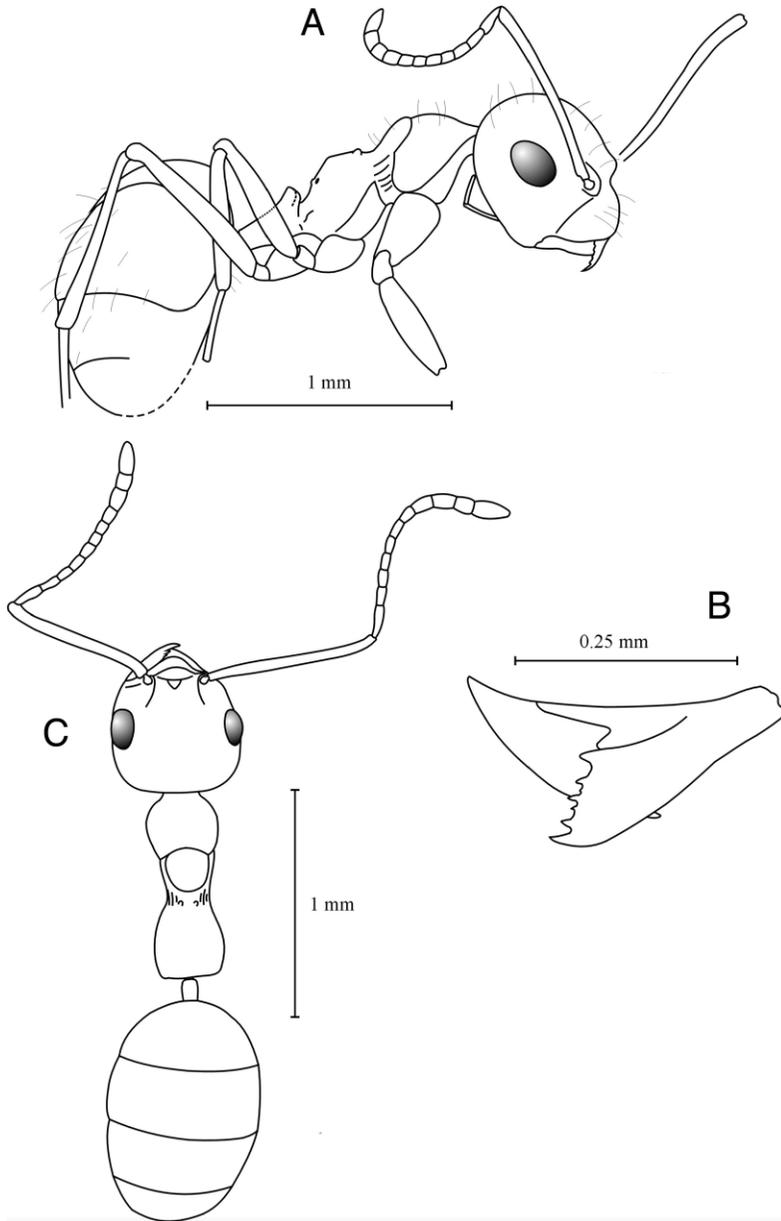


Fig. 4. *Prenolepis henschei* workers from two pieces of Baltic amber (note: pilosity is not depicted in B & C). A) worker in lateral view (PIN no. 964/490) (scape pilosity not shown); B) mandibles (SIZK no K-8672); C) worker in dorsal view (GZG.BST.04215)

SL=0.77, WL=0.70; GZG.BST.04305: WL=0.83; GZG.BST.04319: TL=2.0, TL=2.2, WL=0.75; GZG.BST.04307: SL=0.65, WL=0.67; GZG.BST.04326: TL=2.45, HL=0.53, HW=0.48, TL=2.5, WL=0.90; GZG.BST.04327: SL=0.67, EL=0.15, WL=0.67; SL=0.68, WL=0.73; GZG.BST.04329: GZG.BST.04310: TL=2.3, SL=0.72, TL=2.6, HW=0.58, SL=0.73, WL=0.78; GZG.BST.04316: TL=2.75, WL=0.92; GZG.BST.04333: HL=0.57,

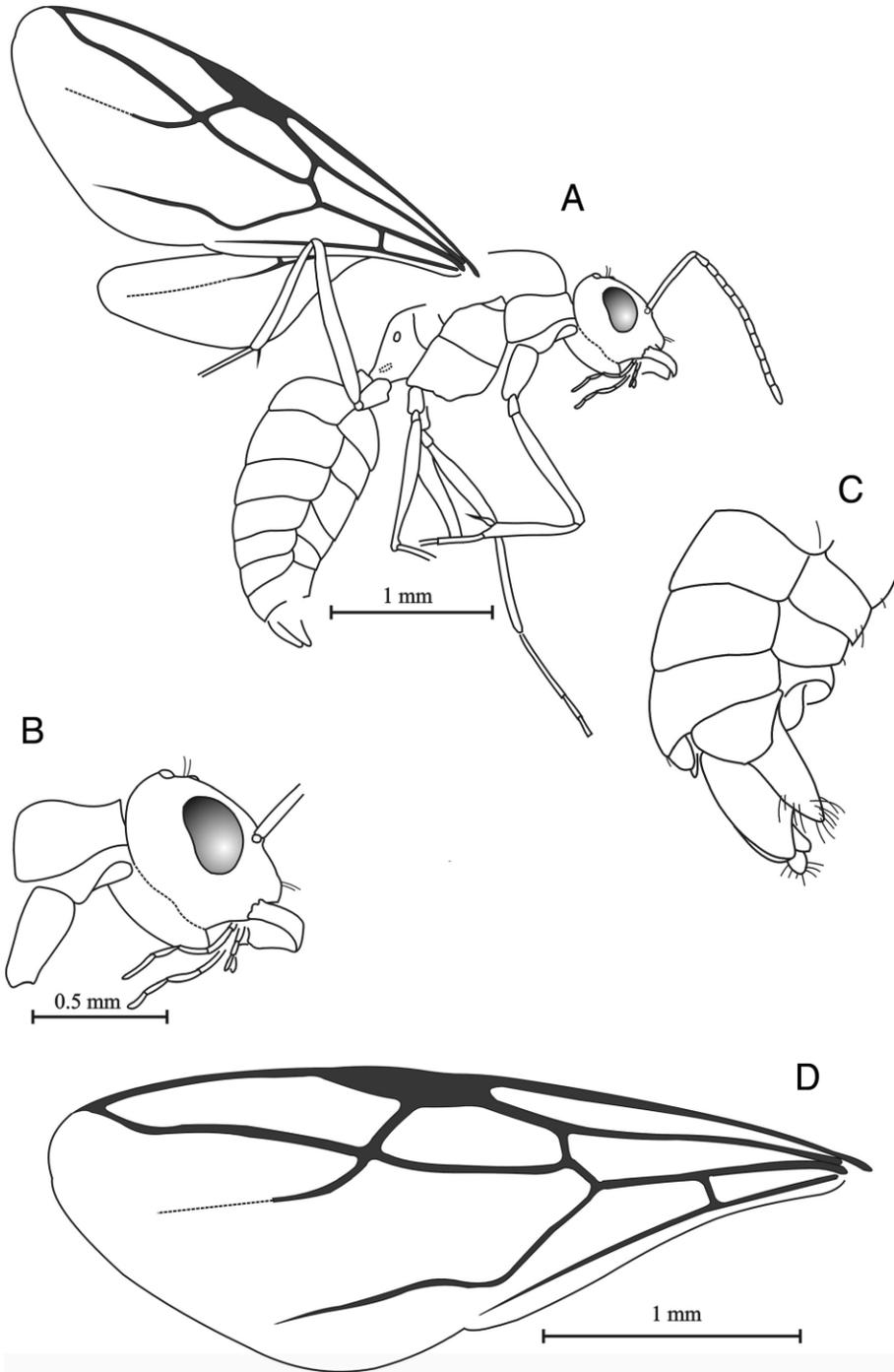


Fig. 5. *Prenolepis henschei* male from Baltic amber (Groehn collection no. 852) (note: pilosity is not fully depicted). A) lateral view; B) head and pronotum; C) gaster with genitalia; D) forewing.

EL=0.17, WL=0.70; PIN # 964/490: TL=2.3, HL=0.56, SL=0.75, EL=0.17, WL=0.83; PIN # 964/489: WL=0.93; SIZK # K-8672: HW 0.56, SL 0.56, WL 0.69.

Male.—*Measurements* (n=3). CGC # 591: TL=2.5, SL=0.53, FWL=2.3; CGC # 852: TL=3.6, HL=0.62, SL=0.49, EL=0.30, FWL=3.3, WL=1.38; ZMUC # 277: TL=2.5, SL=0.53, FWL=2.45, WL=1.12.

Gyne.—*Measurements* (n=2). GZG.BST.04342: TL=3.55, HL=0.67, EL=0.24, FWL=2.85, WL=1.14; GZG.BST.04538: TL=2.8, HL=0.67, SL=0.62, FWL=2.9, WL=1.08.

Pseudogyne.—*Measurements* (n=1). GZG.BST.04631: TL=2.2, HL=0.50, SL=0.57, EL=0.16, WL=0.80.

Type material.—Mayr described this species from 60 workers and 7 males; unfortunately only 5 syntype workers are known to remain: NHMW (Mayr Collection) ## 1984/31/141, 1984/31/142, 1984/31/143 (not studied), and in GZG.BST ## 04215 (370.IV.48), 04216 (3748.IV.96).

Material examined.—Baltic amber: Syntype workers: GZG.BST ## 04215 (370.IV.48), 04216 (3748.IV.96). Workers, determined by W.M. Wheeler as *Pr. henschei*: GZG.BST ## 04281 (G2900), 04283 (K4059, G5178), 04284 (G2893), 04285 (G2905), 04286 (G2875), 04287 (G2911), 04289 (G2897), 04291 (G2924), 04292 (G2896), 04293 (G2935), 04296 (G2889), 04299 (G2917), 04300 (K4495), 04303 (G2937), 04305 (G2921), 04306 (B828), 04307 (B749), 04308 (B696), 04310 (α 75), 04313 (α 32), 04314 (B1008), 04316 (B1741), 04317 (B766), 04318 (B1763), 04319 (α 58), 04326 (B1412), 04327 (B1530), 04328 (B1466), 04329 (B915), 04330 (B1840), 04331 (B1061), 04332 (B937), 04333 (B18566), 04335 (B2043), 04337 (B19188), 04338 (B1874), 04339

(B1905), 04340 (B1850), 04341 (B1873), 04345 (B18397), 04346 (B5190), 04347 (B5190), 04350 (B2143), 04351 (G2890), 04352 (G2922), 04354 (B19879), 04355 (B19886), 04356 (B19030), 04357 (G2884), 04359 (B2066), 04360 (B2672), 04363 (G2876), 04364 (B19971), 04366 (G2887), 04367 (B18557), 04368 (G2878), 04370 (G2883), 04371 (B1212), 04373 (B19064), 04374 (B19949), 04375 (B19970), 04376 (B5496), 04377 (B19181), 04378 (B20000), 04379 (G2888), 04380 (G2877), 04381 (B19681), 04383 (G2886), 04537 (G2879), 04539 (B19824), 04541 (G2933), 04543 (K4204), 04544 (G2881), 04545 (K835), 04546 (K1687), 04549 (G2929), 04552 (K1753), 04555 (G2909), 04557 (K4057, G5190), 04559 (G2925), 04560 (K4051), 04563 (G2927), 04564 (G2926), 04567 (G2920), 04568 (K2901), 04569 (G2902), 04570 (G2919), 04571 (G2918), 04623 (K4198), 04624 (K2647), 04626 (K903), 04627 (K2640), 04628 (K877), 04629 (K881), 04630 (K872), 04632 (K851), 04633 (α 1). Workers, determined by W.M. Wheeler as *Pre-nolepis* sp. (here confirmed as *Pr. henschei*): GZG.BST ## 04311 (B125), 04320 (G4635). Other workers: GZG.BST ## 03833 (K3715), 03845 (K3690), 03865 (K1078), 03868 (K1036), 03870 (K938), 03895 (K2601), 03896 (K1060), 03968 (B18922), 04016 (K4793), 04020 (K4288), 04073 (K5789), 04075 (K6410), 04089 (K5794), 04090 (K5795), 04112 (α 39, K901), 04113 (K4259), 04135 (G3405); PIN ## 364/370, 364/410, 364/422, 964/290–964/294, 964/296–964/306, 964/308–963/313, 964/489, 964/490, 964/2020, 964/2197; MZ ## 1552, 3130, 3641, 4431, 4494, 4594, 5834, 5879, 5889, 7233, 7663, 8030, 8714, 8715, 10355, 14152,

14720, 15448, 15451, 15932, 15954, 16301, 16307, 16309, 16314, 16733, 16734, 17420, 17604, 17857, 19632, 20226, 20228, 20340, 21142, 21546, 21557, 21567, 21568, 22386, 22251a; CGC # 3328; BMNH # PI.II.1097; ZMUC ## 126, 144. Gynes: GZG.BST. ## 04342 (B1101), 04538 (G2880) (determined by W.M. Wheeler). Pseudogyne: GZG.BST # 04631 (K868) (determined by W.M. Wheeler). Males: GZG.BST # 04309 (B245) (determined by W.M. Wheeler); GZG.BST # 04142 (Z526); PIN ## 364/554, 954/304 (together 2 workers in the same sample); CGC ## 591, 852. Bitterfeldian amber: Workers: HM # 16/208; GZG.BST (MKC) # 27.086. Male: HM # 11/294. Rovno amber: SIZK ## K-395 (worker), K-3507 (worker), K-3509 (worker), K-3560 (worker), K-3635 (worker), K-3665 (male), K-3760 (worker), K-4189 (male), K-4232 (male), K-4529 (worker), K-5069 (worker), K-5491 (worker), K-5950 (worker), K-5967 (worker), K-5968 (worker), K-6385 (worker), K-7028 (gyne and male), K-7173 (worker), K-3576b (worker), K-8672 (worker), UA-359 (worker), UA-973 (worker), UA-1340 (male), UA-1697 (worker), UA-2336a (worker); AWC # 25181 (worker). Scandinavian amber: Workers: ZMUC ## 42 (G.V. Henningsen, 16.01.1961), 130 (A.K. Andersen, 28.03.1968), 180 (G.V. Henningsen, 16.01.1961), 181 (G.V. Henningsen, 01.07.1966), 182 (Borge Mortensen, 03.06.1961), 183 (G.V. Henningsen, 28.03.1968), 184 (G.V. Henningsen, 01.07.1966), 185 (A. Henningsen, 09.09.1974), 357 (Thorv.Hansen, 16.01.1961) (workers). Males: ZMUC ## 277 (G.V. Henningsen, 01.04.1970), 278 (G.V. Henningsen, 26.02.1965), 279 (G.V. Henningsen, 24.01.1963), 280 (G.V. Henningsen, 01.05.1967), 281 (G.V. Henningsen, 01.02.1969), 282 (G.V. Henningsen, 01.05.1967),

284 (A.K. Andersen, 01.02.1959), 285 (Borge Mortensen, 21.03.1961).

Notes.—*Pr. henschei* is one of most common ants in Baltic amber. Specimens of this species consist of 4.8–6.7% of all ants in representative collections of Baltic amber, 6.3% in Scandinavian amber, 3.3% in Rovno amber, and 0.3% in Bitterfeldian amber. Inclusions are mainly of workers, which likely means that workers often foraged on tree trunks, as is common with many extant *Prenolepis* species. Another interesting aspect of *Pr. henschei* biology is that mermithid nematodes have been preserved in the process of emerging from ant specimens, indicating that nematode infection of ants dates to at least 40 mya (Poinar 2002).

Wheeler (1930) noted the morphological similarity of *Pr. henschei* to *Pr. imparis* and *Pr. nitens*. The males of *Pr. henschei* and *Pr. imparis* are likewise remarkably similar, with one important difference observed in the parameres. The parameres of *Pr. imparis* are thinner and more setose than observed in *Pr. henschei* specimens.

Protrechina carpenteri Wilson 1985

Protrechina carpenteri is known from a single specimen in mid-Eocene Arkansas amber. Unfortunately, the holotype specimen deposited in the MCZC has deteriorated badly and the amber has become so clouded that it is impossible to see the specimen except for a very faint outline of the body shape. Based on Wilson's (1985) description, the feature used to diagnose this genus from other formicine genera was the lack of a circlet of setae on the acidopore. This lack of setae could have been due to abrasion and needs to be reconfirmed with additional specimens because all other extant and fossil species from the *Prenolepis* genus-group possess setae around the acid-

opore. Hung and Brown (1966) did report that many species of the Campotonini have either reduced or no setae around the acidopore, but that clade is distantly related to the *Prenolepis* genus-group.

Wilson separated *Protrechina* from *Paratrechina* (at that time broadly defined to include what are now three distinct genera: *Nylanderia*, *Paratrechina* and *Paraparatrechina*) by the lack of erect mesosomal setae, but based on the short description and illustration provided in the original paper, *Protrechina carpenteri* could certainly be a *Nylanderia* species. The overall shape of the species and measured characters (taken from Wilson's original description: head width [0.23 mm], scape length [0.48 mm] and pronotal width [0.23 mm]) all fit with a generalized *Nylanderia* morphology. The lack of erect mesosomal setae is problematic as all known *Nylanderia* (extant and fossil species) have erect mesosomal setae. In fact all extant *Prenolepis* genus-group species have at least a few erect mesosomal setae, although they may be fairly short in some species. However, the setae could have been abraded during capture in the resin or during subsequent fossilization. Wilson was unable to count teeth on the mandible, which would have been very helpful for understanding this genus (the vast majority of *Nylanderia* species possess 6 teeth) because mandibular tooth count is an important morphological feature in diagnosing *Prenolepis* genus-group genera (LaPolla et al. 2010).

Because this species cannot be reexamined at the present time it remains difficult to make any decisions regarding the validity of *Protrechina* as a genus. Our inclination is that, based on what we discussed above regarding the observed morphological features, *Protrechina* is really a *Nylanderia* species.

In this study we now have a definitive *Nylanderia* species from Baltic amber, so *Nylanderia* species could have certainly been present when the resins that would eventually become Arkansas amber were produced. For now we maintain *Protrechina* as valid genus within the *Prenolepis* genus-group, but its status remains uncertain until further specimens can be examined.

Pseudolasius boreus

Wheeler, W.M., 1915

(Fig. 6)

Worker.—*Measurements* (n= 10).
 GZG.BST.04574: WL=1.75;
 GZG.BST.04575: SL=1.0, WL=1.125;
 GZG.BST.04576: HL=1.75, HW=1.9;
 GZG.BST.04577: HL=1.25, SL=1.325;
 GZG.BST.04580: SL=1.325, WL=1.4;
 GZG.BST.04581: WL=1.3;
 GZG.BST.04639: HL=0.75,
 WL=1.125; GZG.BST.04645:
 WL=1.75; GZG.BST.04646: HL=1.3,
 HW=1.2; SL=1.075, EL=0.18,
 WL=1.625; NHMW # 1984/31/211:
 HL 1.9, WL 2.1.

Material examined (workers only).—
Baltic amber: Syntypes GZG.BST #
 04574 (G91), 04575 (G92), 04576
 (G96), 04577 (G89), 04578 (G73),
 04579 (G78), 04580 (B1685), 04581
 (G76), 04634 (B18995), 04635
 (B18826), 04636 (B19479), 04637
 (B867), 04638 (B778), 04639
 (B19212), 04640 (B948), 04641
 (B1022), 04642 (B19712), 04643
 (G1543), 04644 (B7177), 04645
 (12216.IV.834), 04646 (B19742),
 04647 (G1544), 04648 (B485), 04649
 (B121), 04650 (14374.IV.1019). Other
 specimen: NHMW # 1984/31/211 (la-
 beled as syntype of *Formica flori*, re-
 determined by Dlussky 2002). Bitter-
 feldian amber: HM # 11/230; Rovno
 amber: SIZK ## UA-2325 (2 workers in
 piece); K-6955 (worker).

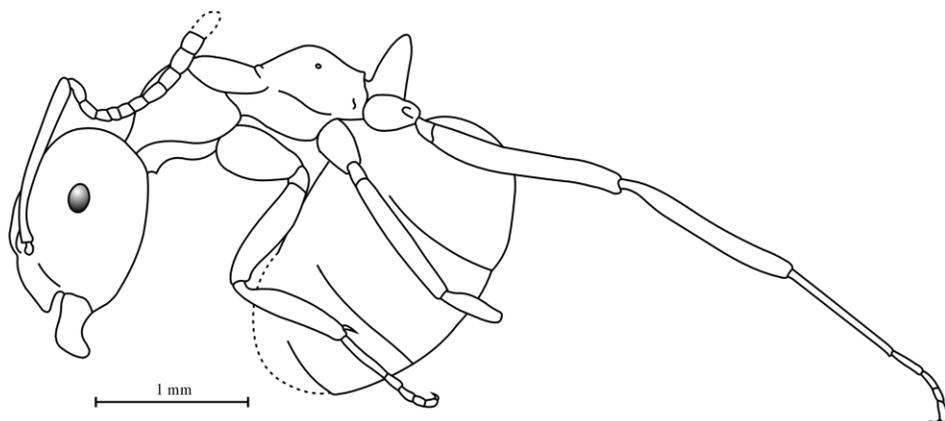


Fig. 6. *Pseudolasius boreus* minor worker from Baltic amber (GZG.BST.04646) (note: pilosity is not depicted).

Notes.—As is the case with some extant species of *Pseudolasius*, it can be difficult to divide workers of this species into a clearly defined minor and major caste, rather it appears that workers are continuously polymorphic (Wheeler 1915). Head length (excluding the mandibles) for example ranges from 0.75 mm to 1.9 mm. It is possible that the specimens measuring closer to the 1.9 mm figure represent what could be called the majors of the species. We have not been able to clearly see the mandibles to count number of teeth present, but Wheeler (1915) reported that the mandibles had 7–8 teeth. Extant species have been observed with between 4–7 teeth present (LaPolla et al. 2010). The other extant genus to which *Ps. boreus* might belong is *Euprenolepis*. Extant *Euprenolepis* and *Pseudolasius* can be difficult to separate, but all extant *Euprenolepis* possess only 5 mandibular teeth (LaPolla 2009). Therefore the high tooth count observed in *Ps. boreus* allows for placement within *Pseudolasius*. The palpal count is usually 2:3 in extant *Pseudolasius* species, but an exact count of the palpal segments cannot be made in any of the fossils observed. What is certain is that

the palps are much shorter than the typical 6:4 segmental count and they do not reach the middle of the head between the mouth and occipital foramen.

EVOLUTIONARY IMPLICATIONS OF FOSSIL TAXA

With the classification of *Nylanderia pygmaea* proposed in this study, it is now clear that all the major lineages of the *Prenolepis* genus-group existed by at least the Eocene (ca. 40 myBP) (Fig. 7). This is consistent with a Paleogene diversification of the ants that has been indicated in previous studies (Wheeler 1915, Grimaldi and Agosti 2000, Brady et al. 2006). Three *Prenolepis* genus-group genera have yet to have any fossil taxa discovered: *Euprenolepis*, *Paraparatrechina* and *Paratrechina*. Since all three of these genera are now found in southeastern Asia (*Euprenolepis* is endemic to the region [LaPolla 2009]), it is possible that fossil taxa could exist within Baltic amber because there is a strong biogeographical affinity between these two regions (Wheeler 1915, Archibald and Farrell 2003). With the exception of *Protrechina carpenteri*, which could not be properly studied

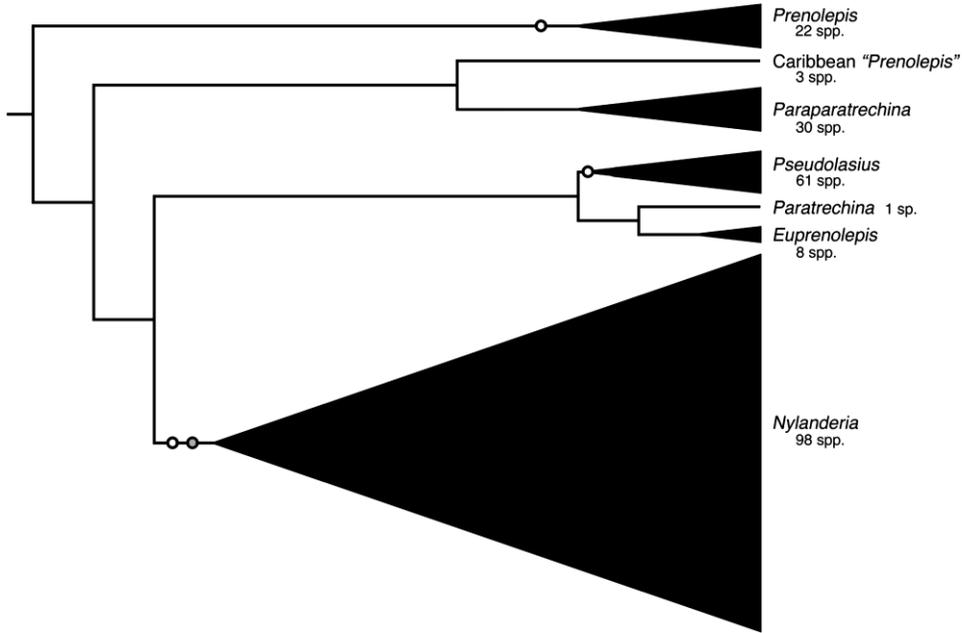


Fig. 7. Phylogeny of the *Prenolepis* genus-group based on LaPolla et al. (2010). Extant species richness numbers are derived from Bolton et al. (2007), LaPolla (2009) and LaPolla et al. (2010), but given that all of the genera are either in various stages of taxonomic revision by JSL and colleagues or in dire need of a modern taxonomic treatment, these numbers will undoubtedly change in the near future. White circles indicate presence of Baltic amber fossils, gray circle indicates presence of Dominican amber fossils.

due to the condition of the fossil, the four remaining species represented in this survey are decidedly modern in appearance. All of them possess morphological features that readily allow for them to be placed within a *Prenolepis* genus-group genus.

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