FIRST RECORD OF *COLLOHMANNIA (C. SCHUSTERI* N. SP.) AND *HERMANNIA* (*H. SELLNICKI* N. SP.) FROM BALTIC AMBER, WITH NOTES ON SELLNICK'S GENERA OF FOSSIL ORIBATID MITES (ACARI: ORIBATIDA)

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HERMANNIA
COLLOHMANNIA,
BALTIC AMBER
FOSSILS
ORIBATID MITES

SUMMARY: Two new species of oribatid mites (Acari: Oribatida) are proposed, each based on single specimens included in Baltic amber. *Collohmannia schusteri* n. sp. and *Hermannia sellnicki* n. sp. represent the first pre-Quaternary fossils of their respective genera. The taxonomic positions of six other oribatid mite genera proposed by Max SELLNICK on the basis of Baltic amber inclusions, which are now lost, are reconsidered due to changes in family concepts since their original proposal. *Scutoribates*, formerly in Carabodidae, is a junior synonym of *Eremaeozetes* Berlese (n. syn.) in the Eremaeozetidae. *Embolacarus* is reassigned to Collohmanniidae. *Tectocymba* and *Gradidorsum* are tentatively retained in Cymbaeremaeidae and Eremaeidae, respectively. *Strieremaeus* and *Plategeocranus* are removed from their current families, Eremaeidae and Carabodidae respectively, but cannot be reassigned based only on original descriptions.

RÉSUMÉ : Deux nouvelles espèces d'oribatides sont présentées à partir de deux spécimens uniques inclus dans une pièce d'ambre de la Baltique. *Collohmannia schusteri* n. sp. et *Hermannia sellnicki* n. sp. sont les premiers fossiles de l'ére quaternaire de chacun des genres. La position taxonomique de six autres genres d'oribate de cet ambre de la baltique, et maintenant perdus, telle que proposée par Max SELLNICK est reconsidérée en raison des changements du concept des familles depuis leur description. *Scutoribates*, précédemment placé dans les Carabodidae est un synonyme junior de *Eremaeozetes* Berlese (n. syn.) au sein des Eremaeozetidae. *Embolacarus* est réassigné aux Collohmanniidae. *Tectocymba* et *Gradidorsum* sont rattachés aux Cymbaeremaeidae et Eremaeidae, respectivement ; *Strieremerus* et *Plategeocranus* sont retirés de leur famille respective (Eremaeidae et Carabodidae) mais ne peuvent être réassignés sur la base de la description originale.

About 100 species of oribatid mites are known as inclusion-fossils in amber, nearly all of which are of Tertiary age (LABANDEIRA *et al.* 1997). More than two-thirds are from Baltic amber, with Max SELL- NICK (1918, 1931) having been the principal describer. The dating of re-deposited inclusion fossils is difficult and inaccurate (WEITSCHAT & WICHARD, 2002), but probably the most reliable age of original rock-matrix

that contains Baltic amber is 44 mya, in the Lutetian Stage of the middle Eocene, as determined by potassium-argon dating (RITZKOWSKI, 1997).

Some oribatid mites from Baltic amber have been identified as representing extant species, but most were considered new at the time of discovery. SELLNICK (1918, 1927, 1931) recognized that the oribatid mite fauna had changed relatively little since the origin of the fossils, and most new species were assigned to extant genera. However, in 1918 he proposed seven new genera based on Baltic amber specimens. These included *Embolacarus*, *Gradidorsum*, *Mulvius*, *Plategeocranus*, *Scutoribates*, *Strieremaeus* and *Tectocymba*. All but *Strieremaeus*, with two species, are monotypic and no other species of these six genera has been described since 1918. Subsequently, SELLNICK (1931) transferred the type species of *Mulvius* (*M. undosus* Sellnick) to the cymbaeremaeid genus *Scapheremaeus*, effectively considering the latter a senior synonym. Herein, I examine the current status and classification of SELLNICK's remaining six genera, with special emphasis on *Embolacarus*. Based on inclusion fossils in newly examined Baltic amber I also propose new species of *Collohmannia* (Collohmanniidae) and *Hermannia* (Hermanniidae), each of which is the first representative of its genus known from the pre-Quaternary fossil record. Because they bear on the identity of *Embolacarus*, the new species are described first.

COLLOHMANNIA SCHUSTERI n. sp.
FIGS. 1-11

Background. *Collohmannia* is an extant genus of very large (over 1 mm), oribatid mites with restricted, probably relictual distributions in the Northern Hemisphere. It is usually included in the middle-derivative paraphyletic group called "Mixonomata" (GRANDJEAN, 1969a). When proposed by SELLNICK (1922), *Collohmannia* was monobasic: type species *C. gigantea* Sellnick. ŠTORKÁN (1925) claimed to have named this species *Phthiracaroides incertus* in 1923, but in fact this name did not appear in the publication and it is a *nomen nudum*. SELLNICK (1932) then proposed a second species, *C. nova*, which SCHUSTER (1962) found to be yet another synonym of *C. gigan-
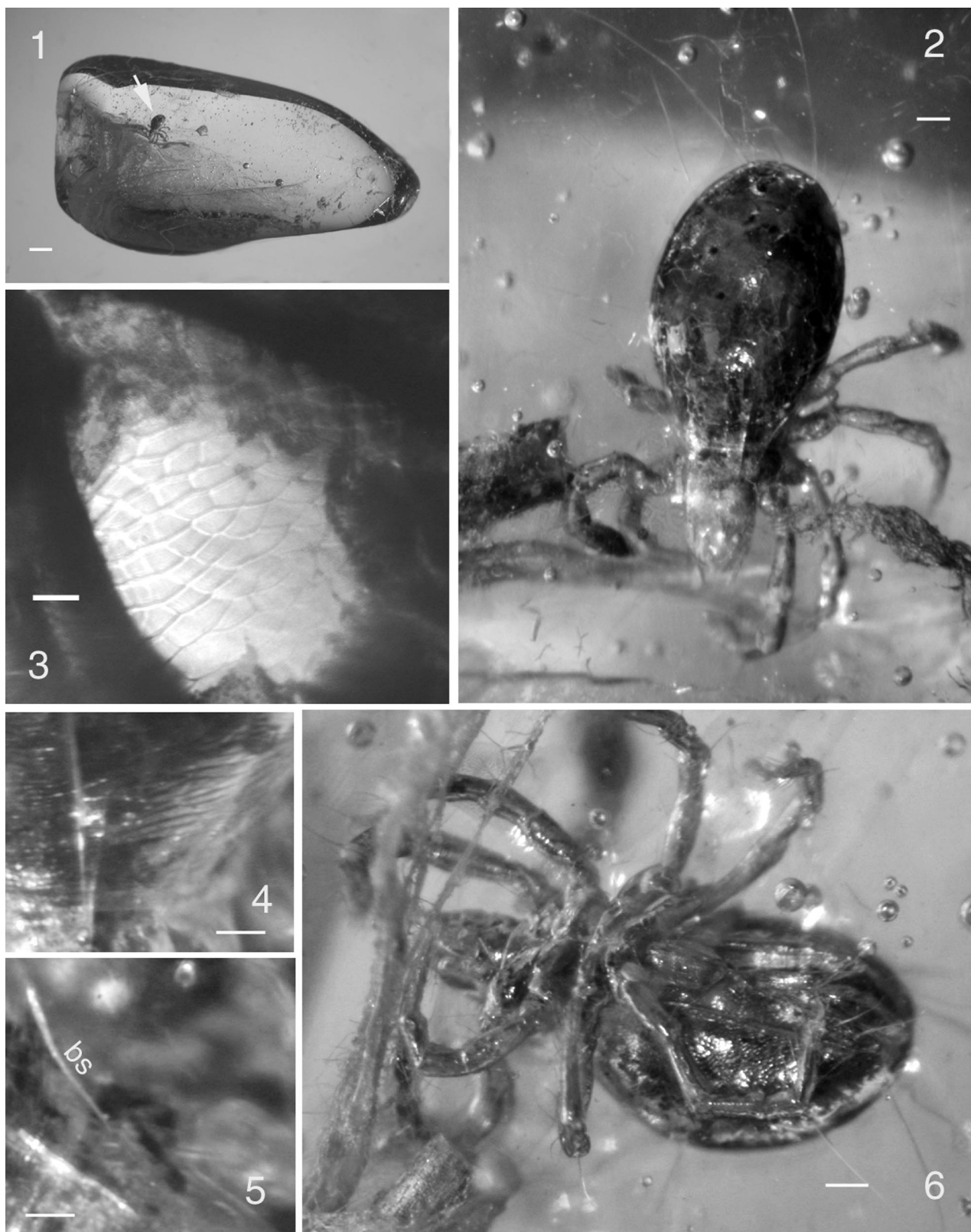
tea*. SELLNICK's error related to the unrecognized presence of strong sexual dimorphism. Since then, one other species has been named — the poorly known *C. asiatica* Krivolutsky & Christov — but undescribed species occur in West Virginia, USA (NORTON, unpublished) and Russia (A. TOLSTIKOV, pers. comm. 1993). *Collohmannia* has been included in four different families: Lohmanniidae (VITZTHUM, 1931, 1942); Eulohmanniidae (BAKER & WHARTON, 1952); Perlohmanniidae (BULANOVA-ZACHVATKINA, 1960) and Collohmanniidae (GRANDJEAN, 1958). The latter is now generally accepted, and includes the single genus.

The strong sexual dimorphism in *Collohmannia* is associated with a mating behavior that is unusual among oribatid mites, most of which transmit sperm indirectly by spermatophores without direct sexual contact. A unique structure of leg IV in males is associated with the presentation of a nuptial food to females (SCHUSTER, 1962; GRANDJEAN, 1966; Alberti and Schuster 2005); this structure is evident in the amber specimen described below, showing conclusively that it is male. Also, the proportion of total length contributed by the hysterosoma of the fossil is similar to that of males (about two-thirds), rather than females (about three-quarters) of *C. gigantea*.
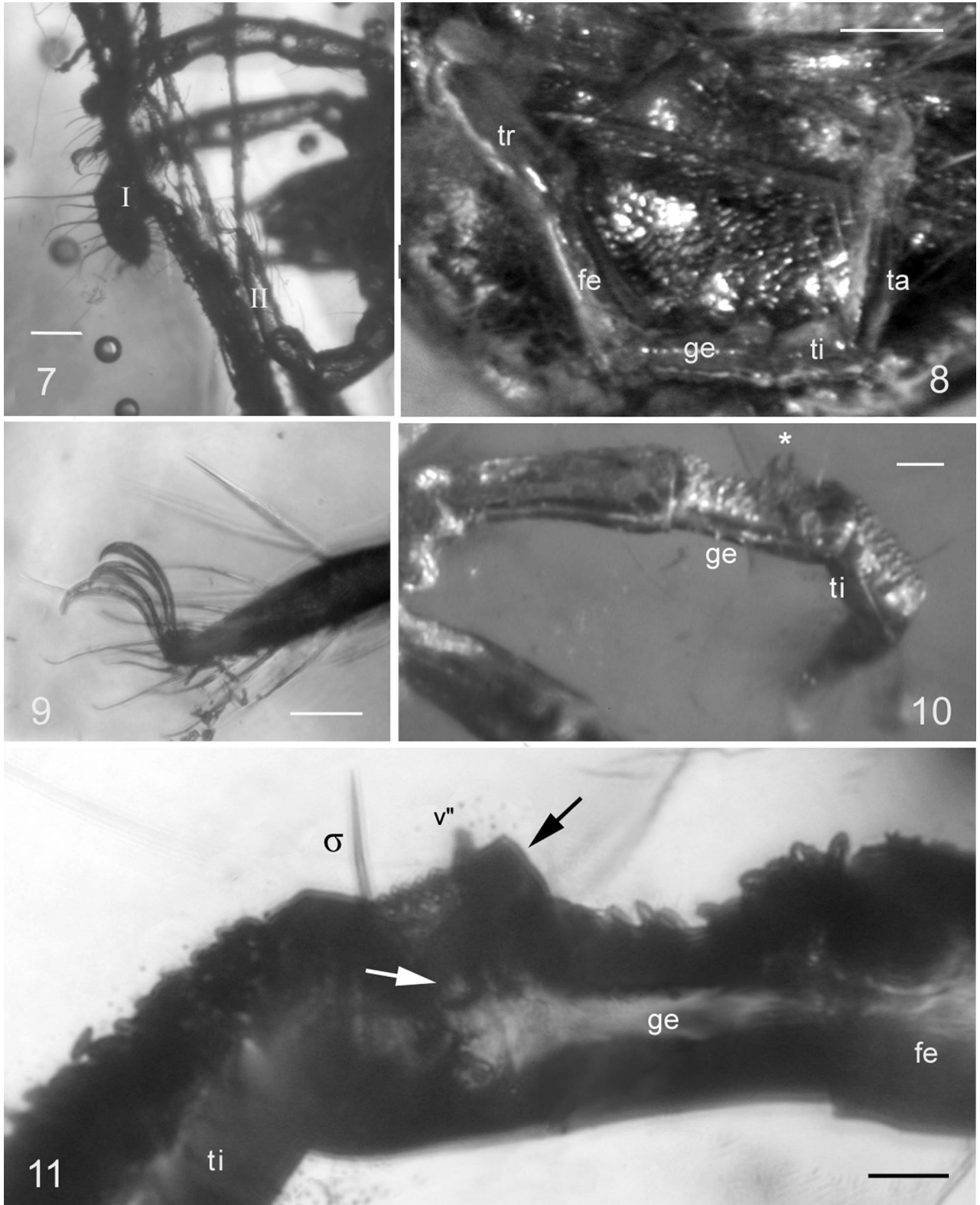
Etymology. *Collohmannia schusteri* n. sp. is named in honor of Prof. Dr. Reinhart SCHUSTER. His accomplishments in the field of acarology and soil biology, combined with those of his students, are truly remarkable. *Collohmannia gigantea* has long been his favorite mite, so this patronym is particularly fitting.

Diagnosis of adult male. Collohmannia species with bothridial seta setiform, not expanded distally. Notogaster with three pairs of flagellate setae (*d2*, *p1*, *h2*). Leg IV with genu almost twice length of tibia, both segments with tuberculate regions; genu with saddle-shaped depression, probably with angular adaxial projection distally and slightly hypertrophied seta *v''*.

Description of adult male (female and immature instars not known). With general traits of *Collohmannia* (see GRANDJEAN, 1966). Color probably medium to dark brown (specimen strongly mottled, affected by preservation). Total length 1.2 mm. Prodorsum widened posteriorly, but otherwise with nearly parallel sides (FIG. 2), rostrum broadly and

FIGS. 1-6. *Collohmannia schusteri* n. sp., holotype male. 1. — Amber piece, arrow indicates specimen (1 mm). 2. — Dorsal aspect, slightly tilted (100 μm). 3. — Notogastral cuticle, colorless region showing imbricate sculpturing (20 μm). 4. — Anterior region of notogaster, same aspect as FIGS. 1, showing elongated imbricate sculpturing (50 μm). 5 –Left bothridial seta (bs), dorsal aspect, anterior to right (50 μm). 6. — Ventral aspect, slightly tilted, anterior to left (100 μm). Length of scale bars in parentheses; FIG. 3 in transmitted light with compound microscope (20× objective); all others in reflected light with stereomicroscope.
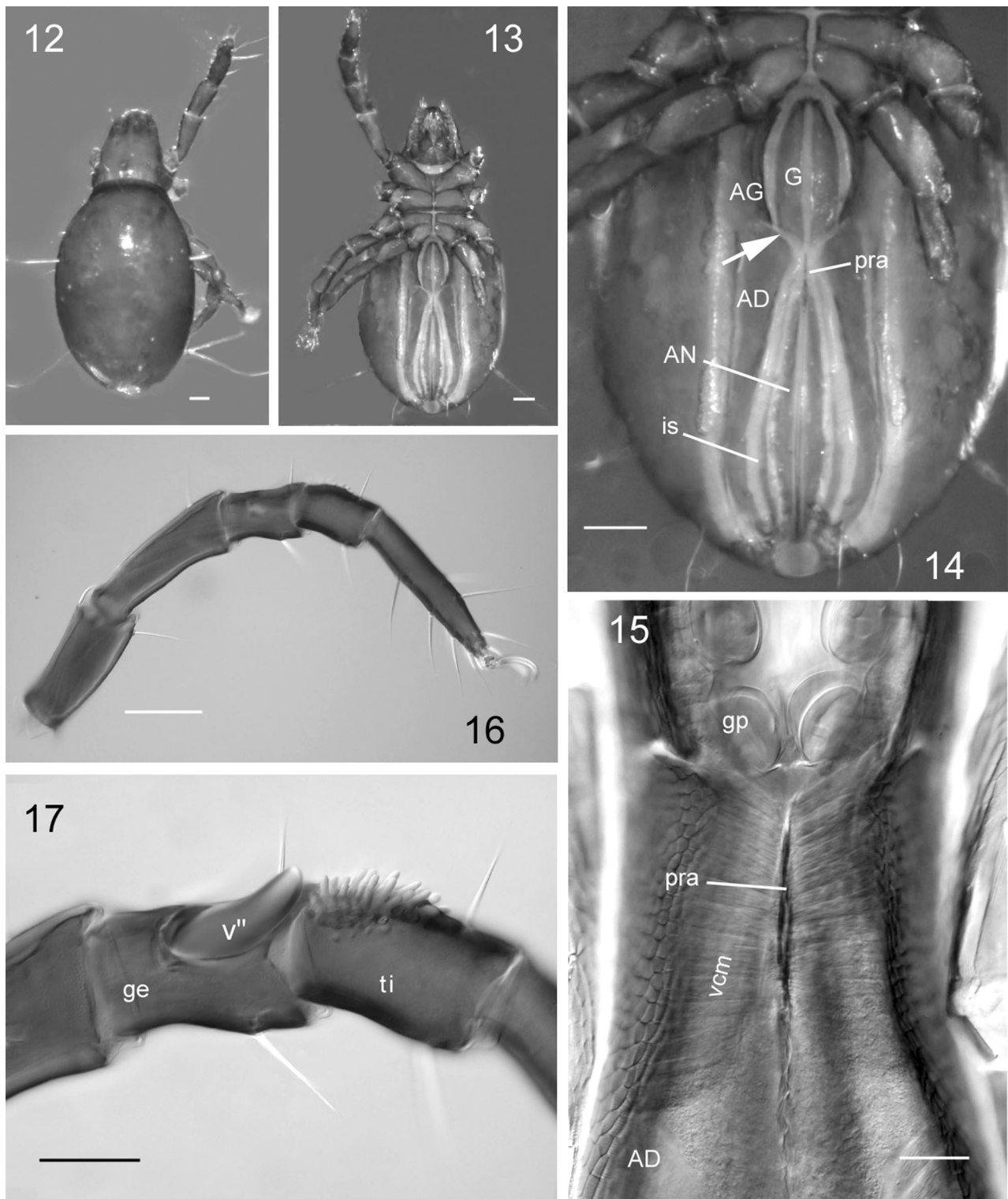
FIGS. 7-11. *Collohmannia schusteri* n. sp., holotype male. 7. — Ventral view of anterior proterosoma, showing legs I and II (100 μm). 8. — Partial ventral aspect of hysterosoma, showing abaxial face of inverted right leg IV (100 μm). 9. — Distal part of left tarsus III, adaxial aspect, showing tridactylous pretarsus (50 μm). 10. — Left leg IV, dorsal (slightly abaxial) aspect showing tubercles of genu and tibia; asterisk marks vague adaxial projections discussed in text (50 μm). 11– Partial left leg IV, ventro-adaxial aspect; layered composite of three images; white arrow marks possible insertion of seta *v''*, black arrow marks cuticular projection (25 μm). Length of scale bars in parentheses; FIGS. 8 &10 in reflected light with stereomicroscope, FIGS. 7, 9 & 11 in transmitted light with compound microscope (10× or 20× objective). Abbreviations: fe (femur), ge (genu), ta (tarsus), ti (tibia), tr (trochanter), *v''* (probable hypertrophied adaxial ventral seta), σ (genu solenidion).

smoothly rounded; length ca. 320 μm, maximum width ca. 250 μm; no surface sculpture discernable. Prodorsal setae thin, smooth (rostral and exobothridial setae not discernable), positioned as in *C. gigantea*; interlamellar seta (*in*) ca. 490 μm (one of pair erect in fossil, one lying flat on body and reaching insertion of notogastral seta *d2*); lamellar seta long, but not measurable, shorter than *in*; bothridial seta (FIG. 5, *bs*) ca. 170 μm, very slightly curved, not tapered, enlarged very slightly in distal half. Notogaster strongly convex, widest near mid-length and nearly elliptical (FIG. 2): length 880 μm, maximum width ca. 540 μm. With strong imbricate sculpture (FIG. 3); anterior quarter with imbricate areas narrower, transversely oriented, giving somewhat striated appearance (FIG. 4). Notogastral setae thin, simple, erect, distributed as in *C. gigantea*; three pairs flagellate: *d2* and *p1* ca. 790 μm, *h2* ca 400 μm. Other setae smaller; measurable examples are *e2* (ca. 180 μm), *h1* (ca. 120 μm), *p2* (ca. 100 μm). Venter (FIG. 6) structured as in *C. gigantea*. Coxisternum with epimera progressively narrower from I to IV; epimeral setation not determined. Anogenital region with imbricate cuticle; overall length ca. 590 μm, of which genital plates occupy ca. 200 μm. Genital and anal plates project obliquely ventrad. Measurable ventral setae include adanal setae *ad1* (ca. 200 μm) and *ad2* (ca. 180 μm), one undetermined anal seta (70 μm) and two undetermined epimeral setae, which are longest on coxisternum (ca 150 μm). Legs with general form as in *C. gigantea*; all tridactylous, with claws similar in size and shape (FIG. 9). Leg I more heavily structured than others: tarsus I about twice as thick as tarsus II (FIG. 7). Leg IV (FIG. 8) ca. 760 μm long; approximate lengths of individual segments as follows: trochanter 180 μm, femur 180 μm, genu 120 μm, tibia 80 μm, tarsus 200 μm. Genu and tibia of leg IV strongly modified (Figs. 10, 11). Proximal half of genu with conspicuous saddle-shaped depression, lined with tubercles dorsally but smooth adaxially. Distal to saddle appears to be angular, adaxially projecting cuticular mass (FIG. 11, black arrow) and what may be hypertrophied seta *v"*, directed dorsally (see remarks in next section). Genu with smaller tubercles in region proximal to solenidion σ; the latter short, erect, similar to that of *C. gigantea*. Tibia IV also with large, dense tubercles dorsally; femur IV distally with small dense tubercles on dorsal surface. Gnathosoma structured as in *C. gigantea*; subcapitulum clearly stenarthric, palps extend slightly beyond end of rostrum; details of chelicerae not discernable.

Remarks on genu IV. Interpretation of this important region — used for the holding of nuptial food in the extant *C. gigantea* and the undescribed American species mentioned above –is uncertain due to general opacity and a partially obscuring flow plane. The projection labeled *v"* in FIG. 11, which is from a compound microscope, is interpreted as the tip of an enlarged seta for two reasons. First, it can be vaguely followed ventrad onto the adaxial face to the light spot, marked with a white arrow, that I interpret as the hollow setal base or its alveolus. Second, the projecting tip of the presumptive *v"* has a thin birefringent margin in polarized light, much like that of *v"* on genu IV of male *Collohmannia gigantea*; in general, setae of the fossil that are in favorable positions show typical birefringence quite clearly. In dorsal view through a stereomicroscope this region is rather vague, but there are two adaxial projections (FIG. 10, asterisk). The more proximal is interpreted as the cuticular projection marked with a black arrow in FIG. 11, the more distal as hypertrophied seta *v"*.

Comparison with other species. *Collohmannia schusteri* is similar to *C. gigantea* (FIGS. 12-17), but males of the two species can be distinguished in several ways. The minimum length of a sample of 20 males of *C. gigantea* from Austria was 1.3 mm; *C. schusteri* is slightly smaller (1.2 mm). The flagellate notogastral setae have different absolute and relative lengths in the two species. In *C. schusteri* setae *d2* and *p1* are almost as long (0.9 times) as the notogaster and are almost twice the length of seta *h2*; in *C. gigantea* males *d2*, *p1* and *h2* are approximately the same size, and no more than 2/3 the notogastral length. The structure of male leg IV also clearly differs between the species. In *C. gigantea* the genu is approximately equal to the tibia in length, and each of the other segments is approximately twice as long (FIG. 16); in *C. schusteri* the genu is twice as long as the tibia, and approximately equals the femur in length (FIG. 8). Both species have tubercles on the tibia, but in *C. schusteri* the tuberculate region runs most of the segment length; in *C. gigantea* it is restricted to the proximal half (FIG. 17). Also, *C. schusteri* has

FIGS. 12-17. *Collohmannia gigantea* Sellnick, male. 12. — Dorsal aspect, several legs removed (100 μm). FIGS. 13. — Ventral aspect, several legs removed for comparison with FIGS. 24 (100 μm). 14. — Hysterosoma, ventral aspect; arrow indicates partial articulation between aggenital and adanal plates (100 μm). 15. — Anogenital region dissected from hysterosoma, in dorsal (internal) aspect, showing transversely oriented compressor muscles that originate on adanal plates and insert on preanal apodeme (100 μm). 16. — Right leg IV, adaxial aspect (100 μm). 17. — Genu and tibia IV, adaxial aspect, composite of four image layers (50 μm). Length of scale bars in parentheses; FIGS. 12-14 in reflected light with stereomicroscope, FIGS. 15-17 in transmitted light with compound microscope (40×, 10×, 20× objective, respectively). Abbreviations: AD (adanal plate), AG (aggenital plate) AN (anal plate), G (genital plate), ge (genu), gp (genital papilla), is (intercalary sclerite), pra (preanal apodeme), ti (tibia), v'' (hypertrophied ventral seta), vcm (ventral compressor muscles).

tubercles on the genu, but *C. gigantea* does not. If the above interpretation of genu IV is correct, *C. schusteri* has an adaxial cuticular projection that *C. gigantea* does not possess, and seta v'' of genu IV is only moderately hypertrophied, not enlarged, thumb-like, as in *C. gigantea* (FIG. 17).

Based on the original description and illustration (CHRISTOV, 1970); *C. asiatica* is relatively small, like *C. schusteri* (mean of three individuals 1.31 mm). However it differs markedly from *C. schusteri* (*Cs*) and *C. gigantea* (*Cg*) as follows: 1) lamellar setae are slightly longer than interlamellar setae (the reverse in *Cs* and *Cg*); 2) the bothridial seta (sensillus) is spindle-form, finely barbed (setiform, nearly isodiametric, and almost smooth in *Cs*, *Cg*); 3) only notogastral seta *h2* is flagellate (*d2* and *p1* also flagellate in *Cs*, *Cg*). The illustrated specimen of *C. asiatica* seems to be male, since the hysterosoma occupies only about one-third the total length, but leg IV was not discussed or drawn. The undescribed species from the USA and Russia differ markedly from *C. schusteri* and *C. gigantea* in the form of male leg IV, as well as other characters.

Remarks on holotype. The amber piece containing the holotype male and only known specimen was purchased by Mr. Joerg WUNDERLICH from a dealer in Baltic amber; its provenance is not known precisely, but he believed that it probably originated from the Kaliningrad (Königsberg) region. The piece (FIG. 1) was originally about 1.5 × 0.7 cm and contained numerous small fracture planes and flow lines, plus a modest amount of debris and plant trichomes. The mite is dorsoventrally oriented, slightly tipped laterally. When first obtained only dorsal features of the mite were visible, so it was trimmed substantially to allow observation of the venter and made thin enough to fit under the 20X objective of a compound microscope, in a temporary glycerin mount; legs and cuticle could then be observed with transmitted light. One other oribatid mite, an unidentified small member of Brachypylina, remains in the piece but in an inconspicuous location, and it is difficult to examine. The piece has been deposited in the Geowissenschaftliches Zentrum der Universität Göttingen Museum, under accession number GZG 001264/1.
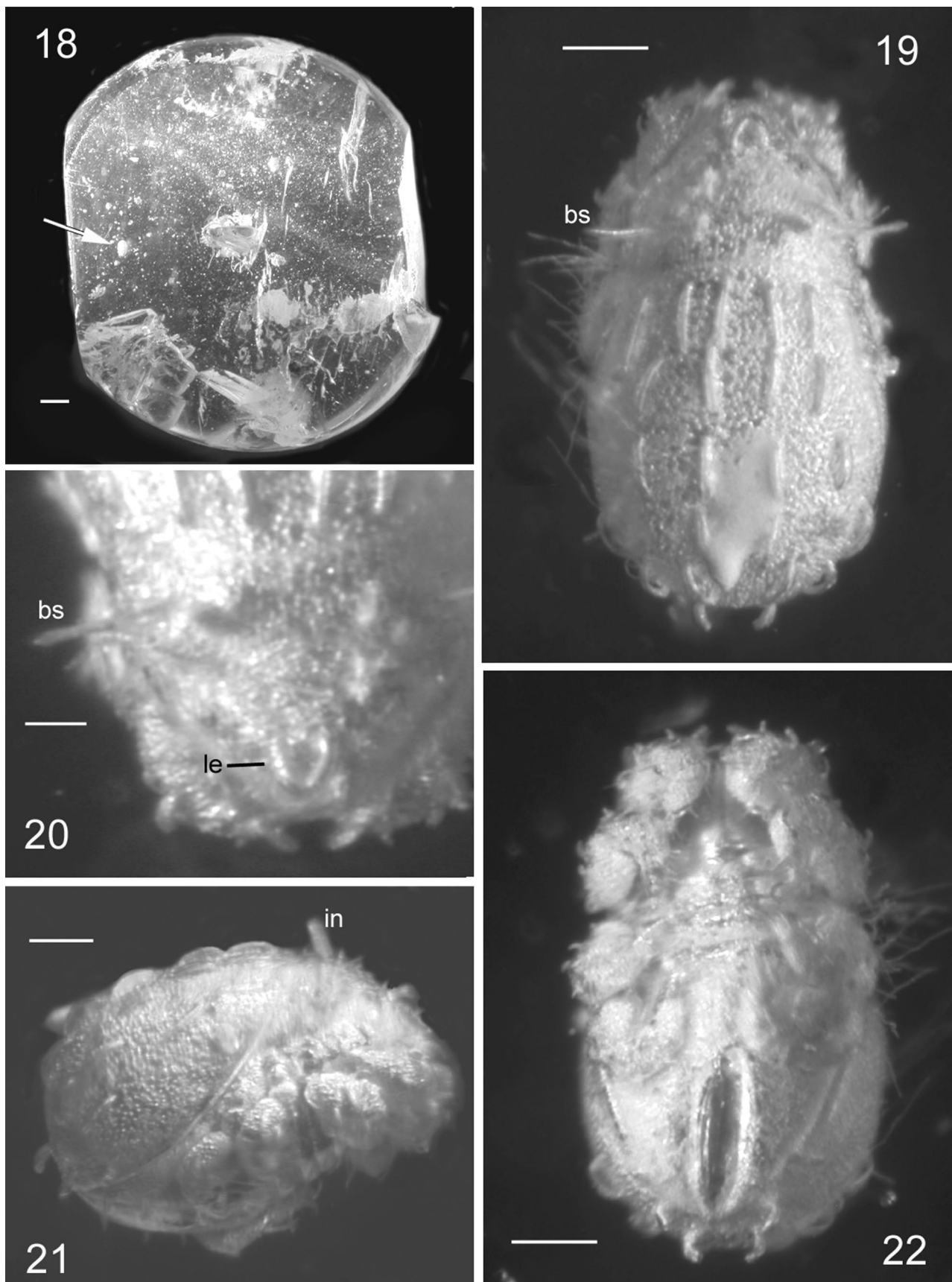
HERMANNIA SELLNICKI N. SP.
FIGS. 18-22

Background. *Hermannia* (sensu lato) is a genus of about 80 named species in the desmonomatan family Hermanniidae (WOAS, 1981, 1992; SUBIAS, 2004). Most species of the subgenera *Hermannia* and *Heterohermannia* are distributed in temperate regions of the Northern Hemisphere, while the rather complementary subgenus *Phyllhermannia* is principally in subtropical to tropical regions, plus temperate regions of the Southern Hemisphere. Characters discernable in the fossil that have been considered diagnostic for species of *Hermannia* include overall shape and size, the nature of bothridial and notogastral setae, cuticular ornamentation, and the shape of legs.

Etymology. *Hermannia sellnicki* is named in honor of the late Dr. Max SELLNICK, who was a major figure in the history of acarology and the first to seriously study fossil oribatid mites.

Diagnosis of adult. Small *Hermannia* species (590 μm) with large cerotegument granules, dense but without pattern. Most prodorsal and notogastral setae broad, not tapered distally; rostral seta not reaching anterior edge of rostrum. Legs I and II with strong ventral carina.

Description of adult (sex unknown, immature instars unknown). Length ca. 590 μm, maximum width ca. 350 μm. Most of cuticle densely covered with large cerotegument granules, or nodules, that lack any apparent pattern (Figs. 19, 21). Prodorsum subtriangular in dorsal aspect. Bothridial seta (*bs*) ca. 100 μm, thin, slightly enlarged in distal half, no ornamentation discernable. Interlamellar seta (FIG. 21, *in*) erect, ca. 90 μm, broad, nearly parallel-sided, rounded distally; inserted very slightly anterior to level of bothridia, with mutual distance of pair about equal to length. Lamellar seta *(le)* equally broad as *in*, but only 50 μm long, clearly not reaching edge of rostrum in dorsal aspect; slightly curved medially, so tips touch (FIG. 20); mutual distance about equal to length. Rostral seta also ca. 50 μm, but much thinner, distally tapered. Notogaster (FIG. 19) about twice length of prodorsum; broadly ovate, 1.2 times longer than wide. Setae all broad, similar in shape to *in*, procumbent, directed posteriorly along body

FIGS. 18-22. *Hermannia sellnicki* n. sp., holotype. 18. — Amber piece, arrow indicates specimen (1 mm). 19. — Dorsal aspect (100 μm). 20. — Prodorsum and part of notogaster, anterior to bottom (50 μm). 21. — Lateral aspect (100 μm). 22. — Ventral aspect (100 μm). Length of scale bars in parentheses; all in reflected light with stereomicroscope; FIGS. 19-22 each layered composite of three images. Abbreviations: bs (bothridial seta), in (interlamellar seta), le (lamellar seta).

contour; most relatively long (90-100 μm), reaching insertion of next more-posterior seta or nearly so. Venter (FIG. 22) appears typical of genus, but no details discernable. Legs (all fully flexed, held against body) with broad femora covered with cerotegument granules (FIGS. 21, 22); large ventral carina discernable on femora I and II.

Comparison with other species. Hermannia sellnicki much resembles the abundant, widespread species *H. gibba* (C. Koch) in having: relatively long, broad notogastral setae; large and dense cerotegument granules which form no pattern; and broad femora, of which I and II have strong ventral carinae. Most *Hermannia* species lack a carina on femora I and II, have notogastral setae that are shorter or differently shaped, and have defined cerotegument patterns. *Hermannia jesti* (Travé) has broad femora, but has shorter notogastral setae and smaller, less dense cerotegument granules than do *H. gibba* and *H. sellnicki*. The latter two species differ much in size; *H. gibba* is 30-60% larger (780-940 μm; WOAS, 1978) than *H. sellnicki*, which is well beyond possible differences based only on gender. *Hermannia gibba* also has noticeably longer and slightly narrower lamellar setae that reach the edge of the rostrum in dorsal aspect. Considering its similarity to *H. gibba*, *H. sellnicki* can be included in the nominate subgenus of *Hermannia*, even though some characters of the group (WOAS, 1992) are not discernable in the fossil.

Remarks on holotype. As with the previous species, the amber piece (FIG. 18) probably comes from the Kaliningrad region and was purchased from a dealer by Mr. Joerg WUNDERLICH. It has been deposited in Geowissenschaftliches Zentrum der Universität Göttingen Museum under accession number GZG 001264/2. The piece also contains two poorly preserved insects and one mesostigmatid mite. The holotype is in good condition, with only a small cloudy region on the notogaster. Unidentified filaments emerge from the left side of the notogaster and the region of the right prodorsal trichobothrium.

FAMILY RELATIONSHIPS OF SELLNICK'S FOSSIL GENERA

Although SELLNICK had suggested vague relationships for several of the genera proposed in his 1918 paper, VITZTHUM (1931) seems to have been the first to explicitly assign them all to families. He included *Tectocymba* in Cymbaeremaeidae, *Plategeocranus* and *Scutoribates* in Carabodidae, *Embolacarus* in Neoliodidae (=Liodidae of many authors), and *Gradidorsum* and *Strieremaeus* in Oribatidae. In VITZTHUM's subsequent major work (1942, Lieferung 5/6) he substituted Oribatidae with Eremaeidae, but the concept of the latter family was quite broad at that time (e.g. WILLMANN, 1931). These affiliations were maintained without comment by authors of mid-century lists and catalogues (RADFORD, 1950; BAKER & WHARTON, 1952; PETRUNKEVITCH, 1955; DUBININ, 1962).

Despite subsequent major changes in family concepts, especially for Carabodidae and Eremaeidae, the placements of the six fossil genera were not adjusted (e.g. KRIVOLUTSKY et al., 1990; SELDEN, 1993) and it seems likely that some of these are now wrongly assigned. Considering that a wide range of highly derived oribatid mites in extant genera existed in the late Eocene (LABANDEIRA et al., 1997), some of the fossil genera are likely to be extant, with synonyms existing among the hundreds of genera proposed since 1918.

The original specimens were part of the amber collections of the Geologisch-paläontologisches Institut, of the Universität Königsberg. It has been assumed that all SELLNICK's specimens were lost (KRIVOLUTSKY & DRUK, 1986), having been destroyed or dispersed during World War II. But based on the list of EZHOVA (1995), some of the material studied for SELLNICK's 1931 paper (representing 17 species) has been accumulated in the Museum of the World Ocean, in that same city (now Kaliningrad). Two of SELLNICK's fossil genera are represented in this material (see below), but attempts to borrow specimens were unsuccessful. Some amber pieces containing types of other arthropod groups from the original Königsberg collection have been rediscovered over the years, in various places. A small possibility remains that some of Sellnick's specimens may reside – unidentified as such – in the Geowissenschaftliches Zentrum der Universität Göttingen Museum, Göttingen, Germany, where part of the Königsberg collection was moved during the war (M. JUDSON, W. MAGOWSKI, M. REICH pers. comm., 2003-2004).

Based on the original descriptions and figures, there is enough information to make definitive or tentative judgments about the family placement of some of SELLNICK's genera, but others will probably remain mysterious until the rediscovery of specimens.

Tectocyma. Specimens identified by SELLNICK himself (1931) as the type species (*T. rara* Sellnick) exist in Kaliningrad (EZHOVA, 1995). Pending their study, *Tectocymba* seems properly placed in Cymbaeremaeide. All described and illustrated traits match various extant genera in that family: these include the rather flattened shape, the oval, strongly sculptured dorsum with centrally raised notogaster, the clavate bothridial setae (sensilli), the venter somewhat angular posteriorly, and the widely spaced genital and anal plates. Also, the family as a whole is characteristic of arboreal habitats, where capture by flowing resin seems most likely (KRIVOLUTSKY et al., 1990).
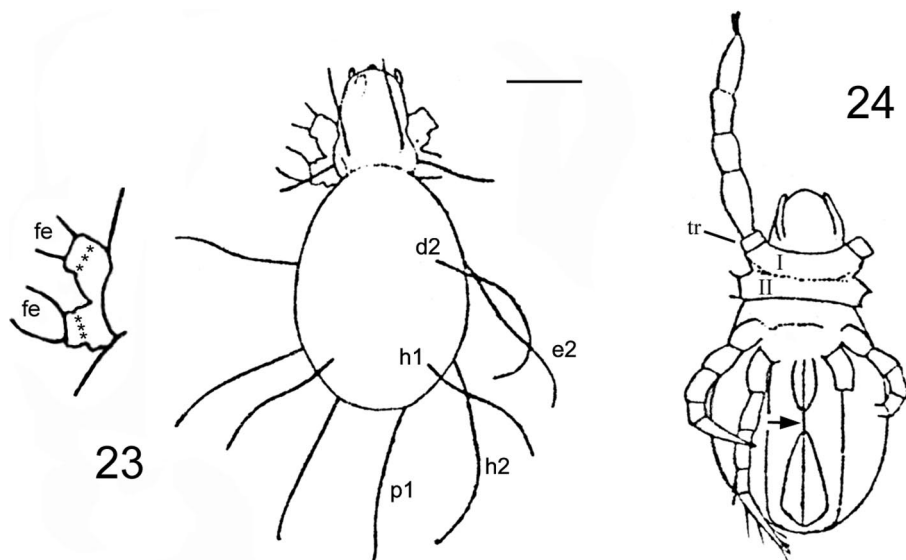
Plategeocranus. Material identified by SELLNICK (1931) as the type species, *P. sulcatus* (Karsch), exists in the Kaliningrad collection (EZHOVA, 1995). Based on SELLNICK's (1918) redescription of the species, *Plategeocranus* can be removed from Carabodidae, in its modern sense (GRANDJEAN, 1954; MAHUNKA, 1986), as it lacks the somewhat elongated body, uniformly broad prodorsum and large, laterally placed lamellae that comprise the facies so characteristic of this family. Also, leg tarsi in Carabodidae are monodactylous, while those of *P. sulcatus* are tridactylous; while the number of claws varies within some oribatid mite families, it seems fixed in Carabodidae. Because few helpful details are available, the genus is left unassigned within Brachypylina, pending reexamination of SELLNICK's specimens.

Scutoribates. This monobasic genus (type species *S. perornatus* Sellnick) is also easily removed from Carabodidae. Besides lacking the carabodid facies noted above, it possesses a lenticulus and pteromorphs, which are unknown in that family. SELLNICK (1918) had suggested the genus was "midway between *Oribates* and *Scutovertex*", but later (1927) noted the similarity of *S. perornatus* with the type species of *Eremaeozetes*, *E. tuberculatus* Berlese. This latter assessment seems accurate, and *Scutoribates* is herein considered a junior subjective synonym of *Eremaeozetes* Berlese 1913 (*n. syn.*), the largest genus in Eremaeozetidae. *Eremaeozetes* has a unique facies – rough appearance (from cerotegument), conspicuous, strongly convex and often elongated lenticulus, large lamellae and pteromorphs – that perfectly matches the original description and figure of *Eremaeozetes perornatus* (Sellnick) (*n. comb*). Based on current distributions, this represents the only obvious warm-climate element of the Baltic amber oribatid mite fauna. *Eremaeozetes* is found throughout tropical and subtropical regions of the world, and even reaches warm-temperate latitudes in Georgia (USA; V. BEHAN-PELLETIER, and H. SCHATZ, pers. comm., 2005). It is moderately diverse with more than 30 species and is known from Chiapas amber, of Miocene to Eocene age (NORTON & POINAR, 1993).

Strieremaeus. Most traits that define Eremaeidae, in its modern sense (GRANDJEAN, 1965; BEHAN-PELLETIER, 1993) were not discussed by SELLNICK (1918), but several that relate to general facies show that *Strieremaeus* should be removed. Unlike Eremaeidae, *Strieremaeus* has lamellae that originate at the bothridia, a narrow tutorium, and no conspicuous notogastral setae. The notogaster of known eremaeid mites is also more elongated, lacking the broad anterior "shoulders" of *Strieremaeus*. Instead, the genus has a dorsal facies much like that of Peloppiidae: they share the short, broad shape, well developed pedotecta I and II, smooth notogaster with few obvious setae, narrow lamellae and absence of pteromorphs. Some members of that family share other traits of the two named *Strieremaeus* species. The type species, *S. illibatus* Sellnick, resembles the arboreal *Dendrozetes caudatus* Aoki in its moderately large size, absence of distinct lamellar cusps, and clavate bothridial setae. The pyriform shape of *S. cordiformis* is unusual for oribatid mites, but resembles that of some *Pyroppia*. However, the anal and genital plates were described as being very close together on the venter, while known peloppiid species have these plates widely separated; this trait varies little within families of brachypyline oribatid mites. Pending rediscovery *Strieremaeus* is left unassigned within Brachypylina, but it probably belongs to some family within Gustavioidea.

Gradidorsum. Unlike *Strieremaeus*, this monotypic genus (type: *G. asper* Sellnick) cannot definitively be removed from Eremaeidae. It appears to lack the prodorsal costula that characterize most, but not all

FIGS. 23-24. *Embolacarus pergratus* Sellnick (reproduced from SELLNICK, 1918). 23. — Dorsal aspect, only base of legs was drawn; left insert is enlarged bases of legs I and II with asterisks added to mark probable articulation between epimeres and trochanters. 24. — Ventral aspect, legs partly drawn. Scale bar = 100 μm. Abbreviations added: fe (femur), tr (trochanter).

members of that family (BEHAN-PELLETIER, 1993). It also is described as having, in essence, fusion between notogaster and prodorsum, which is unknown in extant Eremaeidae. The notogastral setae seem appropriately distributed, but they are short and clavate, while those of described eremaeids are setiform, attenuate. No known eremaeid mite has the pointed rostrum illustrated for *G. asper*. By contrast, consistent with membership in Eremaeidae are the lack of a tutorium, the long clavate bothridial setae and the elongated, anteriorly narrowed anal plates (an uncommon form), well removed from the genital plates. Since some doubt exists, and no other placement seems more appropriate, *Gradidorsum* is tentatively retained in Eremaeidae.

Embolacarus. This genus is a very poor fit in Neoliodidae, which is a basal family of Brachypylina (= Circumdehiscentiae, the so-called "higher" oribatid mites) and clearly should be removed. VITZTHUM (1942) expressed doubt about his initial (1931) family assignment, but suggested no alternative. The doubt is understandable, because the original description and figure (reproduced herein as Figs. 23, 24) present virtually no traits suggestive of membership in this family. Unlike *E. pergratus*, extant Neoliodidae have

roughened, sculptured cuticle that is never smooth, shiny; never have such an elongated body; never have long, attenuate dorsal setae; retain tightly applied notogastral scalps as adults; have epimera that are incorporated into a uniform coxisternum; have a short, broad anogenital region; and have clavate bothridial setae that are positioned well medially on the prodorsum.

Several particular features of *Embolacarus pergratus* that are discussed or illustrated by Sellnick are important in the higher classification of extant oribatid mites. Two are not found in any extant brachypyline family, but are typical of all families with a more early-derivative position, i.e. that are among "macropyline" taxa (SELLNICK, 1929). First is the nature of the coxisternum: the component epimera were illustrated (FIG. 24) as distinct, uniform and transversely oriented, particularly epimera 1 and 2 anterior to the sejugal furrow. In contrast, Brachypylina have a coxisternum that is fully fused, both internally among the epimera and to the ventral plate posteriorly; the various components are usually distinguishable only by internal structures (oblique apodemes, fields of muscle sigilla) that are visible in transmitted light. Second are the legs, which in *E. pergratus* have genua

that are large, similar in size to the tibiae (Fig. 24). Legs of all Brachypylina have a conspicuously reduced genu that functions essentially as a knee.

A third feature is the structure of the anogenital region, which Sellnick described and illustrated as comprising a pair of anal plates and a pair of genital plates, each inserted in a separate ventral plate that articulates laterally and posteriorly with the notogaster (Fig. 24). This seems to represent a typical brachypyline venter, formed from hypertrophied ancestral aggenital and adanal plates that fuse to form a seamless venter in which genital and anal valves lie. Several macropyline taxa either possess or superficially seem to possess a brachypyline venter, and thus blend all three features of *Embolacarus*. The others are discussed below, but one, the desmonomate ("nothroid") family Hermanniidae can be quickly eliminated from consideration. These mites can be large, but no extant species is shaped like *Embolacarus* (cf. Fig. 19); also, the ventral plate is never narrow, the anal and genital plates are never well separated, and the notogaster never possesses long, flagellate setae. Furthermore, Hermanniidae are all holoid mites, i.e. their venter is fused across the sejugal furrow. In strong contrast, Sellnick (1918) suggested that *Embolacarus* was ptychoid (able to withdraw the podosoma and legs into the hysterosoma and deflect the prodorsal aspis ventrad to cover the secondary cavity), which requires a sejugal articulation.

Despite Sellnick's suggestion, it seems virtually impossible that *Embolacarus* was ptychoid. This body form requires a much more reduced, narrow coxisternum and much smaller legs than *Embolacarus* possessed (Sanders & Norton, 2004 and included references). But even the suspicion of ptychoidy tells us that Sellnick envisioned a sejugal articulation (movable "cephalothorax"), and it seems reasonable to infer instead that *Embolacarus pergratus* had a dichoid body form, in which a narrow, circular sejugal band of soft cuticle articulates an anterior propodosoma with a posterior hysterosoma (Grandjean, 1970).

Five extant families of oribatid mites are dichoid and have a one-piece notogaster like that of *Embolacarus*: Eulohmanniidae, Lohmanniidae, Perlohmanniidae, Epilohmanniidae, and Collohmanniidae. All are rather early- to middle-derivative taxa that existed, or probably existed, in the Eocene. The first four bear little resemblance to *Embolacarus*; they have distinctive facies that Sellnick would have recognized (e.g. see Balogh & Balogh, 1992) and certainly would not have considered ptychoid. Eulohmanniidae comprises a single oddly constructed, cylindrical species with a venter much different from that of *Embolacarus* – anal and genital plates adjacent and both far posterior – and it is of medium length, little more than 700 μm. The other families have at least some large representatives that reach the size of *Embolacarus*, which was about 900 μm (combined from Sellnick's measurements of "cephalothorax" and "abdomen"). Lohmanniidae have a unique flattened venter, with pedofossae and a short, broad anogenital region, very unlike that of *Embolacarus*. Perlohmanniidae are also all rather flattened, and all four paired ventral plates (genital, aggenital, anal, adanal) are distinctly separate. Epilohmanniidae have the general shape of *Embolacarus* and one genus, *Epilohmannoides*, even has a ventral structure partly resembling the brachypyline condition. However, unlike *Embolacarus*, epilohmanniid mites have a modified coxisternum, with oblique epimeral borders; they also have broader ventral plates, with the genital aperture posterior to the midline, as do the three previous families. The fifth dichoid family, Collohmanniidae, seems to fit *Embolacarus* quite well.

Inclusion of *Embolacarus* in Collohmanniidae

In dorsal aspect (compare Figs. 2, 12, 23) the overall shapes of *C. gigantea*, *C. schusteri* and *E. pergratus* are virtually identical. Unlike any of the other dichoid taxa mentioned above, *Collohmannia* and *Embolacarus* share several pairs of long, flagellate notogastral setae, with various other setae being much less conspicuous. Tentatively, the five pairs of flagellate setae drawn by Sellnick (1918) can be considered *d2*, *e2*, *h1*, *h2* and *p1*. Those of *C. gigantea* and *C. schusteri* are *d2*, *h2* and *p1*; *e2* and *h1* are longer than remaining setae, but not flagellate. Leg I of both genera is unusually large, with a swollen tarsus. Both genera have narrow, elongated ventral plates (compare Figs. 6, 14, 24). Sellnick drew the

aggenital and adanal plates of *Embolacarus* as fused, with no indication of a transverse articulation between them. Those of *Collohmannia* are fused only near the lateral margins, and more medially the articulation is conspicuous in extant species (Fig. 14, arrow). However, the articulation is hardly visible in the amber specimen of *C. schusteri*, where resoluation is limited by the medium and because the projecting plates are oriented obliquely. If present in *E. pergratus*, the articulation could have easily been missed by Sellnick. The genital aperture of *Collohmannia* is near the middle of the venter (like that of *Embolacarus*) in males but anterior to it in females.

Sellnick drew an unusual, strong medial line between genital and anal apertures of *Embolacarus* (Fig. 24, arrow), indicating the presence of some conspicuous structure that he did not explain. This perfectly matches the surface appearance of a vertical, laminar preanal apodeme in *C. gigantea*, when viewed ventrally (Fig. 14, *pra*). Paired muscles that originate at the lateral margins of the fused aggenital-adanal plate insert on this medial apodeme (Fig. 15). They probably function like the homologous holoventral compressor muscles of the superfamily Euphthiracaroidea (Ptyctima), to compress the venter laterally (Sanders & Norton, 2004). Other than euphthiracaroid mites and *Collohmannia*, no extant oribatid mite taxon has a structure that could be drawn as Sellnick did. While preanal organs are common in Brachypylina, and have a variety of shapes (Grandjean, 1969b), they never appear in ventral view as a thin line that fully connects the two apertures; in fact, under reflected light these internalized structures usually are not visible at all.

The apodeme-muscle complex probably represents a synapomorphy of *Collohmannia* and Euphthiracaroidea. General similarities between the groups were first noted by Štorkán (1925), as reflected in his invalid genus name *Phthiracaroides*. Grandjean (1966, 1967) revisited this idea, and seemed to consider *Collohmannia* a close outgroup of Oribotritiidae (a basal family of Ptyctima), although without using cladistic terminology. It is curious that Sellnick never made this inference himself, when discussing *Collohmannia gigantea*. However, the "subptychoid" facies of *C. gigantea* agrees well with Sel-lnick's (1918) assessment of *Embolacarus* as an intermediate form between the "phthiracarines" (= Ptyctima) and other oribatid mites.

The main obstacle to including *Embolacarus* in Collohmanniidae is the form of the anal region. Sellnick (1918) described and illustrated *Embolacarus* as having adanal plates that fuse behind the anal aperture, and anal plates that are broadest posteriorly. But Sellnick's description and illustration of this region in *E. pergratus* may have been somewhat inaccurate, especially regarding the size and shape of the anal plates. *Collohmannia* species have a narrow intercalary sclerite between the anal and adanal plates, and this sclerite is widest posteriorly (Fig. 14, *is*). If one mentally merges the anal and intercalary plates with the soft surrounding cuticle, their collective outline is strikingly similar to Sellnick's depiction of the anal region in *E. pergratus* (compare Figs. 14, 24). In the fossil the various components may not have been distinguishable. It seems unlikely that the adanal plates fuse behind the anal aperture, but it is certainly possible; macropyline mites as unrelated as Brachychthoniidae and Hermanniidae have separately evolved such a fusion.

Based on the shared "sub-ptychoid" facies, the unusually enlarged leg I, linear preanal apodeme, and the potential that Sellnick (1918) made understandable errors in describing the ventral plates, I include *Embolacarus* in Collohmanniidae. It can be distinguished from *Collohmannia* by having flagellate notogastral setae *e2* and *h1* (one or both are shorter, normal setae in *Collohmannia*). As discussed above, *Embolacarus* may have had adanal plates that fuse behind the anal aperture, but these plates are separate in *Collohmannia*. *Embolacarus* may also have had epimere II broader than epimere I, as Sellnick illustrated (Fig. 26); II is narrower than I in *Collohmannia* (Fig. 13). However, Sellnick may have misrepresented this feature by not drawing the separation between epimere II and trochanter II in the ventral view (Fig. 24); clearly he did not indicate this articulation for either leg in the dorsal view (Fig. 23, added as asterisks in insert). If *Embolacarus* had sexual dimorphism similar to that of *Collohmannia*, then the holotype was probably a male, based on the proportionally small hysterosoma and the mid-body position of the genital aperture. Considering this, the

genera might also be distinguished by size; at about 900 μm, *E. pergratus* is considerably smaller than males of known *Collohmannia* species (minimally 1200 μm; see above).

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