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Arthropods in amber from the Triassic Period

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The occurrence of arthropods in amber exclusively from the Cretaceous and Cenozoic is widely regarded to be a result of the production and preservation of large amounts of tree resin beginning *ca.* 130 million years (Ma) ago. Abundant 230 million-year-old amber from the Late Triassic (Carnian) of northeastern Italy has previously yielded myriad microorganisms, but we report here that it also preserves arthropods some 100 Ma older than the earliest prior records in amber. The Triassic specimens are a nematoceran fly (Diptera) and two disparate species of mites, *Triasacarus fedelei* gen. et sp. nov., and *Ampezzoa triassica* gen. et sp. nov. These mites are the oldest definitive fossils of a group, the Eriophyoidea, which includes the gall mites and comprises at least 3,500 Recent species, 97% of which feed on angiosperms and represents one of the most specialized lineages of phytophagous arthropods. Antiquity of the gall mites in much their extant form was unexpected, particularly with the Triassic species already having many of their present-day features (such as only two pairs of legs); further, it establishes conifer feeding as an ancestral trait. Feeding by the fossil mites may have contributed to the formation of the amber droplets, but we find that the abundance of amber during the Carnian (*ca.* 230 Ma) is globally anomalous for the pre-Cretaceous and may, alternatively, be related to paleoclimate. Further recovery of arthropods in Carnian-aged amber is promising and will have profound implications for understanding the evolution of terrestrial members of the most diverse phylum of organisms.

Acari | Cheirolepidiaceae | phytophagy | Carnian Pluvial Event

The oldest records of arthropods preserved in fossilized resin, or amber, until now have been from the Early Cretaceous of England, Japan, Lebanon, and Jordan (1–3), which coincides with the earliest appearances in the fossil record of large masses of resin *ca.* 130 million years (Ma) ago. This phenomenon is poorly understood, because resins have been produced since the Carboniferous (4) but usually in just trace quantities prior to the Cretaceous. Here we report the first arthropod inclusions in abundant Triassic amber, which extends the geological age of fossil arthropods in amber by approximately 100 million years. Two of the arthropods are members of the highly specialized mite lineage Eriophyoidea (5), which includes the gall mites and is thought to be ancient but lacks any other Mesozoic fossils.

The amber is from the middle part of the Heiligkreuz Formation, which is late Julian to early Tuvalian in age (Late Carnian: *ca.* 230 Ma), based on ammonites and palynology (6, 7). The outcrops occur near the village of Cortina in the Dolomite Alps of northeastern Italy (Fig. 1*A*). These appear to be the most abundant outcrops of Triassic amber in the world, with small droplets 2–6 mm (rarely to 30 mm) in diameter (Fig. 1*F* and Fig. S1) comprising 2–5% by volume of the paleosol in which they are buried. The amber was produced by trees in the extinct conifer family Cheirolepidiaceae (Fig. 1*B*) (6). That attribution is based both on chemistry of dispersed amber and on samples in situ within plant macrofossils, confirmed by abundant pollen and cuticles in the paleosols (Fig. 1 *B*–*E*). This amber has also yielded bacteria, algae, protists, and fungi (8).

Approximately 70,000 droplets (*ca.* 600–700 g) were screened for inclusions, from which three arthropods were discovered and prepared for microscopic study. One arthropod is a nematoceran fly (Diptera) (Fig. 1 *G* and *H* and Fig. S2) and the other two are highly divergent species of eriophyoid mites (Figs. 2 and 3). The midge specimen consists of portions of the head, antennae, thorax, and at least four legs. Most recent infraorders of Diptera (and some extinct ones) existed by the Late Triassic, even though Diptera only represented approximately 1% of all insect compressions during this time period (9). Many of the Triassic Diptera were quite small, which agrees with an estimated body length of the specimen reported herein, some 1.5–2 mm. The most intriguing feature of the midge is the pair of antennae with 10 compact, tapered segments (Fig. 1*H*), found sporadically in nematocerans and basal Brachycera. A detailed account of the specimen is given in *SI Text*.

The mite specimens are entire and preserved with microscopic fidelity (Figs. 2 and 3), such that they could be studied with compound microscopy up to x1,600 magnification. Although the two specimens are visible primarily on one surface, one mite is distinctively elongate and vermiform, with bizarre feeding structures, while the other is fusiform, more compact, with more integrated mouthparts. However, in general body form, with loss of the third and fourth pairs of legs, and presence of highly modified "featherclaws" on the remaining legs, there is no question as to their eriophyoid lineage placement (5).

Systematic Paleontology

Arachnida Cuvier, 1812; Acari Leach, 1817; Eriophyoidea Nalepa, 1898.

Triasacarus fedelei Lindquist and Grimaldi, gen. et sp. nov. (Fig. 2).

Etymology. Generic from *Trias*sic (geological period of origin) and *acarus* (Latin for mite); species name patronymic for Paolo Fedele (Cortina d'Ampezzo), discoverer of the Triassic amber deposit.

Holotype. No. MPG 31343, Museum of Geology and Paleontology, University of Padova.

Locality and horizon. Heiligkreuz Formation, Late Carnian.

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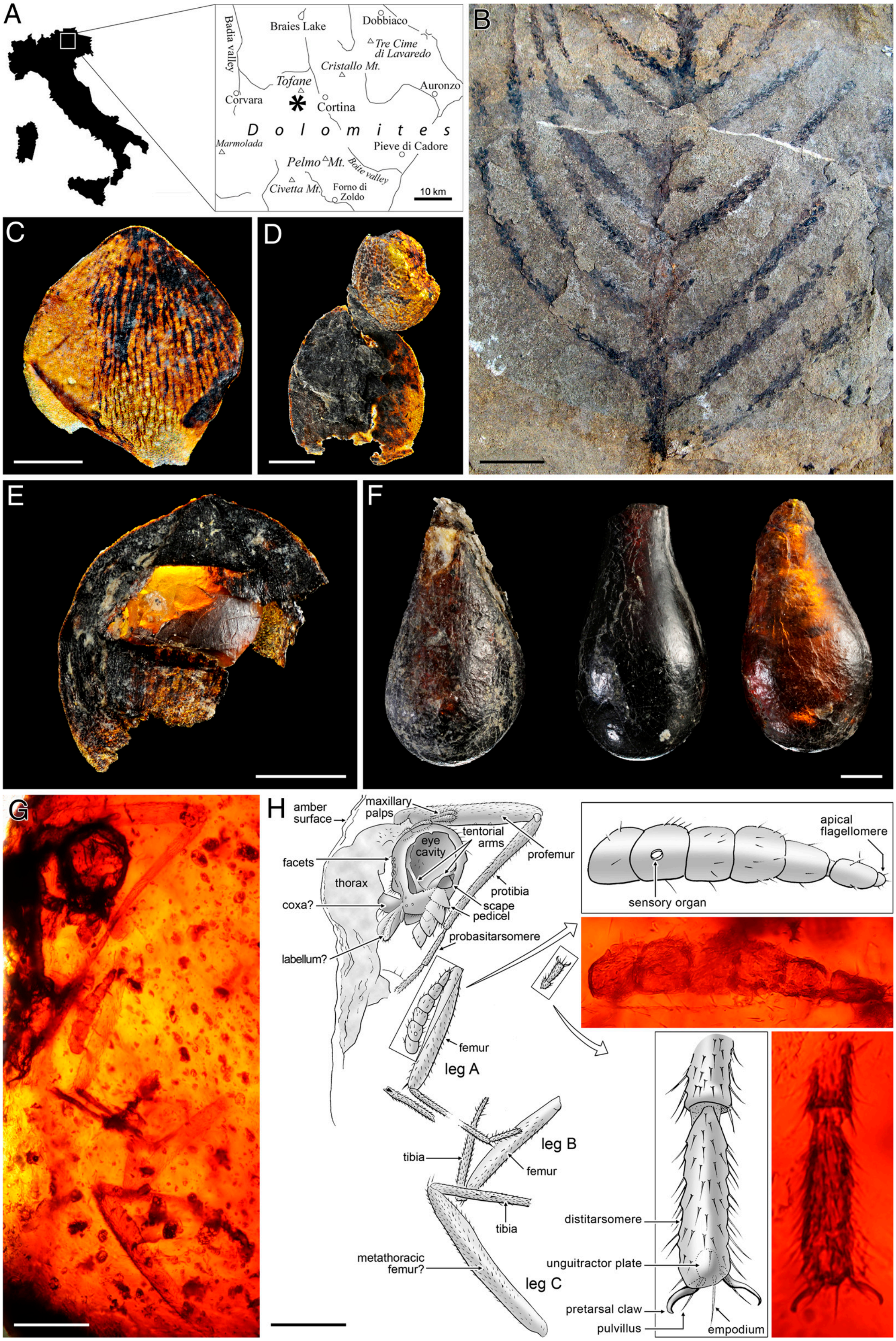

Fig. 1. Triassic (Carnian-aged) amber from the Heiligkreuz Formation of Cortina, northeastern Italy with associated plant and insect remains. (*A*) Location of amber outcrop (asterisk) in the Dolomite Mountains. (*B*) Cheirolepidiaceous shoots associated with amber. Museo delle Regole, Cortina d'Ampezzo, Italy, MRCA 7170. (*C*) Cuticle of the Cheirolepidaceae amber source. Department of Geology, Paleontology, and Geophysics, University of Padova, Italy, DGPGP ER-413c. (*D*) Cheirolepidiaceous foliage associated with in-situ amber. DGPGP ER-413d. (*E*) Resinous pocket in the foliage cuticle. DGPGP ER-365c. (*F*) Typical amber droplets. DGPGP ER-527. (*G* and *H*) Disarticulated nematoceran fly, showing details of antenna and apical tarsomere. Museum of Geology and Paleontology, University of Padova, Italy, MGP 31345. Scale bars: *B*, 2 cm; *C*–*F*, 1 mm; *G* and *H*, 200 μm.

Diagnosis. Body length 210 μm, body shape vermiform; gnathosomatic infracapitulum framed by palpcoxal bases, from which other palpal segments extend freely, on either side of a long proboscis, flanked dorsally by pair of acuminate, possibly cheliceral structures; prodorsal shield with frontal lobe and one pair of setae inserted anterolaterally and one pair inserted posteriorly;

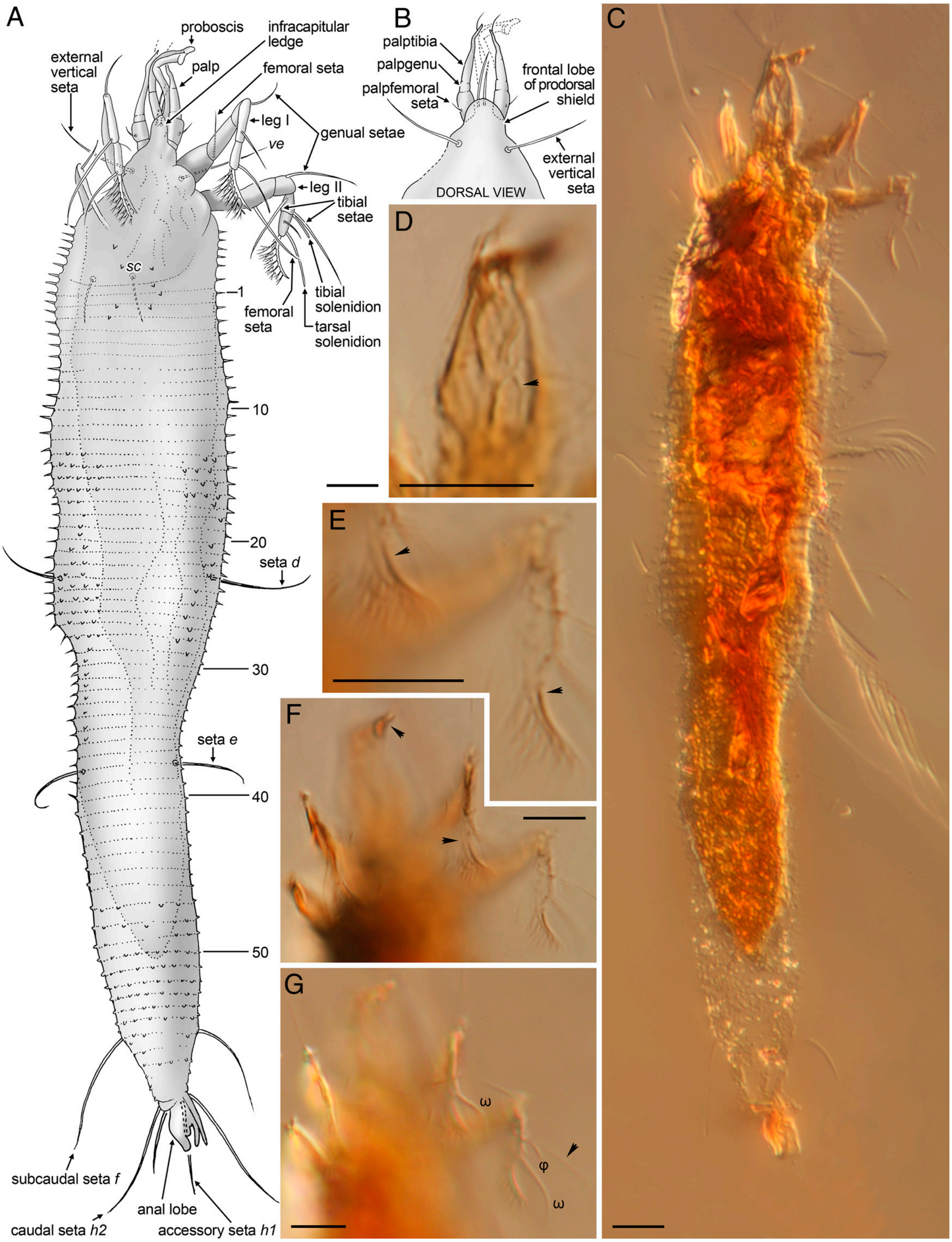

Fig. 2. Eriophyoid mite in the Italian Triassic amber: *Triasacarus fedelei* gen. et sp. nov., Holotype, MGP 31343. (*A* and *C*) Habitus in ventral view [reconstruction and photomicrograph, respectively; photo is a stacked image using differential interference contrast (DIC) illumination]. (*B*) Dorsal structures of anterior region, as viewed ventrally. (*D*) Gnathosoma, arrow pointing to infracapitular ledge [bright field (BF) illumination; f.p (focal plane) 2,347]. (*E*) Detail of *F*; arrows pointing to empodial featherclaws (BF, f.p. 2,324). (*F*) First and second leg pairs, with tip of proboscis in focus (arrow) and empodial featherclaw of first left leg indicated with arrow (BF, f.p. 2,324). (*G*) First and second leg pairs, with some solenidia denoted, tibial one by phi, tarsal ones by omega (DIC, f.p. 2,160). Scale bars: 10 μm.

opisthosoma with *ca.* 55–60 fine annuli circumscribing body, not broadened into tergites dorsally; each with single transverse row of minute spicules; opisthosoma with prominent pair of subcaudal setae *f* and with ventrolateral setae *d*, *e*, and caudal setae *h1* and *h2* seemingly evident; legs I and II with long empodial featherclaws, main shafts divided; legs I and II with a prominent seta on each of femur, genu, tibia (two setae), and a short seta on tarsus (not verifiable on leg I); leg II with a probable solenidion on each of tibia and tarsus (not verifiable on leg I); legs III–IV absent. Detailed description provided in *SI Text*.

Ampezzoa triassica Lindquist and Grimaldi, gen. et sp. nov. (Fig. 3).

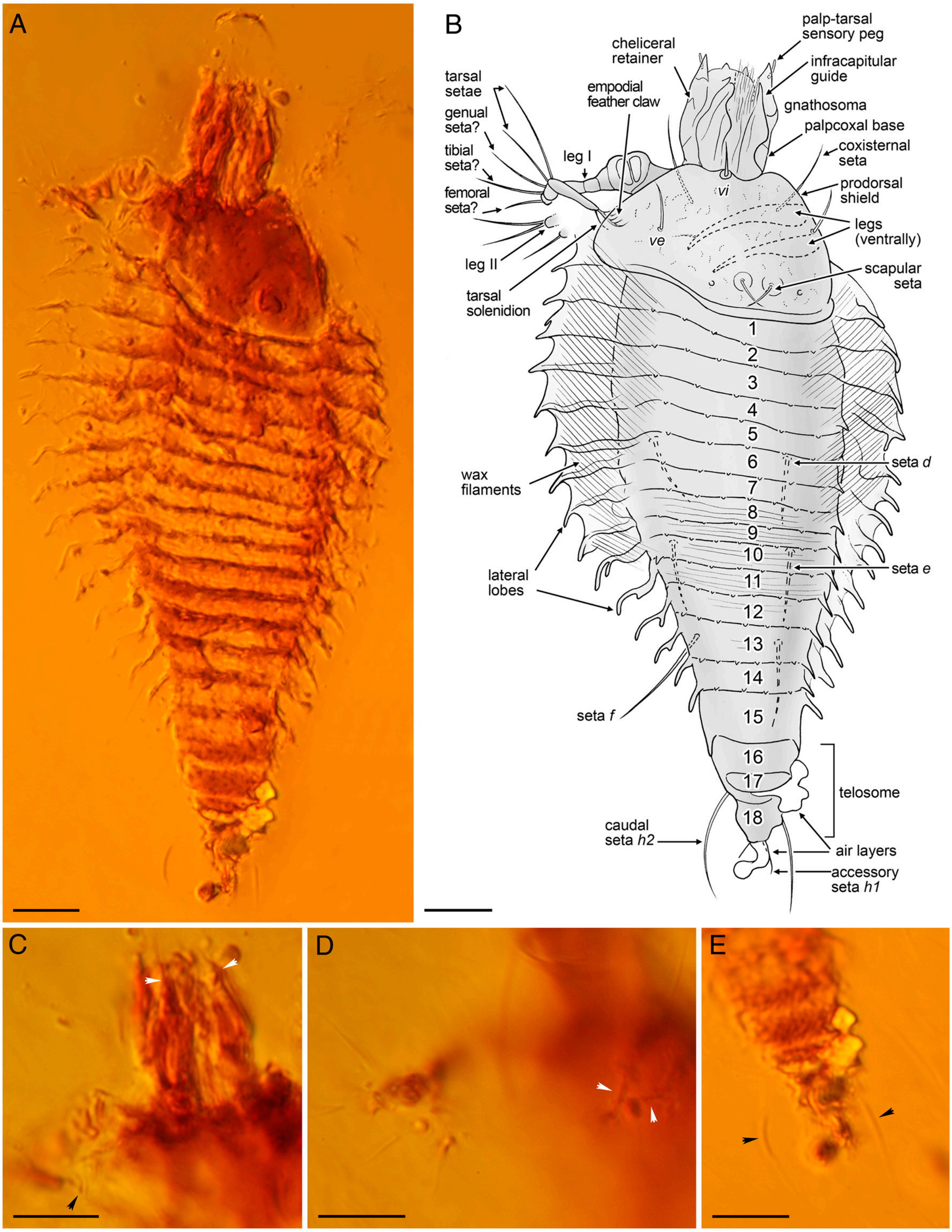

Fig. 3. Eriophyoid mite in the Italian Triassic amber: *Ampezzoa triassica* gen. et sp. nov., Holotype, MGP 31344. (*A* and *B*) Habitus, dorsal view. (*A*) Digitally stacked photomicrographic composite. (*B*) Rendering of complete specimen, as preserved. (*C*) Anterior portion of body, including gnathosoma. White arrows indicate infracapitular guides; black arrow points to second left leg (f.p. 2,904). (*D*) Portion of prodorsal and coxisternal region; arrows point to shadowy images of right legs I and II below prodorsal shield (f.p. 2,692). (*E*) Posterior apex of body; arrows point to caudal setae *h2* (f.p. 2,932). All photos in DIC illumination. Scale bars: 10 µm.

Etymology. Generic from Valle d'Ampezzo in northeastern Italy, source of Triassic amber outcrops; species name for period of geological origin.

Holotype. No. MPG 31344, Museum of Geology and Paleontology, University of Padova.

Locality and horizon. Heiligkreuz Formation, Late Carnian.

Diagnosis. Body length 124 µm; body shape fusiform, dorsoventrally flattened, gnathosomatic infracapitulum framed by adherent inner margins of palpal segments, between which a gutter bears a set of indistinguishable structures (some cheliceral);

prodorsal shield with an unpaired anteromedian seta, one pair of setae inserted midlaterally, and one pair inserted on pair of closely set dorsal tubercles posteriorly. Opisthosoma with ventral annuli broadened into *ca.* 18 tergites, 1–15 bear pair of digitiform, apparently wax-secreting lateral lobes; with prominent pair of caudal setae *h2* and with ventrolateral setae *d*, *e*, *f*, and accessory caudal setae *h1* seemingly evident. Leg I with long, slender tarsus, its empodial featherclaw with main shaft possibly divided; with 5 discernible setae, one each seems to occur on femur, genu, tibia, tarsus, and a second one on tarsus; tarsal solenidion with enlarged tip, tibial solenidion indiscernible. Leg pair II present but structure not discernible; legs III–IV absent. Detailed description provided in *SI Text*.

Discussion

Both rounded, vermiform, and flattened, fusiform gall mites occur throughout disparate genera of the three extant families of Eriophyoidea. Vermiform mites generally live in sequestered spaces (sheaths, galls, buds) that protect them from desiccation, while a fusiform body correlates with a vagrant lifestyle on exposed surfaces of plants. *Ampezzoa* displays faint, parallel striations that extend over the dorsum of the body and do not appear to be cuticular (Fig. 3 *A* and *B*). We interpret these striations as waxy filaments, secretion of which occurs sporadically in vagrant Eriophyoidea (5). In fact, the modern New Zealand species *Cymeda zealandica* Manson & Gerson, which feeds on tree ferns, also has lateral fringes of wax and a body shape very similar to this Triassic species. Just as in other terrestrial arthropods, secretions of flocculent wax are believed to be an adaptation of external plant feeders against desiccation, rain, predation, and parasitism.

The fossils reported here extend the geological record of the eriophyoid lineage by approximately 185 Ma. They cannot be assigned to any of the three extant families, partly due to inadequate classification in this superfamily, as well as to some unusual attributes of the fossils. The very divergent body structure of the fossils indicates they are distantly related, which is further supported by *Triasacarus* lacking integrated feeding appendages. This, and the presence of a tibial solenidion on leg II in *Triasacarus* (Fig. 2 *A* and *G*), are plesiomorphically unique in the lineage Eriophyoidea. It is very possible that this taxon is a stem group eriophyoid, indicating that significant divergence occurred in Eriophyoidea prior to the Late Triassic.

The Eriophyoidea is the most highly specialized lineage of phytophagous mites, indeed of any arthropods except certain insects such as scales (Hemiptera: Coccoidea). Most eriophyoid species are extremely host specific, typically confined to a species or genus of host plants (5). Despite the common name of gall mites, only about one-third of the species actually induce formation of galls or other abnormal plant growths. The remaining species are leaf vagrants or they live sequestered within sheaths, buds, and flowers. Of the *ca.* 3,500 described species of extant world eriophyoids, 97% use angiosperms as hosts (5); the other 3% feed on conifers and ferns, with even two mite species feeding on *Ephedra* and *Equisetum*, respectively. Fern feeding is considered to be secondary (5), because all are disparate species in 11 genera of the more derived family Eriophyidae.

Feeding on conifers is typically interpreted as an ancient association in Eriophyoidea (5), because half of the extant species in the putatively primitive family Phytoptidae subsist on conifers. Of the conifer hosts, more than 90% are Pinaceae and Cupressaceae. Only one eriophyoid, *Pentasetacus araucariae* Schliesske, is presently known to feed on the relict conifer family Araucariaceae, and that mite is morphologically quite primitive (10, 11). Monocotyledonous plants have also been considered as a group of hosts upon which eriophyoid mites arose, because several putatively early derivative genera of Phytoptidae are restricted to palmaceous or graminaceous hosts (5).

The Triassic fossils clearly reveal that eriophyoids preceded angiosperms by at least 100 million years and fed on conifers. There is evidence that the tiny amber droplets from the Heiligkreuz Formation were formed on the leaf surfaces of the source cheirolepidiaceous tree (7) (Fig. 1 *D* and *E*), so it is likely that the fossilized mites were either sheath dwellers or surface vagrants feeding on the foliage. Mites like *Triasacarus* may have produced galls, as some of the morphologically most primitive forms of extant vermiform mites induce galls on twig and bark surfaces of their conifer hosts (10, 12). Also, some conifer-feeding eriophyoids today cause leaf/needle yellowing, browning, necrosis, dehiscence, and even russetting and deformation, so it is possible that the fossil mites induced formation of the Triassic amber droplets, although we are unaware of any eriophyoids today inducing resin production.

The discovery of eriophyoid mites in Triassic amber substantiates the lineage's antiquity, in contrast to some previous notions about this being a more recently derived group linked with tetranychoid (spider mites and relatives) or other raphignathine superfamilies (5). The fossils further demonstrate eriophyoids as ancient because they had already achieved their specialized body plan by the Triassic, especially the loss of the third and fourth pairs of legs. The current notion is thus exceedingly unlikely of finding a transitional extant form (that retains at least the third pair of legs) on some unsampled primitive conifer such as one of the Araucariaceae (13). Whether this obligate plant-feeding lineage of mites preceded the origin of the conifers in the Late Carboniferous, *ca.* 300 Ma, becomes a new speculation, specifically if Paleozoic progymnosperms or early seed ferns were ancestral host plants.

The Triassic eriophyoid mites provide additional evidence for the antiquity of acariform mites (subclass Acari, superorder Acariformes), which have a fossil record beginning in the Early Devonian (14, 15), although records of Carboniferous, Triassic, and Jurassic mites are scarce. Mites in Cretaceous and Cenozoic amber are very diverse (3, 5, 16), albeit poorly studied, and virtually all of them belong to modern families. The Triassic amber gall mites confirm the hypothesized antiquity of Trombidiform mites (a lineage within Acariformes that includes the Eriophyoidea), which were estimated to have diverged in the Devonian based on molecular evidence (17). The only other definitive fossil Eriophyoidea is a specimen preserved as cuticle in clay from the Middle Eocene of South Australia (18). A few galls on fossil leaves from the Cenozoic have been attributed to eriophyoid mites (19, 20) and galls on gnetopsid and peltasperm plants from the Late Triassic have been attributed to "foliar gall mites" (21), although these records lack definitive evidence of mites themselves.

Interestingly, virtually all amber recovered from the Triassic occurs within the narrow 10-million-year interval of the Carnian, 230 Ma (Fig. S3). Widespread amber occurrence during this time period may be a result of the Carnian Pluvial Event (7, 22), a global episode of atmospheric perturbation linked to massive volcanism associated with the Wrangellian Large Igneous Province (23) as well as profound changes in a monsoonal climate (7, 24). The Cheirolepidiaceae plant remains in the amber-bearing paleosol, primarily cuticles with possible affinities to the genera *Brachypyllum* and *Pagiophyllum* (25), exhibit the typical xerophytic features of this family (6, 7); however, the dominance of hygrophytic forms in the palynological morphospecies found generally in the Carnian suggests climate changes. The decrease of xerophytic taxa and the increase of hygrophytic associations attributable to ferns, clubmosses, horsetails, and the Cycadeoidales indicate multiple humid climate pulses within the Carnian Pluvial Event (7). Paleosol analyses confirmed that this climatic event can be considered as a supraregional climate shift with increased rainfall during the late Early Carnian, followed by a decrease in the Late Carnian (22). Such a climate is probably ideal for the secretion of large amounts of resins (6, 7, 26) as well as for the formation of fluvial sediments that optimally preserve amber. Perhaps a similar climatic change is responsible for the enigmatic abundance of amber beginning in the Early Cretaceous, although other hypotheses include the advent of certain conifers, along with groups of wood-infesting beetles and fungi (27).

The Triassic is a transformative period in the evolutionary history of terrestrial arthropods, because taxa from this period are much more modern in their relationships than are taxa from the Permian (1). Indeed, the earliest representatives of the insect orders Diptera, Hymenoptera, Thysanoptera (thrips), and Trichoptera (caddisflies) are Triassic, which is also when diverse crown-group beetles (Coleoptera) appear. Presumably, the end-Permian extinctions had a significant effect on insects (1). The discovery of other significant terrestrial arthropods in the Triassic Italian amber is very promising. Although size of inclusions within amber droplets is limited to 1–3 mm, diverse arthropods occur in this body size. In particular, Sternorrhyncha (a group that includes modern whiteflies, aphids, and scale insects), Psocodea (bark lice), and Thysanoptera (thrips) are typically small insects living on plant surfaces, for which stem-group Triassic species occur as compressions (1). Given the microscopic fidelity of preservation within amber, any specimens of these insect groups in Dolomite amber would greatly illuminate their early evolution.

Materials and Methods

Collection and Screening. Amber-bearing paleosol was field collected and elutriated in water; amber droplets were separated from plant remains and placed in water on glass microscope slides with moulds (Menzel Inc.), covered by a glass coverslip and screened for inclusions under a Carl Zeiss AxioScope A1 compound microscope.

Preparation. Three small amber droplets, approximately 3 mm in diameter and 2–3 mm in length, each containing an arthropod, were individually embedded in a high-grade epoxy resin (Buehler Epoxicure), in a procedure modified from the protocols described in ref. 28. Samples were trimmed and polished on opposite sides using a series of emery papers with decreasing grit sizes (P1200, P1500, P2500: Buehler) on a Buehler Ecomet-3 variable speed flat lapidary wheel, with a fine stream of water. The amber surface was gradually removed from opposite sides of each amber droplet, such that flattened surfaces were parallel to the broadest surfaces of each arthropod inclusion; each flattened surface was brought to about 100 μm of the inclusion to optimize microscopic examination.

Photomicrography. Prepared specimens were applied to a glass microscope slide with a drop of water, with another drop applied to the upper surface of the amber, covered with a 0.06–0.08 mm thickness glass coverslip (Menzel Inc.). This reduces light scattering from fine surface scratches and improves optical resolution (contact of the amber with oil or organic liquid should be avoided because it may be deleterious to the amber). Optical immersion oil was allowed to contact only the glass coverslip, not the amber surface. Specimens were photographed with a Carl Zeiss AxioScope A1 compound microscope, using 640 to 1,600x (oil immersion) magnification and either bright field (BF) or differential interference contrast (DIC) illumination. A series of over 3,000 individual photomicrographs were taken of the three specimens at various magnifications and in successive focal planes using a Canon 450 D digital camera; images were then digitally compiled using Helicon Focus 5.0 software. Finest structures, such as fine setae, were best resolved using individual slices/photos, so for the descriptions of the eriophyoid mites (e.g., Figs. 2 and 3) individual focal planes ("f.p.") are referenced when discussing certain structures. The complete set of digital image files is available to qualified researchers upon request to the corresponding author. Illustrations were made by first tracing high-resolution printouts of images compiled from the stacked images, then filling in details using the photos from individual focal planes taken at 1,600x magnification (which had the greatest resolution), as well as with direct observation of the specimens under 1,000x magnification using a Nikon Eclipse E600 compound microscope. Morphological terminology follows that of Lindquist (5) for the Eriophyoidea, and (29) for the midge.

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Supporting Information

Schmidt et al. 10.1073/pnas.1208464109

SI Text

Systematics.

Class: INSECTA
Order: DIPTERA
Family: Indet.:
(Fig. 1 *G* and *H* and Fig. S2)

General description. Specimen is fragmentary, consisting of a partial head with portions of some appendages still attached; an antenna (most of it disarticulated from its base); a dorsal portion of the thorax; remnants of at least four legs (principally the femora and tibiae but some basitarsomeres as well), including a dissociated distitarsomere (Fig. 1 *G* and *H* and Fig. S2*A*). The dorsal surface of the thorax lies just under or perhaps breaches the surface of the amber; the head is flexed under the thorax, and some of the head appendages (e.g., maxillary palps) apparently shifted during immersion in the resin. There are no remains of wings, halteres, or an abdomen.

Head: Slightly pear-shaped, with the presumed dorsal portion being widest; greatest length 0.25 mm. A cavity on the right side (0.20 × 0.15 mm) appears to have been formed by the decay of the eye, which exposes a portion of the posterior tentorial arm and what is possibly an anterior tentorial arm (Fig. 1*H*). The only eye facets that are preserved appear to be a small group of six (diameter *ca.* 10 μm) near the posterior or ventral surface of the head capsule. Putative eye cavity is pear-shaped (slightly emarginate), with a smaller cavity anterior and close to the emarginate portion (greatest length 0.06 mm). The small cavity is probably the insertion base of the antenna, such as the scape. Distal to the putative scape is a row of four apparent antennomeres; a roughly triangular basal segment (the pedicel?), then a trapezoidal segment (the largest segment, probably the first flagellar segment), and then two smaller segments shaped like parallelograms (Fig. 1*H* and Fig. S2*B*). Total length of connected antennal section is 0.19 mm. Disarticulated from these segments, and lying some 0.10 mm away, is the remainder of the antenna, composed of seven flagellomeres that diminish in size apicad (Fig. 1*H* and Fig. S2*C*); total length of disarticulated section is 0.27 mm. Basal segments of the disarticulated antennal section are barrel-shaped, distal two segments narrowed apicad; apical segment minute, approximately 0.25x the length, 0.3x the width of penultimate segment. Flagellomeres with sparse setulae, with slightly thicker and longer setae forming a possible subapical whorl. Second flagellomere in disarticulated portion of antenna with small, ring-like sensory organ (doubtfully the Johnston's Organ, which occurs on the pedicel). If all antennal segments are preserved, flagellum is comprised of 10 flagellomeres; total length 0.59 mm. Possible labellum lying between head capsule and thorax, a slightly irregular, very slightly sclerotized structure 0.11 mm length, with apparently two opposing, setulose lobes; no pseudotracheae are visible (Fig. 1*H*). Distal portions of possible maxillary palps are deflexed over the head capsule (best seen in view from left side), total preserved length 0.18 mm; distal three palpomeres preserved, each palpomere with fine, dense, erect setulae; palpomeres approximately equal in length (0.05–0.06 mm), apical one slightly fusiform in shape.

Thorax: Remains of at least four legs are preserved (Fig. 1*H* and Fig. S2 *D*–*F*), though all but one are disarticulated from body and thus not identifiable as to pro-, meso- or metathoracic in origin. All leg segments with numerous microtrichia, which are denser on the tibiae than on femora. Left proleg with femur, tibia, and basal two tarsomeres preserved; leg lies over dorsal surface of head and is folded around head capsule. Prothoracic leg long and slender; lengths of profemur and protibia equal (0.43 mm); width of femur up to twice that of tibia. Protarsomeres slender, thinner than apex of tibia; length of probasitarsomere 0.10 mm (segmentation of more distal tarsomeres is obscure). Protibia and tibia of unidentified leg (leg C in Fig. 1*H*) with dorsal and median longitudinal row of 4–5 slightly longer, thicker, and more erect setulae. No apical tibial spurs present, though a thick, short seta occurs at apex of tibia on leg A. No apical comb present on tibiae. Proportions of podomeres on disarticulated legs: leg A femur 0.37 mm, tibia 0.28 mm; leg B femur 0.41 mm [tibial apex ambiguous]; leg C femur 0.55 mm [tibia incomplete] (Fig. 1*H*). Leg C is possibly the hind leg, since these are generally the longest legs in many adult insects. A single distitarsomere, with portion of penultimate tarsomere, is preserved, with excellent detail; it is detached and distant from most other parts. Distitarsomere setulose, 0.06 mm length; with pair of simple pretarsal claws (i.e., not toothed or serrate); length of each claw approximately equal to width of tarsomere; unguitractor plate visible as light area through dorsal surface. Most significantly: Empodium and pair of flanking pulvilli are setiform (definitely not branched, feathered, or pulvilliform); empodium slightly longer than pulvilli (Fig. 1*H* and Fig. S2*D*).

Specimen. MGP 31345, Museum of Geology and Paleontology, University of Padova, Italy.

Comments. An ordinal-level attribution of the fossil can be made via a process of exclusion, as well as by use of the few specialized features that are preserved.

Ephemeroptera and Odonata can be excluded, based on antennal structure (these orders have an aristate flagellum, and Odonata are much larger). Polyneoptera (orthopteroids and Dictyoptera) can be excluded based on tarsal structure (i.e., in these orders an arolium and often a pad-like pulvillus are present as well as plantular lobes on the more proximal tarsomeres); absence in the fossil of large, spine-like setae on the legs as well as the absence of mandibles. Insect mandibles are typically toothed and among the most heavily sclerotized/chitinized structures on the body and so, if originally present, would have been preserved along with the less durable cephalic appendages. Polyneoptera also typically have long, flagellate antennae with filiform antennomeres. Hemiptera is excluded by the lack of a sucking beak and by the presence of maxillary palps. Among Holometabola, the mandibulate orders (Coleoptera, Neuropterida, Hymenoptera) can be excluded based on lack of mandibles in the fossil. Coleoptera can further be excluded since the fossil has long, slender legs and does not have a heavily sclerotized, shield-like pronotum. Hymenoptera have conspicuous, setulose tibial spurs, and the only Triassic Hymenoptera known are a few rare fossils of the most basal living sawfly family, Xyelidae. Amphiesmenoptera (Trichoptera and Lepidoptera) can be excluded because these two orders also possess conspicuous tibial spurs as well as a densely setose or scaled body; long, multiarticulate antennae; and in Lepidoptera (except a few basal families) a proboscis composed of long, coiled galeae. While Trichoptera are of Triassic age (and some even possess labellum-like mouthparts), Lepidoptera can be further excluded since this appears to be a particularly young order, no older than Jurassic (1).

In lieu of definitive synapomorphies being preserved (e.g., wing venation, halteres), attribution to the Diptera is based on a combination of features that is most consistent with this order or groups within this order. These features are the following: long, slender, setulose legs; antennal flagellum with apparently a reduced number [10] of flagellomeres; antennal flagellum short, compact, with differentiated flagellomeres (decreased in size apicad); pretarsal structure, particularly the absence of a lobe-like arolium or pulvilliform empodium; and the presence of a putative labellum.

Long, slender, setulose legs are widespread in the basal ("nematocerous") families of Diptera, and a fleshy labellum (if correctly identified) is actually a defining feature of the order. Lack of tibial spurs and short coxae preclude most Sciaroidea (Cecidomyiidae is an exception) and Anisopodidae sensu lato, but otherwise this is a widespread condition among nematocerans. The monophyletic group Brachycera can be excluded based on flagellomere number, because the groundplan for this suborder is eight flagellomeres. A shortened, compacted antenna with thick segments occurs sporadically throughout Diptera. The pretarsus is unusual, because the empodium and pulvilli are all setiform. Generally, pulvilli are pad-like (pulvilliform) or at least branched and feathery in most Recent Diptera, although sometimes quite small. A setiform empodium occurs in the nematoceran infraorder Culicomorpha (and many Brachycera), and pulvilli are lacking altogether in the nematoceran infraorders Tipulomorpha and Psychodomorpha.

The antennal flagellum has a reduced number [10] of compact, differentiated flagellomeres, which occur sporadically throughout nematocerans [e.g., Simuliidae (blackflies), Axymyiidae, Scatopsidae], and in basal Brachycera (e.g., Stratiomyiidae, Xylomyiidae, etc.), although Recent Brachycera have only eight or fewer flagellomeres. Culicomorpha are preserved as compressions (mostly just wings) in Late Triassic sedimentary deposits from the Anisian to Rhaetian, and stem-group Brachycera (lacking the antennal specialization of recent brachycerans) are known from the Carnian (2).

Five principal Late Triassic sedimentary deposits have preserved diverse Diptera compressions from the Anisian to Rhaetian (reviewed in ref. 2). These deposits are Mt. Crosby, Queensland (Australia); Stransham, UK; Vosges, France; Dzhailoucho, Kyrgyzstan; and the solite quarries of Virginia (the last three deposits have produced 80% of the species). Most recent infraorders of Diptera (and some extinct ones) existed by the Carnian, even though Diptera only represented approximately 1% of all insect compressions during the Triassic (2). Many of the Triassic Diptera were quite small, which agrees with an estimated body length of the specimen reported herein, some 1.5–2 mm. By the Early Jurassic Diptera comprised 20–30% of all fossil insect compressions, and nearly half of all inclusions in amber from the Cretaceous and Tertiary.

Class: ARACHNIDA
Subclass: ACARI
Superorder: ACARIFORMES
Order: TROMBIDIFORMES
Infraorder: TETRAPODILI
Superfamily: Eriophyoidea

Gnathosoma prognathous, with stylet-like cheliceral structures. Cheliceral bases not enlarged, not forming a stylophore. Palpi maximally four-segmented, without thumb-claw process and without spine-like or elongated setae. Prodorsum covered by a prodorsal shield bearing maximally five simple setae, none bothridial. Opisthosoma more or less vermiform, with numerous narrow annuli ventrally and sometimes dorsally, or dorsal annuli consolidated into a series of fewer, thicker, less flexible "tergites"; annuli provided at least ventrally with a single transverse row of minute spicules. Opisthosomatic setation reduced to maximally eight pairs of setae, of which 3–4 lateral pairs displaced ventrolaterally to resemble ventral setae. Caudally, opisthosoma terminating with adhesive structure flanked dorsally by pair of elongate caudal setae. With only two pairs of anteriorly inserted legs, lacking pairs III–IV. Legs lacking true (paired) claws but with a well-developed, unpaired empodial featherclaw. Leg setation reduced to maximum of seven setae each, none bothridial; tarsi I-II consistently with a solenidion, usually inserted dorsodistally and often curved, rod-like in form.

Contains three living families: Eriophyidae, Diptilomiopidae, and Phytopidae. Relationships and classification of the two Triassic genera within the Eriophyoidea lineage, below, will be treated in a separate paper.

Triasacarus **Lindquist and Grimaldi, new genus.**

Diagnosis. A vermiform eriophyoid with prognathous gnathosoma; gnathosoma with infracapitulum framed by palpcoxal bases, from which other palpal segments extend freely, well separated, on either side of a long proboscis flanked dorsally by another pair of acuminate, possibly cheliceral structures; prodorsal shield with anterior margin projected into a frontal lobe; shield with two pairs of setae, one pair inserted anterolaterally in area usually occupied by external vertical setae and one pair inserted posteriorly in area occupied by scapular setae; opisthosoma with ca 55–60 fine annuli that circumscribe body, annuli subequal dorsoventrally, not broadened into tergites dorsally; each annulus with single transverse row of minute spicules; opisthosoma with prominent pair of subcaudal setae *f* and with ventrolateral setae *d*, *e*, and caudal setae *h1* and *h2* seemingly evident, other setae indiscernible; legs I and II with empodial featherclaws long, not bushy, main shaft divided, tips of each branch bifurcate; legs I and II with a prominent seta on each of femur, genu, tibia (two setae), and a short seta on tarsus (not all these verifiable on leg I); leg II with a probable solenidion on each of tibia and tarsus (these not verifiable on leg I); legs III and IV absent.

Type species: *T. fedelei*, sp. nov.

Etymology. Generic from *Trias*sic (geological period of origin) and *acarus* (Latin for mite); species name patronymic for Paolo Fedele (Cortina d'Ampezzo), discoverer of the Triassic amber deposit.

Triasacarus fedelei Lindquist and Grimaldi, new species. (Fig. 2)

Diagnosis. As for genus (monotypic).

Description. Body shape vermiform, cylindrical, total length 210 μm (6.5x greatest width). Body observable mostly just ventrally. Gnathosoma distinctly prognathous, with infracapitulum framed by fused palpcoxal bases. Among some image focal planes ("f.p."), infracapitulum with an anterior, underlying ledge with narrowly rounded anterior margin (f.p. 2,346–49, 2,448–50), above which a long proboscis, seeming with paired structures, projects anteriorly and then somewhat ventrally, between freely standing apical segments of palpi (Fig. 2 *A*, *B*, and *D*). A pair of acuminate, possibly cheliceral structures flank proboscis dorsolaterally. Palpi with freely extending segments well separated on either side, slightly convergent apically, each with slightly elbowed, slender palp-femur, longer than wide, bearing a short seta; palp-genu shorter than wide, indistinctly delineated from more apical segments; palp-tibia and -tarsus partly fused, elongate, with short apical seta, and seeming to end in a sinuous, blunt apex (f.p. 2,337–50). Coxisternal region of legs I and II apparently consolidated, but structural details, including setae, not discernible. Prodorsal shield details observed with difficulty in ventral view; anterior margin of shield projected as narrowly rounded frontal lobe over base of gnathosoma (f.p. 2,351–54); faint indications of one pair of long vertical setae discernible and projecting anterolaterally from *ve* position (f.p. 2,179–80, 2,356–58), and pair of shorter scapular setae *sc*, projecting posteriorly, more discernibly on right side (f.p. 2,359–63, 2,429). Opisthosoma elongate, with *ca.* 55–60 fine, transverse annuli that encircle the body circumference and are not differentiated dorsoventrally. Annuli each with single transverse row of minute spicules; these longer, spiniform laterally, decreased in size posteriad. Pair of long, fine subcaudal setae *f* present at level of dorsal opisthosomatic annuli 55–56, their tips reaching to level of opisthosomatic apex. Other opisthosomatic setae not readily discernible, but indications of them evident among some focal planes and also based on positions of faint indications of their insertions, as follow: *d* at level of annuli 22–23 (f.p. 2,022–38, 2,156–83), *e* at level of annuli 37–38 (f.p. 1,926–31, 2,156–83, 2,022–38, 2,482–85), and elongate caudal setae *h2* and short accessory setae *h1* on terminal annuli before anal lobe (f.p. 2,206–13, 2,412–16, and 2,479–89). Anal lobe small, slender, with possible accessory lobes. Genital opening and setae not observable. Legs slender, without spine-like projections or serrations evident on any segments; trochanter and femur thickest segments on legs I and II; tibia I longer (*ca.* 1.4x) than tibia II. Femur of legs I–II with long, fine, ventral seta (f.p. 2,323–26, 2,447–50); genu of legs I–II short, with long, dorsal seta (f.p. 2,335–40); tibia of legs I–II slightly longer than tarsus, with a long ventrobasal seta and a long, fine, dorsoapical seta and adjacent lateroapical solenidion (f.p. 2,330–37) (solenidion and ventral seta not discernible on tibia I). Tarsus of legs I–II with short dorsal seta and moderately long, curved, blunt-tipped solenidion subapically (about 1.2x longer than empodial featherclaw) (f.p. 2,330–33; Fig. 2). Empodial featherclaw long, length approximately equal to that of tibia + tarsus on leg II, 8- or 9-rayed, rays simply branched, with central shaft divided (f.p. 1,989–92, 2,022–23, 2,068–69, 2,323–26, 2,336–37; Fig. 2 *A* and *E*–*G*).

Type. Holotype, no. MGP 31343, in amber from outcrops of the Heiligkreuz Formation [late Julian to early Tuvalian in age (Late Carnian: *ca.* 230 Ma)] near the village of Cortina in the Dolomite Alps of northeastern Italy. Museum of Geology and Paleontology, University of Padova, Italy.

Comments. A superfamily-level attribution of the fossil can be made via a process of exclusion as well as by use of the specialized features that are preserved. Among acariform mites, no other taxon than Eriophyoidea is characterized by the apomorphic attributes of an elongated, vermiform body that terminates caudally with an adhesive anal structure, loss of legs III–IV, and the remaining legs equipped with empodial featherclaws (3). Within the superfamily, the immediately most notable attributes are the presence of a ventral seta and a solenidion on tibia II (the presence of these structures on leg I could not be confirmed). Among extant taxa of Eriophyoidea, the presence (retention) of a tibial seta has been noted as an atavism in only one species of the relatively derived eriophyid genus *Abacarus* (4), while a tibial solenidion is found only among some of the genera of the putatively early-derived family Phytoptidae and, even among these taxa, only on leg I. Therefore, the presence of these structures on the tibia of leg II is thought to be even more ancestral within the lineage. The presence of a pair of prodorsal setae with insertions in the area occupied by the pair of external vertical setae, *ve*, is also notable, because only a handful of genera in the same family Phytoptidae retain these setae. Other attributes characteristic of Phytoptidae are not discernible in the fossil of *Triasacarus*, in particular the form of the female genitalia, with spermathecal tubes longer than the diameter of the spermathecal sacs. Not only are these structures internal (and therefore not visible externally in the fossil), but what surfaces are visible do not allow determining whether the specimen is a female, or indeed, even an adult.

At the superfamilial level, the fossil appears to lack an integration of gnathosomatic structures into the form that characterizes all known extant members of the superfamily Eriophyoidea. Although details of form of the cheliceral and associated stylet-like structures are not discernible, the palpi are not formed as thickened, truncated structures appressed to the infracapitulum and partially enclosing and guiding the feeding structures. Also, the palpal apices are not truncated distally into adhesive lips that flank the feeding structures. This less specialized form of the gnathosoma may be viewed as basal (or primitive) to that which characterizes the superfamily and argue for a separate taxon within a higher category that has long been recognized by various authors as the Tetrapodili.

Ampezzoa Lindquist and Grimaldi, new genus.

Diagnosis. A distinctive fusiform eriophyoid with prognathous gnathosoma; gnathosoma framed by lateral margins of palpal segments, between which an infracapitular gutter bears a set of indistinguishable structures (some cheliceral); anterior portion of idiosoma broad, posterior end tapered; body dorsoventrally flattened; prodorsal shield well developed, with posterior margin well defined, posterior region of shield possessing pair of closely set dorsal tubercles, each with scapular seta; shield also with possible indications of an unpaired internal vertical seta anteriomedially and a pair of external vertical setae midlaterally; opisthosoma with approximately 18 tergites, 1–15 bear pair of digitiform lateral lobes; lateral lobes and portions of opisthosomatic tergites apparently wax-secreting; telosome with prominent pair of caudal setae *h2*; opisthosoma with ventrolateral setae *d*, *e*, *f*, and accessory caudal setae *h1* seemingly evident, other setae indiscernible; leg I with 5 discernible setae, of which one appears to emanate from each of femur, genu, tibia, tarsus, and a second one from tarsus; tarsal solenidion with enlarged tip; tarsus I long and slender; empodial featherclaw moderately long, not bushy, main shaft possibly divided, tips of each branch bifurcate; leg pair II present, but structure not discernible; legs III and IV absent.

Type species: *A. triassica*, n. sp.

Etymology. Generic from Valle d'Ampezzo (Anpezo in local dialect) in northeastern Italy, source of Triassic amber outcrops; species name for period of geological origin.

Ampezzoa triassica Lindquist and Grimaldi, new species (Fig. 3)

Diagnosis. As for genus (monotypic).

Description. Body fusiform, dorsoventrally flattened, total length 124 μm, greatest width *ca.* 50 μm (Fig. 3*A* and *B*). Body as preserved is largely just visible from dorsal surface. Gnathosoma prognathous, clearly demarcated from idiosoma. Greatest width of gnathosoma 0.4x that of prodorsal shield; length of sclerotized portion of gnathosoma slightly less than that of prodorsal shield. Infracapitulum with an anterior, underlying ledge with broadly rounded anterior margin (f.p. 2,606–09; 3,006–09). Lateral margins of gnathosoma outlined by palpcoxal bases and outer margins of apparently three segments (palpal trochanter-femorogenu, palp-tibia, palp-tarsus). Within these margins is a pair of undulate dorsal ridges that may represent walls of a stylet sheath or infracapitular gutter (Fig. 3 *A*–*C*), within which lie a complex of structures; each ridge bears a bluntly rounded dorsal projection, alongside the palp-tibial base, that may represent a cheliceral retainer. Chelicerae not discernible amidst adjacent gnathosomatic structures. Prodorsal shield large, well sclerotized, somewhat trapezoidal in shape, with anterior margin as shortest side, lateral margins divergent posteriad, posterior margin longest and slightly convex (Fig. 3 *A* and *B*). Pair of low, paramedian dorsal tubercles near posterior margin of prodorsal shield, each tubercle with short internal scapular seta *sc* directed posteromedially; length of seta ca. 2x the diameter of tubercle; possible indications of other prodorsal setae evident among a few focal plane images—i.e., unpaired internal vertical seta *vi* anteromedially (f.p. 2,607–09, 3,006–08)—paired external vertical setae *ve* midlaterally (f.p. 2,597–2,601, 2,663–68, 2,999–3,002). Opisthosoma pyriform, with caudal end tapered narrowly (telosome width *ca.* 0.3x that of anteriormost segment); with 18 fully transverse, delineated tergites. Tergites 1–14 each with single transverse row of minute spicules along posterior margin, and laterally projecting into thin digitiform lobes (some perhaps bifurcate at apex, e.g., t10–13; Fig. 3 *A* and *B*). Very fine, transparent, striated "webbing" appears to connect between lobes and extends dorsally over opisthosoma in places; striations oblique, but fine striations over t8–12 transverse. Tergite 15 without denticles or striations, but with pair of sharp, posterolateral, spine-like lobes. Tergites 16 and 17 simple. Pair of long caudal setae *h2* present (having ventral insertion) (f.p. 2,533–35; Fig. 3 *B* and *E*), lengths approximately equal to lengths of segments 15 + 16 + 17. Other opisthosomatic setae not readily discernible but possible indications evident among some focal plane images—i.e., ventrolateral seta *d* on both sides at level under tergite 6 or 7 (f.p. 2,597–98, 2,952–53), ventrolateral seta *e* on right side at level under tergite 10 (f.p. 2,596–99, 2,892–94, 2,952–54, 2,999–3,000), ventrolateral seta *f* on both sides at level under tergite 13 (f.p. 2,589–92, 2,945–48, 2,994–95), on right side (f.p. 2,632–34, 2,873–74) and on left side (f.p. 2,780–81, 2,832–34, 2,886–88), and short accessory caudal seta *h1* (f.p. 2,529–30, 2,765–66). A pair of long coxisternal setae, either *1a* or *2a*, seem evident in a few images (f.p. 2,561–66). Leg pairs I and II present (right legs obscured beneath prodorsal shield), left leg I best revealed, some segmentation preserved but basal segments difficult to interpret (Fig. 3*B* and *D*). Leg I with 5 long, fine setae discernible, of which one each interpreted to insert on femur (ventrally), genu (dorsally) and tibia (dorsally), and two on tarsus (dorsobasally) (f.p. 2,690–94, 2,752–57, 3,015–19). Leg I tarsus long, slender, length 1.75x that of empodial featherclaw; featherclaw simply branched (central shaft possibly divided) (f.p. 2,611–12, 2,904–06), not bushy; tarsal solenidion with enlarged tip (f.p. 2,755–57, 2,916–19, 3,020–21). Minute portion of left leg II preserved with attached setae.

Type. Holotype, no. MGP 31344, in amber from outcrops of the Heiligkreuz Formation [late Julian to early Tuvalian in age (Late Carnian: *ca.* 230 Ma)] near the village of Cortina in the Dolomite Alps of northeastern Italy. Museum of Geology and Paleontology, University of Padova, Italy.

Comments. A superfamily-level attribution of the fossil can be made with the same rationale given above for *Triasacarus*. The most notable attribute of this specimen is the form of the opisthosoma, with its thickened tergites individually extended into lateral projections that appear to be capable of forming waxy secretions. Among extant taxa of Eriophyoidea, the body form of *Cymeda zealandica* Manson & Gerson (5) is remarkably similar to this fossil. A monotypic genus in the tribe Acaricalini (subfamily Phyllocoptinae, family Eriophyidae), this taxon is known only from ferns in New Zealand (6). As in the fossil *Ampezzoa*, derived but possibly homoplasious attributes characteristic of extant Acaricalini are the empodial featherclaw of legs I–II moderately to deeply divided, and the dorsal opisthosomatic annuli coalesced into fewer, enlarged tergite-like thickenings, sometimes extended laterally as lobes (7, 8). However, none of the extant acaricalines retains either of the vertical pairs of prodorsal setae. Although details of the ventral surface of the fossil are not clear enough to determine whether it is an adult (with external genital structures) or immature (without them), it is likely an adult, because the presence of strongly differentiated tergites is generally expressed only in the adult stage of eriophyoid mites.

Unlike *Triasacarus*, the specimen of *Ampezzoa* presents an integration of gnathosomatic structures into much of the form that is apotypical of all known extant members of the superfamily Eriophyoidea. Therefore, these two fossil taxa may be regarded as only distantly related to one another in the eriophyoid lineage of the Tetrapodili, with no possibility of their being dimorphic forms of the same species. Although details of structure of the cheliceral and associated stylet-like structures are not discernible, in *Ampezzoa* the palpi are formed as thickened, truncated structures appressed to the infracapitulum and partially enclosing and guiding the feeding structures. In contrast, in *Triasacarus*, the palpi appear to be well-separated, free-standing structures somewhat reminiscent of the form seen in some cunaxid mites.

Amber from the Late Triassic (Carnian) of Europe and Other Sites in the World

Two types of Triassic amber have been found in the Dolomite outcrops. The first occurs as fractured brittle pieces of up to 30-mm size embedded in sandstone and hybrid-sandstone, mixed with shells of large bivalves. These fossils indicate a marginal marine environment. Abundant plant fragments, including horsetails, conifer twigs, wood, and leaflets, suggest a rich coastal vegetation (9). This resin was transported prior to deposition. The second amber type is represented by abundant, isolated, and well-preserved autochthonous drops, which occur in large number within a lignitic paleosol (2–5% by volume). These amber droplets are ovoid to elongated (Fig. 1*F* and Fig. S1) and mostly 2–6 mm in size. Their color ranges from yellow to russet and they possess a resinous luster. The surface of the amber droplets often shows reticulate desiccation marks, suggesting exposure to air or sun that caused a fast evaporation of volatile components in the resin. The small size of the amber droplets and the presence of a small peduncle suggest a narrow point of exudation from the plant. Coeval findings of Triassic amber (see Fig. S3) suggest that small droplets are typical for Triassic ambers. Although strong compression due to the weight of superimposed sediments occurred during the geological history of the Dolomites (the paleosol is interposed between compact white dolomite levels), the softness of the sediment constituting the paleosol (mainly clay and cuticle remains) permitted optimal preservation of the amber. Considering the sometimes larger size of the first amber type embedded in the sandstone (9), we might hypothesize that future field work within the paleosol will give access to hydrodynamically selected larger amber pieces that might consequently be a source of larger Triassic arthropods.

Triassic amber from the Dolomite Alps of Italy is preserved in the Heiligkreuz Formation, which corresponds to an interval between the Early and Late Carnian. In Italy, Triassic amber has also been found in a second distinct stratigraphic unit in the Southern Alps [Rio del Lago Formation in the Julian Alps; Fig. S3 (9)]. Both sites are located in the westernmost Tethyan margin of the Eurasian plate during the Mesozoic. In the same chronostratigraphic interval, amber outcrops have also been found in several other areas of Europe, including Austria [Raibler Schichten (10), Lunzerschichten (11)], Hungary [Sándorhegy Formation (12)], Spain [Keuper facies, Alicante (13)], and Switzerland [Schilfsandstein Formation (14–16)]. A comparative stratigraphic section shows that the occurrence of Triassic amber in Europe as well as in other parts of the world (Arizona, South America, and South Africa) was roughly contemporaneous in the Carnian (Fig. S3; refs. 17–21; stratigraphy based on ref. 22).

These findings suggest three possible scenarios for the Carnian amber anomaly: (*i*) changes in sedimentation that facilitated the preservation of resins; (*ii*) increased production of resins; and (*iii*) both factors acting together. After the Permian mass extinction, and the following slow recovery of environments and biota in the

Early Triassic, the Middle and Late Triassic was a relatively stable period, interrupted only by a global episode of wet conditions (23), with a consequent transition to more mesic floras (24) and an increase in the production of conifer resins (9). As recently demonstrated (25), major climatic changes and mass extinctions appear to be associated with C-isotope anomalies in the atmosphere-ocean system. In this context, amber is potentially a paleoclimatic indicator (9, 26).

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Fig. S1. Typical appearance of numerous amber droplets found in the paleosol of the Dolomite Alps Triassic outcrop. Scale bar: 5 mm.

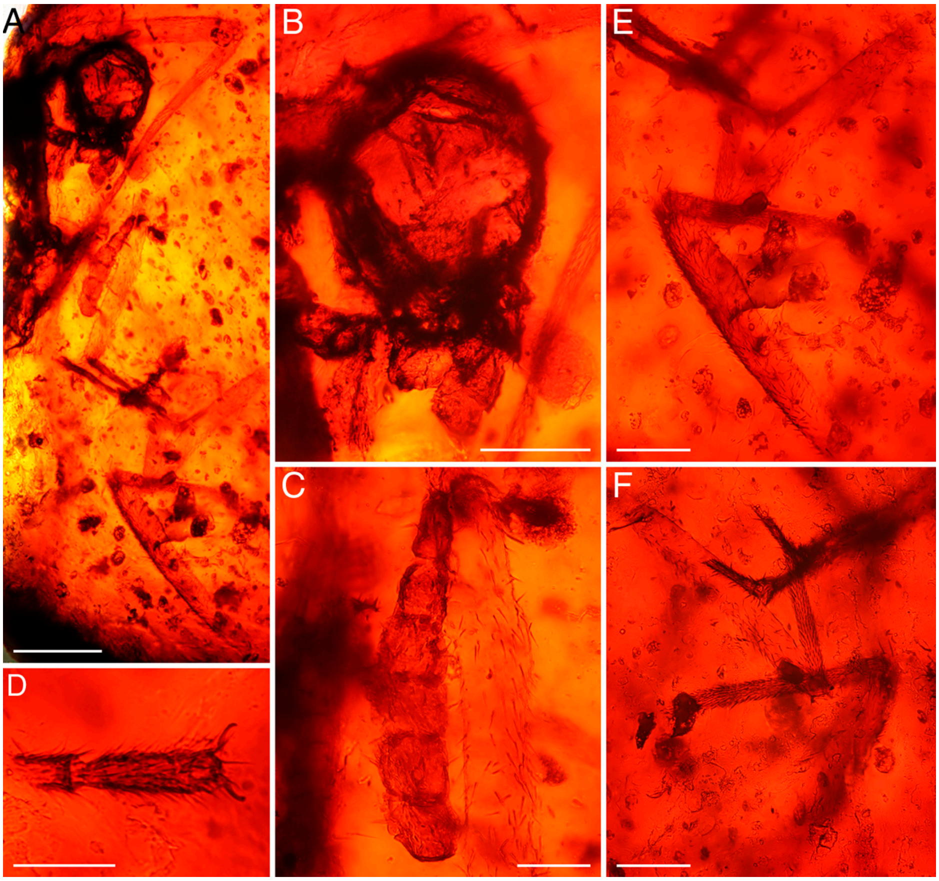

Fig. S2. Photomicrographs of Diptera specimen in Dolomite Triassic amber, MGP (Museum of Geology and Paleontology, University of Padova, Italy) 31345. (*A*) Entire specimen with dissociated appendages. (*B*) Head, detail. (*C*) Detail of antenna and adjacent leg, showing oval sensory area, possibly Johnston's organ. (*D*) Detail of dissociated distitarsus. (*E*) Dissociated legs. (*F*) Same dissociated legs as in E, from opposite side and taken before embedding preparation. All photos using bright field (BF) illumination; all images are stacked composites of individual focal planes. Scale bars: *A*, 200 μm; *B*, *E*, and *F*, 100 μm; *C* and *D*, 50 μm.

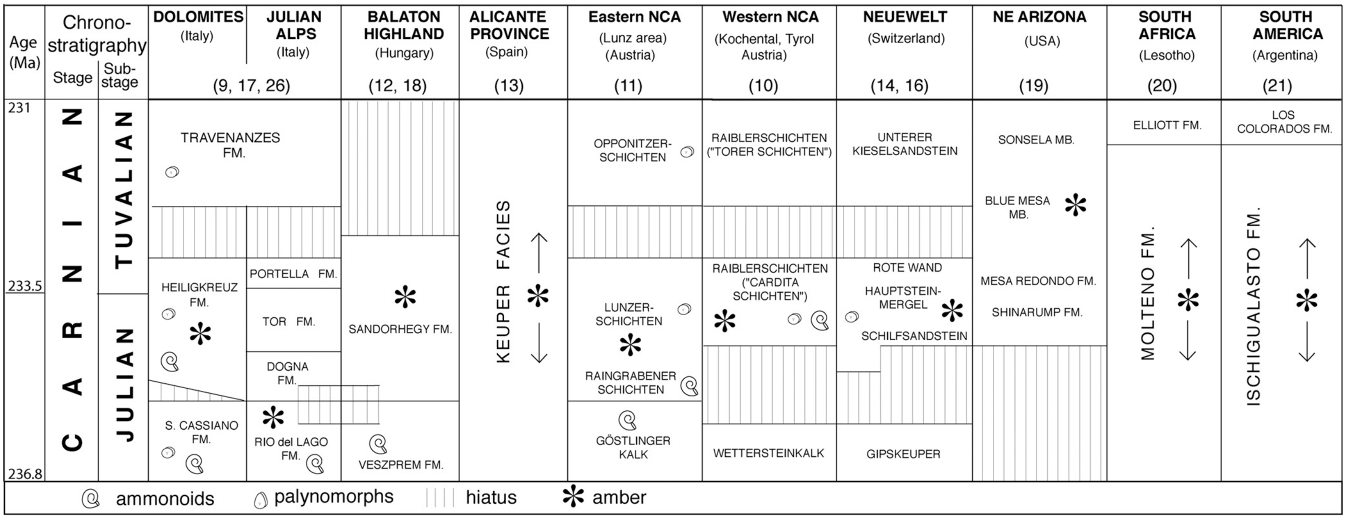

Fig. S3. Stratigraphic chart of the main Triassic amber deposits of the world. NCA, Northern Calcareous Alps; FM., Formation; MB., Member. References are indicated in parentheses. Geochronological scale according to Ogg et al. (22).