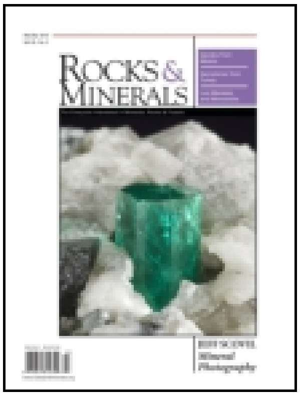

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The Amazing Fossil Insects of the Eocene Kishenehn Formation in Northwestern Montana

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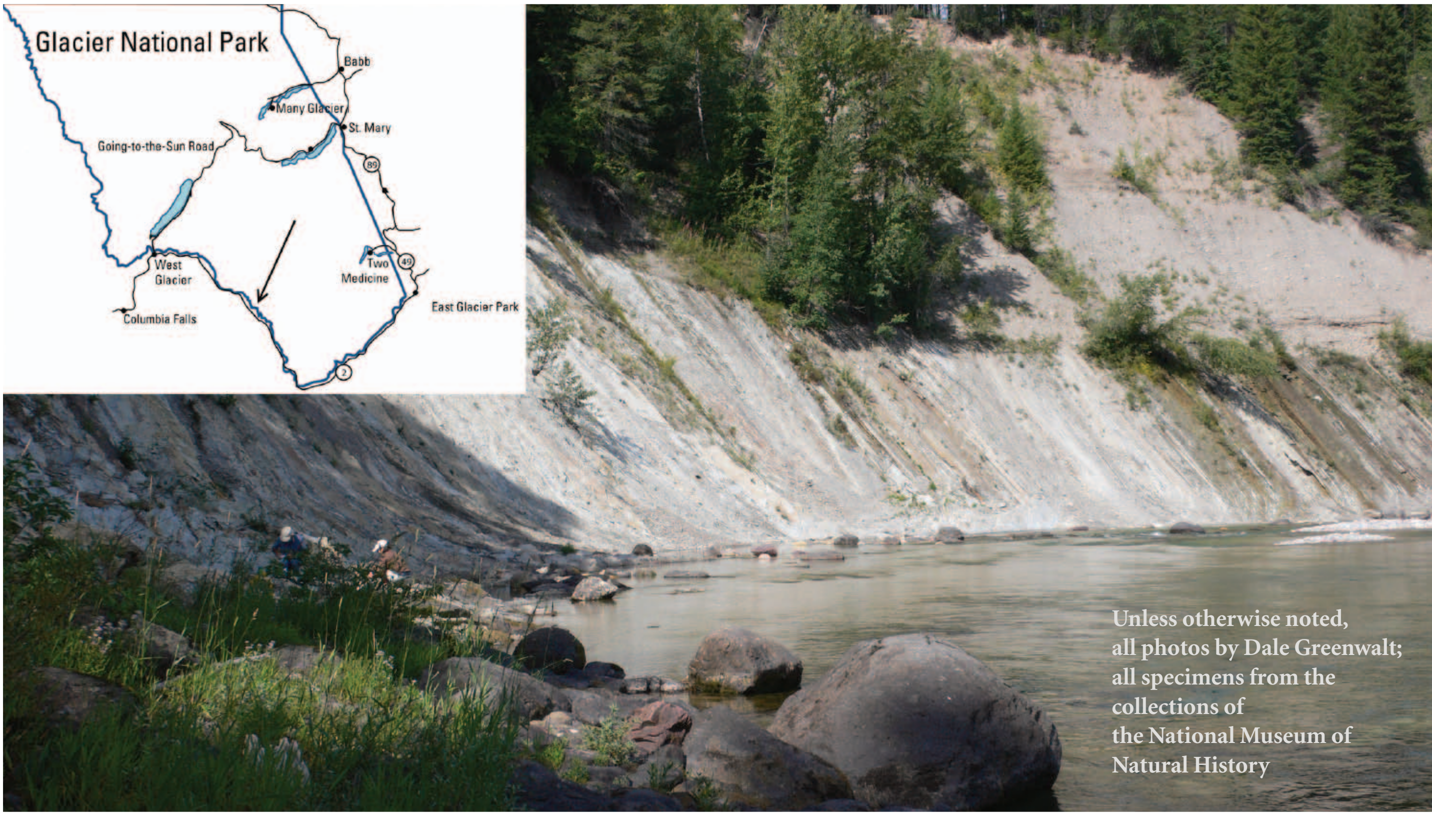
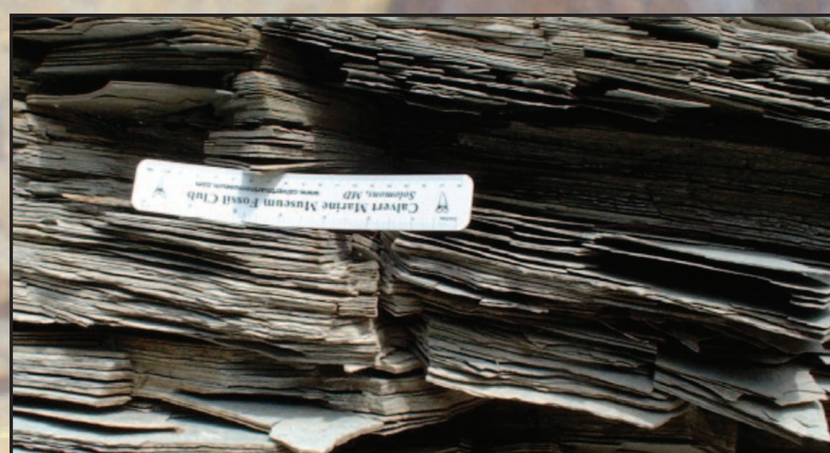


Unless otherwise noted, all photos by Dale Greenwalt; all specimens from the collections of the National Museum of Natural History

Figure 1 (above). The first author (DG) and Sarah Dakin collecting at the Dakin site along the Middle Fork of the Flathead River in Montana. Note the unconformity between the steeply angled shale at the river's edge and the overlying layers of Quaternary gravel at the treeline. Bill Dakin photo. _Insert:_ A map of Glacier National Park with an arrow denoting the region of the Flathead River near which fossil insects were collected.

Figure 2 (right). An outcrop of weathered fissile oil shale. The ruler is 18 cm long.



The Amazing Fossil Insects

Of the Eocene Kishenehn Formation in Northwestern Montana

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Figure 3. **A cross-section of a 1.8-mm-thick piece of oil shale from the Coal Creek Member of the Kishenehn Formation reveals twelve varves with thicknesses from 75 to 250 microns. Scale bar = 1 mm.**

APPROXIMATELY 46 MILLION YEARS AGO, shortly after the green and red mudstones that now form the mountains of Glacier National Park completed their slow slide eastward from Canada, a series of strong earthquakes created a long north-south rift valley along what is now the western border of the park. As the valley filled with run-off from adjacent mountains, Lake Kishenehn, a 100-mile-long lake, was formed. Today, the North and Middle forks of the Flathead River erode their way through the mile-thick sediments of that ancient lake and expose carbon-rich oil shale and siltstone that comprise the steep cliffs on either side of the river. It is within these shales of the Kishenehn Formation that scientists from the Smithsonian Institution are collecting what are arguably some of the most exceptional insect fossils in the world.

Although fossil gastropods were reported from the Kishenehn Formation in the early 1900s (Daly 1912), fossil insects are a more recent discovery. The first specimens of fossilized insects were found along the Flathead River in the early 1980s when a young geology student, Kurt Constenius, decided to write his master's thesis in geology on the origins of the Kishenehn Basin (Constenius et al. 1989). Constenius lived in the nearby town of Whitefish, Montana, and spent many weekends rafting the river with his parents. Over the course of several summers, they documented the presence of fossil insects at a number of different sites and made a collection, much of which was recently donated to the Department of Paleobiology in the Smithsonian's National Museum of Natural History. Today, only a few trout fisherman ply the waters of the Middle Fork, unaware of the fascinating history of the rift valley and its ancestral lake.

The oil shales of the Kishenehn Formation, interbedded with massive siltstone and sandstone, are exposed as large and sometimes nearly vertical cliffs along several miles of the Middle Fork of the Flathead River. The shale outcrops are occasionally horizontal, but in many areas they are uplifted to a near-vertical position. In most cases, the shale is covered with thick layers of Quaternary alluvial fan and fan-delta sediments (fig. 1). The fossiliferous oil shale is often exposed as weathered planar laminae that are 1 mm to several millimeters in thickness (fig. 2). The fissile shale can be split to reveal unweathered surfaces. However, the insect fossils are not readily visible; the shale must be wetted and, given the small size of the average Kishenehn Formation insect fossil, examined with a hand lens.

The middle sequence of the Coal Creek Member has been estimated to be 46.2 ± 0.4 million years old (early Middle Eocene) by ^{40}Ar/^{39}Ar analysis and 43.5 ± 4.9 million years old by fission-track analysis (Constenius 1996). Several lines of evidence suggest that during that time the climate was wet tropical to subtropical with a mean annual temperature significantly higher than it is now. Lake Kishenehn was a large body of water, with both deep-water and marsh environments. The molluscan fauna of the Kishenehn Formation includes a group exemplified by *Gastrocopta minuscule* Pierce. *Gastrocopta pellucid* Pfeiffer, selected as the extant analogue of *G. minuscula*, currently lives in an environment characterized by a mean annual temperature of 25°–27°C (Pierce and Constenius 2001). The early arboreal primate *Tarkadectes montanensis* McKenna 1990, of the extinct family Omomyidae, has also been described from the Coal Creek Member (McKenna 1990; Ni et al. 2010). This tiny primate

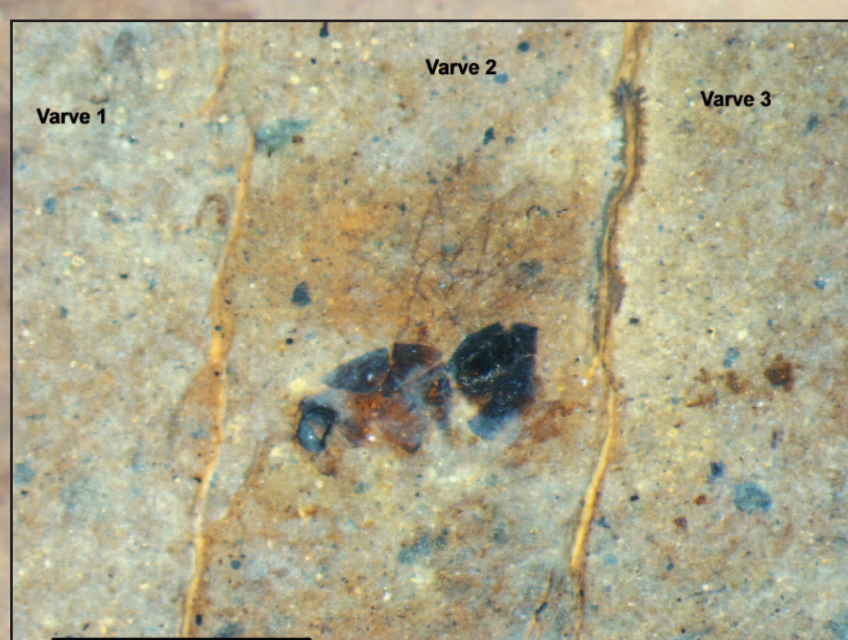

Figure 4. **When Kishenehn Formation oil shale is split, colored varve surfaces that appear glassy in texture are exposed. In this specimen, the shale has split through multiple planes to expose the surfaces of several varves and reveal a fossil wasp. USNM (United States National Museum) 553702. Scale bar = 2 mm.**

Figure 5. **This fairy wasp (family Mymaridae) is distinguished by its clubbed antennae, long narrow hind wings, and a fringe of long delicate setae at the margins of its wings. USNM 553689. Scale bar = 1 mm.**

is closely related to the insectivorous Tarsiidae, extant species of which are currently restricted to islands of Southeast Asia (Groves and Shekelle 2010).

During the past four summers, 5,245 pieces of shale containing approximately 16,000 fossil insects have been collected from the Coal Creek Member of the Kishenehn Formation. To date, fourteen different orders of fossil insects have been identified. However, the insect fauna of the Coal Creek Member is not particularly diverse. Diptera (flies) make up 55 percent of all fossil insects in the collection; of these, more than 80 percent are chironomids (non-biting midges) and representatives of other closely related families. An additional 15 percent of all the fossil insects are water boatmen (family Corixidae), true bugs that spend their entire life either in or on the surface of lakes, ponds, and streams. Seven orders of insects (including Odonata [dragonflies], Lepidoptera [butterflies and moths], Dermaptera [earwigs], Isoptera [termites], Collembola [springtails], Psocoptera [bark lice], and Neuroptera [lacewings and others]) account for less than 0.2 percent of all the Kishenehn fossil insects. Several factors may have contributed to this distribution of insect types. Members of the families Lepidoptera, Dermaptera, Isoptera, Psocoptera, and Collembola are not aquatic insects, and their near absence from the sediments of Lake Kishenehn is not unexpected. Perhaps the most important factor involved in the selective preservation of Kishenehn insects is their size.

When the oil shale is sectioned and viewed under a microscope, well-defined structures (varves) that represent annual layers of sediment are visible (fig. 3). The alternating light and dark layers represent seasonal accumulations of detrital mud and sand (light layers) and organic carbon-rich remnants of algal and/or bacterial "mats" (dark layers) that proliferated in the warmer summer months. It is within or on the thinner dark layer that the fossil insects are found. The varves are very thin (50–250 microns) and provide a narrow taphonomic filter that biases preservation in favor of tiny insects. Large insects, such as grasshoppers and dragonflies, are too big to be buried by a single layer of sediment and are therefore exposed to predation and other processes that de-

Figure 6 (above). **A female of the recently described mosquito (family Culicidae) species *Culiseta kishenehn* Harbach and Greenwalt 2012. Many extant species of the genus *Culisita* feed on birds—note the long specialized mouthparts (proboscis). USNM 546529. Scale bar = 2 mm.**

Figure 7 (left). **A female of the recently described mosquito species *Culiseta lemniscata* Harbach and Greenwalt 2012. USNM 547065. Scale bar = 2 mm.**

Figure 8 (below). **A female of the newly described mosquito species *Culiseta kishenehn.* Note the tiny crystals of pyrite in the head, thorax, and legs of this specimen. USNM 547066. Scale bar = 2 mm.**

stroy the insect before it can be entombed. The only fossils of dragonflies in the Kishenehn Formation are wing fragments, structures that are very flat and thin that can be embedded within a single layer. The shale can occasionally be split along or within the plane of the mat to reveal a smooth siliceous surface that is often colored. The colors of the mat surfaces, the geochemical basis of which is unknown, range from gray to yellow to dark purple. Figure 4 shows several reddish mat surfaces and a cross-section of each respective varve where they have broken to expose lighter larger-grained detrital layers. A fossil wasp lies on a surface of varve two. The colored mat surfaces are unique to the Kishenehn and are not characteristic of the fossiliferous shales found at other North American *Lagerstätten* such as the Green River (Wyoming) and Florissant (Colorado) sites.

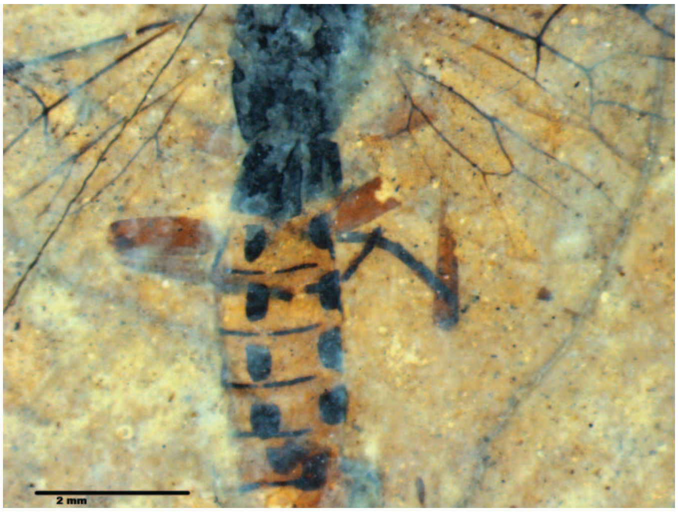

***Figure 9 (above).* Color preservation in a specimen of the Hymenopteran family Ichneumonidae. Reddish legs, an orange abdomen with two large black spots on each abdominal segment, and a jet-black thorax highlight this specimen. USNM 553690. Scale bar = 2 mm.**

***Figure 12.* A specimen of the Hymenopteran family Proctotrupidae. Note the very broad ovipositor (the egg-laying device at the end of the abdomen) and the distinct wing venation pattern. USNM 545295. Scale bar = 1 mm.**

***Figure 10 (right).* A well-preserved rove beetle (family Staphylinidae) fossilized in the siliceous surface of the Kishenehn Formation oil shale. Note the long delicate hairs at the terminus of the abdomen, a characteristic of many of the species of this family. USNM 553691. Scale bar = 1 mm.**

On average, the insect fossils are very small, typically 1–5 mm in length. The very first fairy wasps (Hymenoptera: Mymaridae) ever to be described from compression fossils have recently been found in Kishenehn oil shale (Huber and Greenwalt 2011). Six new species were designated, all approximately 1 mm or less in length. Prior to their description, fossil mymarids were known only as inclusions in amber. Note the very small size and the long setae (hairs) along the margins of the wings of the mymarid in figure 5. The species *Ptenidium kishenehnsis* Shockley and Greenwalt 2013, a featherwing beetle in the family Ptiliidae, is less than 0.7 mm in length and has also been recently described from the Kishenehn Formation (Shockley and Greenwalt 2013).

Relatively large numbers of beautifully preserved mosquitoes (Diptera: Culicidae) have been found in the Kishenehn Formation; ten of these have recently been described as two new species in the genus *Culisita* (Harbach and Greenwalt 2012). The Kishenehn Formation may be the most prolific source of high-quality mosquito fossils in the world (figs. 6–8). Note the minute crystals of pyrite throughout the specimen in figure 8. The presence of pyrite is evidence of the

***Figure 11 (below).* One of the numerous tiny parasitic wasps of the superfamily Chalcidoidea. Like many chalcidoids, this wasp has a uniformly jet-black body and very reduced wing venation. USNM 553692. Scale bar = 1 mm.**

Figure 13. **Although this fossilized wasp (family Diapriidae) appears to be in amber, it is in fact a compression fossil. USNM 553693. Scale bar = 1 mm.**

Figure 14. **An exceptional specimen of the family Diapriidae, subfamily Belytinae. Note the similarity of the wing venation patterns in figures 11–13. USNM 553694. Scale bar = 1 mm.**

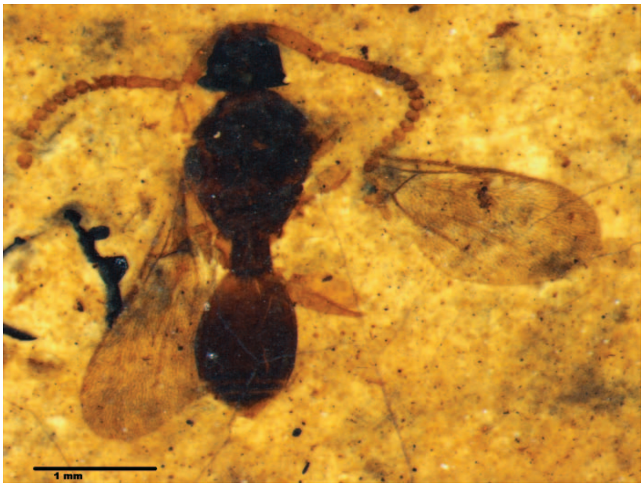

Figure 15. **A belytinid wasp. Note the very long first segment of the antennae and the "beads-on-a-string" morphology of the segments of the terminal half of the antennae. USNM 553695. Scale bar = 1 mm.**

anoxic environment in which the fossil formed. The lack of oxygen is an absolute requirement for quality preservation, as it prevents oxygen-mediated degradation of the insect.

Another remarkable aspect of the Kishenehn Formation fossil insects is their color. This phenomenon is best depicted by the highly sclerotized fossil wasps, the chitinous exoskeleton of which was an important factor in their preservation once they were buried in the anoxic sediments of ancient Lake Kishenehn. The stunning orange abdomen, reddish legs, and jet-black head and thorax of the Ichneumonid wasp pictured in figure 9 are good examples of color preservation. This particular specimen, with a body length of nearly 1 cm, is also unusually large for a Kishenehn fossil insect. The coloration of insects, as well as that of many other organisms, is based on two very different phenomena that have been appreciated since the nineteenth century (Hagen 1882). Color can be based on the presence of pigments, such as melanin, that absorb and reflect different wavelengths of light, or on multilayered nanostructures that generate color via interference of scattered light. Both mechanisms have been shown to exist in fossil bird feathers, from which melanic functional groups, melanin-derived organocopper compounds, and fossilized melanosomes have been documented (Barden et al. 2011; Vinther et al. 2008; Wogelius et al. 2011). Structure-based color has been documented in both metallic/iridescent fossil beetles (McNamara et al. 2011, 2012; McNamara, Briggs, and Orr 2012; Tanaka et al. 2010) and moths (McNamara et al. 2011). However, evidence for pigment-based coloration in insects is lacking. The staphylinid beetle pictured in figure 10 displays an array of colors that help to define the details of its abdominal segments. The structures and/or pigments responsible for the red, orange, and yellow colors of the insects from the Kishenehn Formation have yet to be investigated.

The Kishenehn fossil wasps best depict the great detail and color preservation of these insects. These parasitic wasps were very small—they laid their eggs in the larvae or eggs of other insects. There are large numbers of wasps of the superfamily Chalcidoidea. In addition to the fairy wasp pictured in figure 5, this group of insects is also depicted in figure 11. Their average size is less than 2 mm and nearly two hundred specimens of this superfamily have been collected from the Kishenehn Formation. Figure 12 depicts a member of the wasp family Proctotrupidae. Note the very stout and strongly sclerotized ovipositor; these wasps, as do extant species of this family, probably laid their eggs in beetle larvae. It is the family Diapriidae, however, that is not only the most beautiful, but also the most plentiful of all fossil Hymenoptera (bees and wasps). The diapriid wasp in figure 13 looks as if it were an inclusion in a piece of amber. In figure 14, nearly every detail of the wasp is beautifully preserved including the intricate sculpturing of its red thorax. More than 10 percent of all Kishenehn Hymenoptera belong to the diapriid subfamily Belytinae. The size and shape of the individual segments (flagellomeres) of the antennae allow assignment of the specimen in figure 15 to this subfamily.

Figure 16 depicts a rare example of a "snapshot in time" in which a fossil represents a dynamic process. In this case, that process is eclosion—that is, the exit of an adult midge

Figure 16. **A fossil of the process of eclosion—the emergence of an adult insect from its pupal case. The pupal abdomen of this midge, represented only by setae, extends toward the bottom of the photo, and an incompletely enlarged wing extends to the right. USNM 553696. Scale bar = 1 mm.**

from its pupal shell or exuvium. The long legs of the midge have pulled out from the confines of the exuvium as has one wing that is still quite small and yet to be expanded to its full size. The empty pupal abdomen, covered with setae, is at the bottom of the photograph.

The Kishenehn Formation fossil insects are unique and of significant scientific value. In addition to the high degree of preservational detail and the preservation of color, the collection contains insects that are smaller than those in most other collections of compression fossils. Several studies are underway that will describe new species. These include the first compression fossils from North America of the Dixidae, a family of aquatic flies closely related to mosquitoes, and the smallest fossil wasp ever found in the family Proctotrupidae. Another remarkable aspect of the Eocene fossil insects is their high degree of similarity to those species that are alive today. Although the consensus is that the life-span of an insect species is 3–10 million years (Grimaldi and Engel 2005), after 46 million years, it is difficult to distinguish one from another, a feature that was previously mentioned in an analysis of fossil insect diversity (Labandeira and Sepkoski 1993). An exception is a very rare pelecinid wasp (Hymenoptera: Pelecinidae) from the Kishenehn Formation that differs significantly from the single living representative of this family.

The North and Middle forks of the Flathead River have been designated as Wild and Scenic Rivers by the U.S. Congress; as a result, collection of geological specimens, including fossils, is strictly regulated by the U.S. Forest Service, which is responsible for protecting the river. The specimens figured in this article were collected under the auspices of USFS permit number HUN281.

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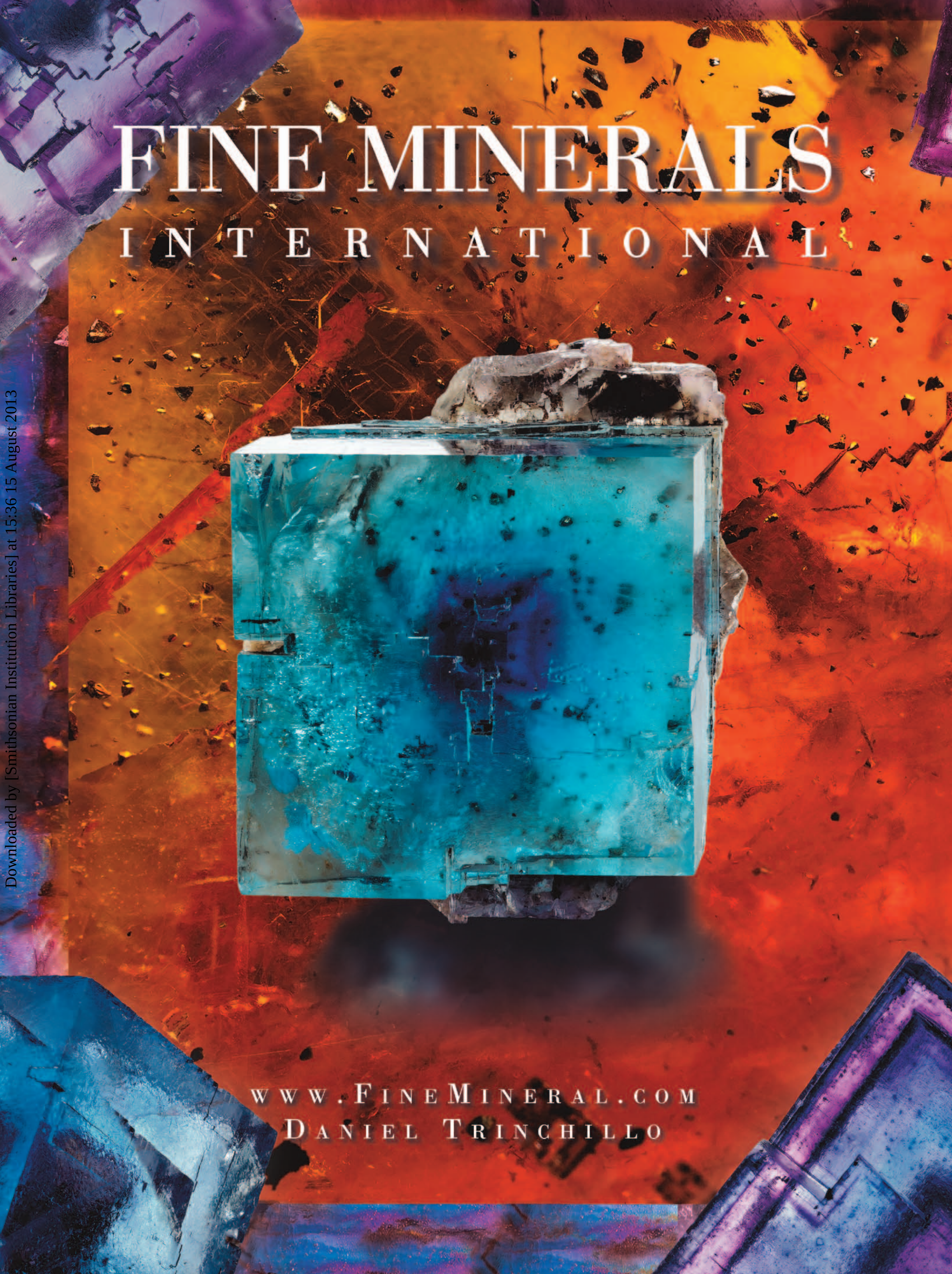
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