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from the Upper Miocene of Ardèche,
southern France

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Insecta,
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Spinarge,
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southern France,
Cenozoic,
new species.

ABSTRACT

Spinarge miocenicus n. sp., first fossil representative of an extant argine genus, is described from the Upper Miocene lacustrine maar of montagne d'Andance (Coiron Massif, Ardèche, France). The extant species of *Spinarge* Wei, 1998 are distributed from Japan, China, Korea, and eastern Siberia to Europe and live on broad-leaved trees, which are well represented in this paleoflora. During the Late Miocene the area of the Coiron Massif was probably quite favorable for Argidae Konow, 1890 as two of the three described fossil argids also originate from this area and period.

RÉSUMÉ

Un troisième fossile de mouche-à-scie argide (Hymenoptera, Tenthredinoidea) du Miocène supérieur d'Ardèche, Sud de la France.

MOTS CLÉS
Insecta,
Symphyta,
Arginae,
Spinarge,
Ardèche,
Sud de la France,
Cénozoïque,
espèce nouvelle.

Spinarge miocenicus n. sp., premier représentant fossile d'un genre actuel d'Arginae Konow, 1890, est décrit du maar lacustre du Miocène supérieur de la montagne d'Andance (massif du Coiron, Ardèche, France). Les espèces actuelles de *Spinarge* Wei, 1998 sont réparties du Japon, de la Chine, de la Corée et de la Sibérie orientale jusqu'en Europe et vivent sur des feuillus, qui sont bien représentés dans cette paléoflore. Au cours du Miocène supérieur, la zone du massif du Coiron était probablement assez favorable aux Argidae Konow, 1890, car deux des trois argides fossiles décrits sont également originaires de cette zone et de cette période.

INTRODUCTION

With approximately 913 species and 60 genera, Argidae Konow, 1890 are the second-most diverse family of the symphytan grade of Hymenoptera Linnaeus, 1758, lagging behind Tenthredinidae Latreille, 1818 (Taeger *et al.* 2018). This is paralleled in their known fossil occurrences, with many more fossil tenthredinids known than for Argidae. Only two fossil argid species are currently described, viz. *Mioarge azari* Nel, 2004 (Arginae Konow, 1890: Upper Miocene of Mont-Charay, Ardèche, France) and *Sterictiphora konowi* Rohwer, 1908 (Sterictiphorinae Konow, 1890: Eocene-Oligocene boundary, Florissant Formation, Colorado, USA). Douglas (1991: fig. V-18) and Douglas & Stockey (1996) figured an incomplete forewing they attributed to 'Argidae/Diprionidae' from the middle Eocene of the USA. Lastly, Smith & Poinar (1992) recorded an argid larva in Early Miocene amber from the Dominican Republic.

Here we describe a third adult of a fossil argid sawfly from the Upper Miocene of montagne d'Andance (Ardèche, France). It is also the first known fossil representative of an extant genus of Arginae.

MATERIAL AND METHODS

The holotype of *Spinarge miocenicus* n. sp. originates from the Miocene Konservat- Lagerstätte of the montagne d'Andance (Saint-Bauzile, Ardèche, France). The montagne d'Andance (altitude 552 m) is located on the site of an ancient maar dating from the Miocene epoch and linked to the Coiron basalt complex. The diatomitic unit from which the specimen originated was deposited in a lake formed by the maar crater (Demarcq *et al.* 1989), under a warm and humid climate (Brice 1965), with a possibly seasonal character. This lake was probably calm and shallow (Ehrlich 1966), surrounded by a deciduous forest with an undergrowth of ferns (Grangeon 1958; Riou 1988). Over time, this lake was filled with diatomite, forming rock strata up to 30 m thick in some localities (Serieyssol & Gasse 1991). This diatomite is a soft siliceous rock in which were preserved the insects that drowned in the lake at the time. These stratigraphic layers of diatomite represent a reducing environment that has allowed a remarkable conservation of mummified organic matter. The age of this deposit corresponds to the late Tortonian, 7.54 ± 0.06 Mya (Pastre *et al.* 2004). The new fossil was collected by two of us (VNM and BR) during fieldwork in summer 2024, with the authorization of Chemviron France Company, owner of the Quarry of montagne d'Andance. The fossil was fixed using wallpaper glue.

Two extant representatives of the genus were observed for comparison with the fossil:

– *Arge meliosmae* Shinohara & Hara, 2011, MNHN.FEY38826 (Fig. 3);

– *Spinarge (Arge) metallica* Klug, 1834, MNHN.FEY42476 (Fig. 4).

Specimens were observed using a Leica M205C stereomicroscope and photographed using a Sony alpha 7RIV camera. Photographs were exported in NEF format and processed with Nikon NX Studio software. All images are digitally stacked photomicrographic composites of several individual focal planes that were obtained using Helicon Focus 6.7 software.

We follow the list of genera of Argidae of Taeger *et al.* (2010, 2018), and the wing venation nomenclature was adapted from Goulet & Hubert (1993).

ABBREVIATIONS

Mya	Million years ago;
MDA	Muséum de l'Ardèche, Balazuc;
MNHN	Muséum national d'Histoire naturelle, Paris.

Morphology

A	anal vein;
C	costal vein;
Cu	cubital vein;
cu-a	transverse between Cu and A;
M	medial vein;
m-cu	transverse between M and Cu;
R	radial vein;
Rs	radial sector vein;
rs-m	transverse between Rs and M;
Sc	intercostal vein.

SYSTEMATICS

Class INSECTA Linnaeus, 1758
Order HYMENOPTERA Linnaeus, 1758
Family ARGIDAE Konow, 1890
Subfamily ARGINAE Konow, 1890

Genus *Spinarge* Wei, 1998

Spinarge miocenicus n. sp.
(Figs 1; 2)

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TYPE MATERIAL. — **Holotype.** France • body rather well-preserved with thorax, abdomen, one antenna, two complete forewings and partly preserved hind wings; Upper Miocene; montagne d'Andance paleomaar, diatomites, Saint-Bauzile, Ardèche; MDA.R2024.8.1.

TYPE STRATIGRAPHY AND LOCALITY. — Upper Miocene (7.54 Mya), montagne d'Andance paleomaar, diatomites, Saint-Bauzile, F-07210 Ardèche, France.

DIAGNOSIS. — In addition to the characters of the genus (see Discussion), third antennomere simple, elongate and slightly curved, $6.3\times$ as long as wide; fore- and hind wings brown in basal half, more yellow in distal half.

DESCRIPTION

Head hidden in matrix; third antennomere elongate and slightly curved, 1.9 mm long, 0.3 mm wide. Thorax 3.4 mm long, 1.9 mm wide; mesoscutellar appendage fused to mesoscutellum. Forewing complete, 8.8 mm long, 3.1 mm wide; brown in basal half, more yellow in distal half; short anterior

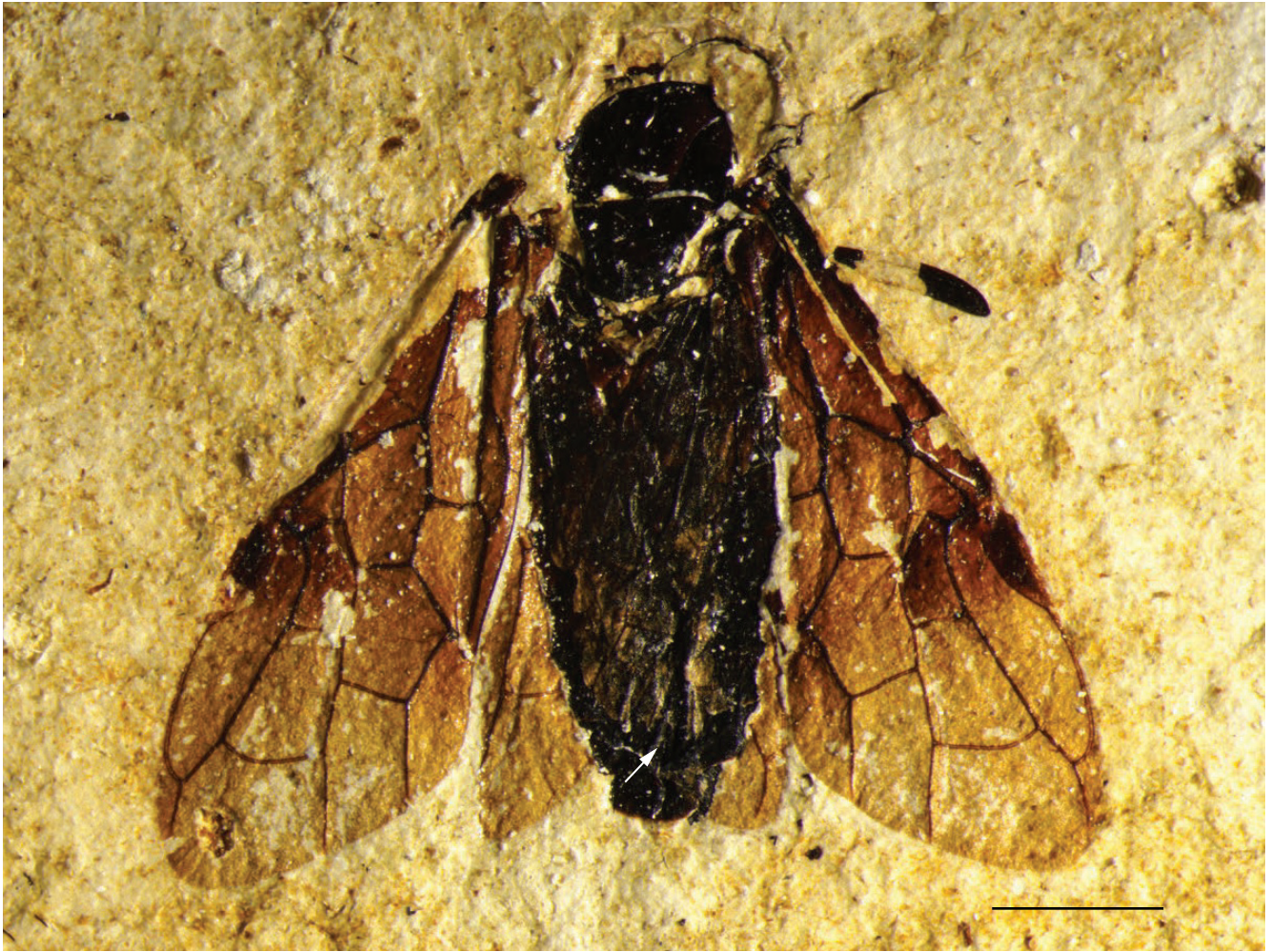


FIG. 1. — *Spinarge miocenicus* n. sp., holotype MDA.R2024.8.1. Photograph of general habitus. **White arrow**, median process on the 5th tergum, poorly preserved. Scale bar: 2 mm.

Sc branch (intercostal vein) located slightly anterior to Sc+R and 1M junction; pterostigma 1.5 mm long, 0.4 mm wide, strongly arched along cell 2R1, slightly arched along anterior wing margin; M+Cu slightly curved; 1M slightly longer than 1Cu, curved basally; R clearly deviating between junctions of Sc and 1M; fusion of R with M exceedingly short; R meeting 2M much less than halfway between short anterior branch of Sc and pterostigma; 2M slightly longer than 1rs-m; Rs emerging at pterostigmal base; 2Rs strongly curved, shorter than 3Rs; no r-rs crossvein; cell 2R1 with a distal abscissa ending in wing margin; cell 1R1 trapezoidal, 0.5 mm long; cell 1Rs 1.2 mm long, enclosed distally by subvertical 2rs-m (the latter slightly longer than 1rs-m); 3M shorter than 4M; cell 2Rs 1.5 mm long, distinctly wider along curved 3rs-m; 1Cu and 2Cu nearly straight, 1Cu as long as 2Cu; 1m-cu meeting Cu at an angle of ca 90°, 1M and 1m-cu converging; cell 1Cu elongate, longer than cell R; 1cu-a (nervulus) located at middle of cell 1M, distinctly distad point of fusion of R with 1M; cell 2Cu long, trapezoidal; cell 2M fully enclosed distally by long and slightly sinusoidal 2m-cu; 1A long, nearly straight; basal anal cell 1A distally closed; a long fusion of

2A+3A with 1A; cell 2A quite long. Hind wings only partly visible, 6.8 mm long, brown in basal half and more yellow in distal half; cell R1 with a distal abscissa not ending in wing margin; cell Rs distinctly longer than cell 1M, both distally closed. Abdomen 5.7 mm long, 2.8 mm wide; fifth tergum with a long median process; genitalia not visible.

DISCUSSION

Following the key to symphytan families of Goulet & Hubert (1993), the current fossil falls within the Argidae *sensu lato* because of the following characters: mesoscutellar appendage fused to mesoscutellum; forewing without 2r-rs; forewing base of 2A+3A present; antenna with one flagellomere. In addition, the forewing venation is quite similar to those of extant Argidae (Fig. 3: *Arge meliosmae* Shinohara & Hara, 2011).

Malagón-Aldana *et al.* (2021) separated the genus *Zenarge* Rohwer, 1918 from other Argidae, elevating the Zenarginae Rohwer, 1918 as family Zenargidae Rohwer, 1918. The new fossil differs from *Zenarge* in a shorter 2A+3A,



Fig. 2. — *Spinarge miocenicus* n. sp., holotype MDA.R2024.8.1: **A**, photograph of third antennomere (note that part of the antennomere is missing) and forewing; **B**, with nervation indications. Abbreviations: see Material and methods. Scale bar: 2 mm.

distal part of Rs as long as Rs+M (vs quite shorter), Rs+M making a strong angle with cell R1 (Malagón-Aldana *et al.* 2021: fig. 5).

The Argidae *sensu stricto* are currently divided into Arginae Konow, 1890, Athermantinae Benson, 1938, Atomocerinae Benson, 1938, Dielocerinae Benson, 1938, Erigeninae Rohwer,

1911, and Sterictiphorinae Rohwer, 1911 (Taeger *et al.* 2010, 2018). The Erigleninae, Atomacerinae, and Sterictiphorinae have the forewing cell 2R1 and the R1 of hind wing open apically, unlike the new fossil (Benson 1938; Malaise 1937, 1955; Smith 1969). The presence of the intercostal vein also excludes affinities with the Sterictiphorinae (Benson 1938,



FIG. 3. — *Arge meliosmae* Shinohara & Hara, 2011, MNHN.FEY38826. Photograph of general habitus in dorsal view, together with the cocoon from which the imago emerged. Scale bar: 1 mm.

Smith 1969; Togashi 1990, 1997). The Neotropical Dielocerinae also have the hind wing cell R1 opened (Fernández & Sharkey 2006).

Benson (1938) first separated the Athermantinae from the Arginae on the basis of the presence vs absence of preapical spurs on the meso- and metatibiae (but see Liston *et al.*, 2017). Both groups share with the new fossil the presence of the intercostal vein and the forewing radial cell closed apically. In the Athermantinae, *Pampsilota* Konow, 1899 has nearly the same forewing venation as the new fossil (Koch 2006; Liston *et al.* 2017), as do the genera *Athermantus* Kirby, 1882 and *Pseudosinarge* Saini, Thind & Kaur, 1998 (Wei 1997; Saini *et al.* 1998). *Pampsilota* and *Athermantus* have a third antennomere much longer compared to its width than in the fossil (Liston *et al.* 2017; Luo *et al.* 2019). *Athermantus* also has the forewing cell 2R1 distinctly broadened basally, not less than half breadth of cell 2R1, unlike in the new fossil. *Pseudosinarge* differs from the new fossil in the much longer

and thin third antennomere, point of fusion of R with 1M situated opposite 1cu-a, and an abscissa of forewing cell 2R1. *Cibdela* Konow, 1899 also has R+M as long as or longer than the anterior branch of Sc. *Sinarge* Forsius, 1934 and *Tanyphatnidea* Rohwer, 1912 have R+M punctiform, which is unlike the new fossil.

Within the Arginae, the tribes Argini Konow, 1890 and Scobinini Benson 1963 are separated on the basis of characters not visible in this fossil (leg and head structures) (Benson 1963). In the Scobinini, the Australian genus *Antargidium* Morice, 1919 is characterized by characters not visible in the new fossil (Benson, 1963), and they share an open appendiculate cell in hind wing (Benson 1934). Nevertheless, *Antargidium* has a third antennomere only twice as long as broad (Benson 1934). *Scobina* Lepeletier de Saint Fargeau & Audinet-Serville, 1828 differs from the new fossil in the exceedingly weak angle between R1 and R+M (Smith 2008: figs 1-2).



FIG. 4. — *Spinarge metallica* Klug, 1834, MNHN.FEY42476. Photograph of general habitus of female in dorsal view. Third antennomeres and right forewing missing. Scale bar: 1mm.

Following the key to Palaearctic and Oriental genera of Argidae (Wei 1997: 296-297), the new fossil would fall in the Argini because of the following characters: short anterior SC branch (intercostal vein) present; forewing and hind wing cells R1 closed with an appendiculate cell. In this group affinities with *Alloscenia* Enderlein, 1919 are excluded because the anterior branch of Sc is well defined, not faint. *Kokujewia* Konow, 1902 has the forewing 1rs-m absent and the basal anal cell open, as in *Asiarge* Gussakovskij, 1935. *Sjoestedtia* Konow, 1907 has the forewing basal anal cell absent (Liston *et al.* 2017). *Triarge* Forsius, 1931 has the forewing 2rs-m absent (Koch, 2006; Liston *et al.* 2017). *Pseudarge* Gussakovskij, 1935 has the forewing basal anal cell open distally and R+M distinctly longer than in the new fossil (Koch & Goerger 2008).

Arge Schrank, 1802 (*Calarge* Enslin, 1911 is a junior synonym of *Arge* after Liston *et al.* (2017)) and *Chyparge* Pasteels, 1963 have very similar wing venation (Pasteels 1963). The new fossil has a forewing venation similar to those of the species in *Arge* (Choi *et al.* 2016). *Spinarge* Wei, 1998 shares with the new fossil R+M shorter than the anterior branch of Sc and the venation of the new fossil is quite similar to those of the species in this genus (Liu *et al.* 2022). Furthermore, the new fossil has a long median process on the fifth tergum (Fig. 1), typical of males in the genus *Spinarge* (Hara & Shi-

nohara 2006: fig. 7). Liu *et al.* (2022: 231) indicated that '[t]he validity of this genus needs further study on the generic phylogeny of Arginae'. *Spinarge* seems to be close to *Arge*. The different species of *Spinarge* are separated on the basis of wing coloration, viz. yellowish orange in *S. chrysoptera* vs hyaline, dark, yellowish or brownish in the other species (Hara & Shinohara 2006). The new fossil has brown-yellow wings, but their present coloration may be different from that of the living animal during the Miocene. It is thus nearly impossible to specify its exact affinities in the genus.

Extant representatives of the genus *Spinarge* include three Chinese species and 11 Palearctic species. The only species reported in France (South of France, Ariège) is *Spinarge metallica* Klug, 1834 (Hara & Shinohara 2006; Noblecourt 2020), a country-wise rare species (Fig. 4). Species of *Spinarge* live on broad-leaved trees such as *Betula* L., 1753, *Prunus* L., 1753, *Sorbus* L., 1753, *Tilia* L., 1753 (Hara & Shinohara 2006; Savina & Chevin 2012; Liu *et al.* 2022). The yellow larvae of *Spinarge metallica* were observed in two localities (Aulus-les-Bains and Bethmale, Ariège piedmont) by Henri Savina on July 2010, and were feeding on *Betula* (Savina & Chevin, 2012). At least *Betula* and *Tilia* have been recorded from the outcrop of Saint-Bauzile (Brice 1965; Riou 1996), representing potential host plants for the fossil species occurring in this paleobiota.

CONCLUSION

Even though several extant genera in Arginae and Athermantinae have wing venations similar to the new fossil, we could discriminate them and attribute the extinct species to *Spinarge* on the basis of the structure of the abdominal tergum. Although we lack significant characters to separate the fossil from the extant species in this genus, we propose to name it because it is the first known fossil representative of an extant genus of Arginae. *Spinarge miocenicus* n. sp. is the earliest occurrence of the genus *Spinarge*, 7.54 Mya, and may serve as a calibration point for phylogenetic analyses.

It is rather remarkable that the new fossil comes from an outcrop quite close to that from where *Mioarge azari* was recovered. The diatomite outcrop of montagne d'Andance is dated around 7.54 ± 0.06 Mya (Pastre *et al.* 2004), while the basaltic Coiron Massif (including the interstratified diatomite of Mont-Charay) would be slightly younger, around 6 Mya. The sediments in the two outcrops are quite different. In the Mont-Charay outcrop the diatomite is exceptionally hard and filled with a stacking of numerous angiosperm leaves, while at the montagne d'Andance outcrop the matrix is much softer and there is no such stacking of leaves. The localities may correspond to two different paleolakes, though paleoenvironment and paleoclimate were probably similar. It remains puzzling to find so few fossil Argidae in Miocene outcrops. The scarcity of Argidae in the French Miocene outcrops may mirror the scarcity of species diversity among existing argid sawflies in France.

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