beams does not change the beam amplitude because Δω is a small fraction of the bandwidth of typical ultrasound transducers. For instance, the bandwidth of the ultrasound transducer may be greater than 1 MHz, whereas Δω might be around 10 kHz.
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# Flower-Associated Brachycera Flies as Fossil Evidence for Jurassic Angiosperm Origins

Dong Ren

**Pollinating insects played a decisive role in the origin and early evolution of the angiosperms. Pollinating orthorrhaphous Brachycera fossils (short-horned flies) collected from Late Jurassic rocks in Liaoning Province of northeast China provide evidence for a pre-Cretaceous origin of angiosperms. Functional morphology and comparison with modern confamilial taxa show that the orthorrhaphous Brachycera were some of the most ancient pollinators. These data thus imply that angiosperms originated during the Late Jurassic and were represented by at least two floral types.**

The ancestors and time of appearance of angiosperms remain obscure (*1*–*5*). The earliest fossil evidence of nectar secretory tissue is provided by the Santonian-Campanian flowers from Sweden (*6*). The oldest angiosperm pollen grains have been found in Israel, in strata of Early Cretaceous time (Late Valanginian to Early Hauterivian) (*7*). The earliest recognized angiosperm inflorescences have been recovered from rocks of Late Hauterivian Age at Jixi, China (*8*).

The origin and early evolution of flowering plants are probably related to the coevolution of insect pollinators (*9*–*11*). Cretaceous and Tertiary flower-visiting insects were diverse and include an impressive variety of Coleoptera (beetles), Diptera (true flies), Lepidoptera (moths), Hymenoptera (wasps and bees), and other less diverse taxa, such as Thysanoptera (thrips). Some highly faithful pollinators such as butterflies and cyclorraphan flies appeared in the middle Tertiary (*12*). Few pre-Cretaceous pollinating insects are known. Small insects, especially flies and parasitoid wasps, may have been important then and thus in the origin and evolution of angiosperm pollination (*13*). Here I describe Late Jurassic pollinating orthorrhaphous Brachycera with well-preserved nectaring mouthparts.

Early pollinating insects have long tubular mouthparts designed for feeding on or extracting nectar from long tubular flowers (*9*–*11*). Other examples of Jurassic insects having this type of mouthpart include nemonychid weevils, which probably fed on bennettitaleans or cycads (*14*), and a monotrysian Lepidopteran with a siphonate proboscis (*15*, *16*).

I collected the fossil Brachycera at a locality near Beipiao City, Liaoning Province, China, from nonmarine sedimentary rocks of the Yixian Formation (*17*). These rocks contain abundant remains of insects (*18*, *19*), fishes, conchostracans, reptiles, birds, and mammals of Late Jurassic (approximately Tithonian) age (*20*).

Extant Brachycera comprise a wide variety of flower visitors (*9*, *10*). Most orthorrhaphous Brachycera feed on flowers as adults. The new fossil orthorrhaphous Brachycera (*19*) include deer flies (Pangoniinae of Tabanidae), flower-loving flies (Apioceridae), and tangleveined flies (Nemestrinidae).

Most extant pangoniines are exclusively flower feeders (*21*). They often hover over flowers on the borders of dense vegetation (*9*, *10*). Both males and females subsist on nectar and on the juice of flowers. The female proboscis of some species is flexible and suitable only for imbibation of nectar (*22*, *23*), and is three or four times the length of the body. One of the Jurassic fossils, described as *Palaepangonius eupterus* Ren, 1998, includes a complete body and an associated well-developed long proboscis (Fig. 1) (*19*). These fossils provide direct evidence for the mid-Mesozoic diversification within Tabanidae of subclades with nectaring mouthparts. *Palaepangonius* not only provides evidence for the extraction of nectar from flowers or flowerlike structures but also demostrates that the Pangoniinae have existed since the Late Jurassic. Another brachyceran clade, the Nemestrinidae, are important pollinators of flowers (*9*, *10*). Modern members are often collected when feeding on blossoms or hovering over them while imbibing nectar (*24*). Many Late Jurassic examples were collected and were described as *Protonemestrius jurassicus* Ren, 1998. These had a proboscis about 5.2 mm long, which would have been especially suitable for visiting long tubular flowers (Fig. 2). *Florinemestrius pulcherrimus* was also an important flower visitor. Its long stout proboscis seems to have been suited to extracting nectar from open or short tubular flowers (Fig. 3). Similar proboscides have been reported from the Late Jurassic of Karatau, Kazakhstan (*25*).

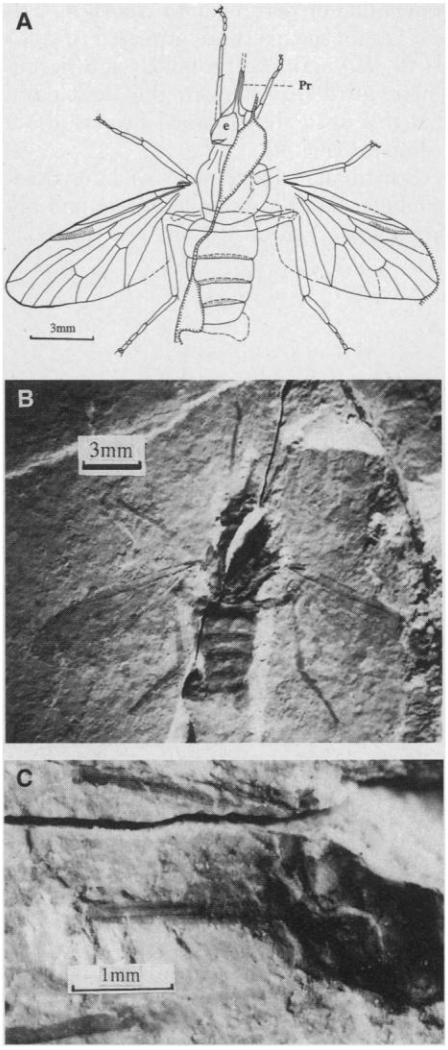

**Fig. 1.** *Palaepangonius eupterus* Ren, 1998. (**A**) Camera lucida drawing of specimen LB97017. (**B**) Photograph of body, LB97017. (**C**) Photograph of proboscis, LB97017. Abbreviations: e, compound eye; Pr, proboscis.

A representative of the stem group of the Apioceridae has also been found (Fig. 4) and called *Protapiocera megista* Ren, 1998. Its body bears dense hairs, a feature used in

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National Geological Museum of China, Xisi, Beijing 100034, China.

confamilial modern taxa for collecting pollen. Extant members are attracted to flowers (*9*, *10*) and feed on pollen and nectar. These attributes support the conclusion that this fossil short-horned fly was also a pollinator (Fig. 4).

Structural features such as long fluid-imbibing mouthparts and densely and appropriately positioned hairs on the body surface imply that the behavior of some Late Jurassic brachyceran flies was related to flower visiting and pollination. Insects with nectaring mouthparts would have been adapted to consume nectar from flowers, extrafloral nectaries, or flowerlike structures such as those documented from contemporaneous and fossil anthophytes. Such structures today are associated with cross-pollination (*6*).

Apart from the three fossil taxa mentioned above, many other short-horned flies, particularly the Stratiomyidae, Athericidae, Vermileonidae, Mydidae, Acroceridae, Mythicomyiidae, Bombyliidae, Empididae, and Dolichopodidae, are known to feed on modern flowers (*9*, *10*, *26*). Species from these taxa are primarily adapted to consume pollen and nectar and have an effective role in pollination. This interaction is particularly important because the fossil records of these flies also extend to the Late Jurassic and early Cretaceous (*27*, *28*) (Fig. 5).

These paleoentomological records indicate that the oldest known anthophilous orthorrhaphous Brachycera existed during the Middle to Late Jurassic. During the Late

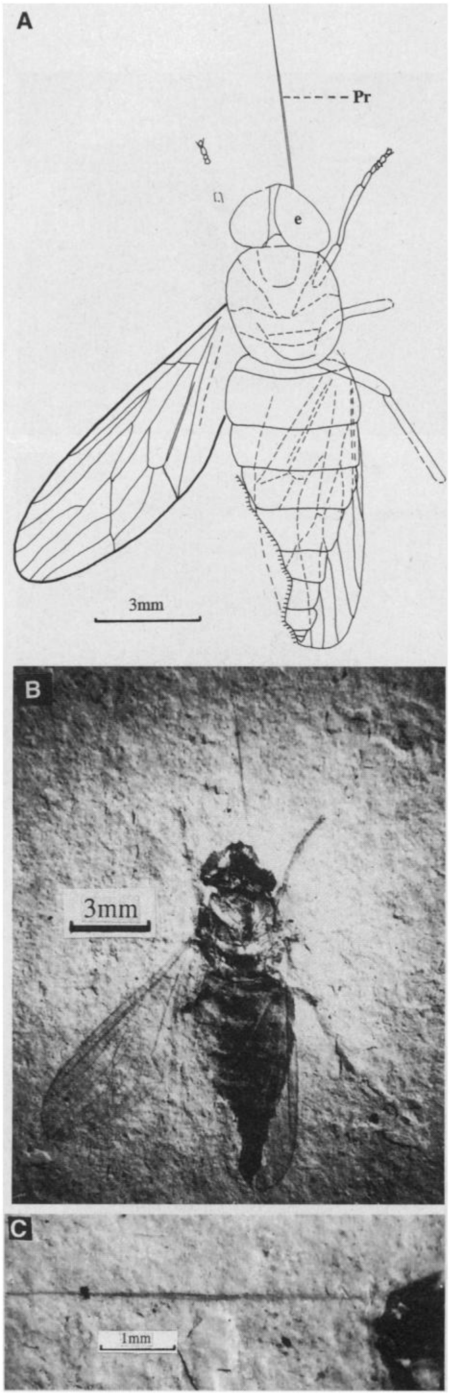

**Fig. 2.** *Protonemestrius jurassicus* Ren, 1998. (**A**) Camera lucida drawing of specimen LB97005. (**B**) Photograph, LB97005. (**C**) Photograph of proboscis, LB97005.

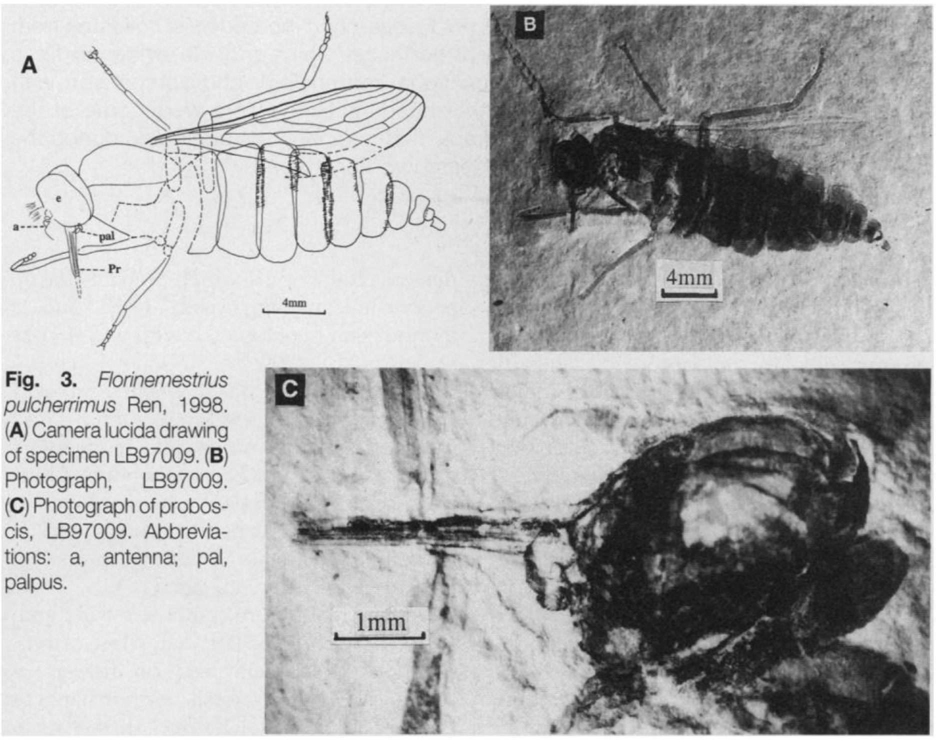

**Fig. 3.** *Florinemestrius pulcherrimus* Ren, 1998. (**A**) Camera lucida drawing of specimen LB97009. (**B**) Photograph, LB97009. (**C**) Photograph of proboscis, LB97009. Abbreviations: a, antenna; pal, palpus.

**Table 1.** Geographical distribution of Middle and Late Jurassic main orthorrhaphous Brachycera. Solid circles indicate locations where fossils were found.

| Family | Genus (*n*) | Species (*n*) | Liaoning | Shandong | Siberia | Karatau | Solnhofen |
|---|---|---|---|---|---|---|---|
| Protobrachycerontidae | 1 | 1 | | | | | + |
| Archisargidae | 2 | 5 | | | | + | |
| Kovalevisargidae | 2 | 2 | | | | + | |
| Palaeostratiomyiidae | 1 | 1 | | | | + | |
| Eomyiidae | 1 | 1 | | | | + | |
| Xylomyidae | 1 | 1 | | + | | | |
| Eostratiomyiidae | 1 | 1 | | | | + | |
| Rhagionidae | 16 | 16 | + | + | + | + | |
| Tabanidae | 3 | 3 | +● | | | | |
| Acroceridae | 1 | 1 | | | | + | |
| Nemestrinidae | 6 | 11 | +● | + | | + | + |
| Bombyliidae | 1 | 1 | | | + | | |
| Vermileonidae | 1 | 1 | | | + | | |
| Eremochaetidae | 4 | 5 | + | | | + | |
| Protempididae | 2 | 4 | + | | | + | |
| Protomphralidae | 1 | 1 | | | | + | |
| Protapioceridae | 1 | 2 | +● | | | | |
| Mythicomyiidae | 1 | 1 | | | + | | |

Jurassic, the orthorrhaphous Brachycera underwent an explosive radiation (*29*, *30*). Hitherto, about 46 genera and 58 species within 18 families have been reported (*19*, *27*, *31*, *32*) (Table 1). Most of these fossils have been recovered from Late Jurassic rocks of Eurasia, principally from northeast China, Karatau, Baissa, and Siberia.

Although anthophytes (including Bennettitales, Gnetales, and angiosperms) also have flowerlike reproductive structures, the flower is one of the defining characteristics of angiosperms. Insects probably visited the flowers of primitive angiosperms mainly because of their pollen and nectar (*1*, *10*). I conclude that the presence of nectar-collecting Brachycera during the Late Jurassic provides direct evidence of the occurrence of nectariferous angiosperms during this time interval. This conclusion is supported by a tricarpous female angiosperm reproductive fossil (*33*) recently collected from the same bed that contains the Brachycera fossils. It is also possible that these pollinating short-horned flies were pollinators of nonangiospermous anthophytes. Comparative morphology of the mouthparts suggests that at least two types of general morphotypes of nectar-feeding proboscides of orthorrhaphous Brachycera existed during the Late Jurassic. One was a stout proboscis, typical of *Palaepangoninius euptera* and *Florinemestrius pulcherrimus*, suitable for feeding on open and short tubular structures that contained fluid. Another was a slender proboscis that was suited to extracting nectar from long tubular structures. In view of the presence of early (primitive) pollen feeders or pollinators with mandibulate mouthparts (*14*), the orthorrhaphous Brachycera pollinators with nectar-imbibing mouthparts seem to have been considerably advanced by the Late Jurassic. They were sufficiently diverse by the Late Jurassic that an earlier origin of angiosperms seems possible.

These fossils thus imply that either angiosperms originated during the Middle Jurassic and flourished in the Late Jurassic or, which is less likely, that other clades of anthophytes were responsible for the pollination syndromes exhibited by these orthorrhaphous Diptera. This possibility also can be supported by the final phase of mouthpart class expansion that occurred during the Late Jurassic and perhaps as early as the early Middle Jurassic, in which surface-fluid–feeding mouthpart classes evolved; these became important during the subsequent ecological expansion of angiosperms (*12*). The origin and diversification of the orthorrhaphous Brachycera during the Jurassic may offer support for either the hypothesis of a Middle Jurassic origin of angiosperms (preferred) or the existence of anthophyte seed plants with reproductive biologies that required pollinating insects, similar to those documented for extant cycads and gnetaleans (less likely). The paleogeographical distribution of anthophilous orthorrhaphous Brachycera fossils from the Late Jurassic (Table 1) and other fossil insects, such as scorpionflies of the family Bittacidae (*20*), indicate that central Asia (China and Siberia) split from Neopangea (Pangea without China and Siberia) not earlier than the Middle Jurassic (*34*). If angiosperms are monophyletic, they should have originated no later than the Middle Jurassic; otherwise, their ancestors could not have dispersed to the other continents. These paleogeographical patterns, together with the observation that most extant primitive angiosperms occur in the southwestern Pacific (*5*), imply that the earliest angiosperms originated in eastern Laurasia.

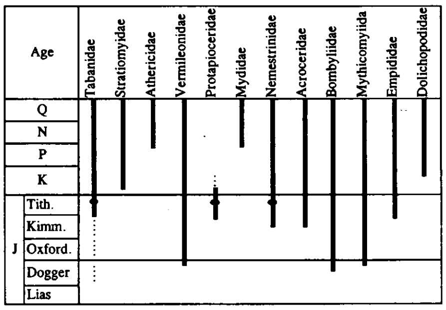

**Fig. 5.** Stratigraphic distribution of flower-associated orthorrhaphous Brachycera. Solid ellipses indicate the fossils of this study. Abbreviations: J, Jurassic; K, Cretaceous; N, Neogene; P, Paleogene; Q, Quaternary.

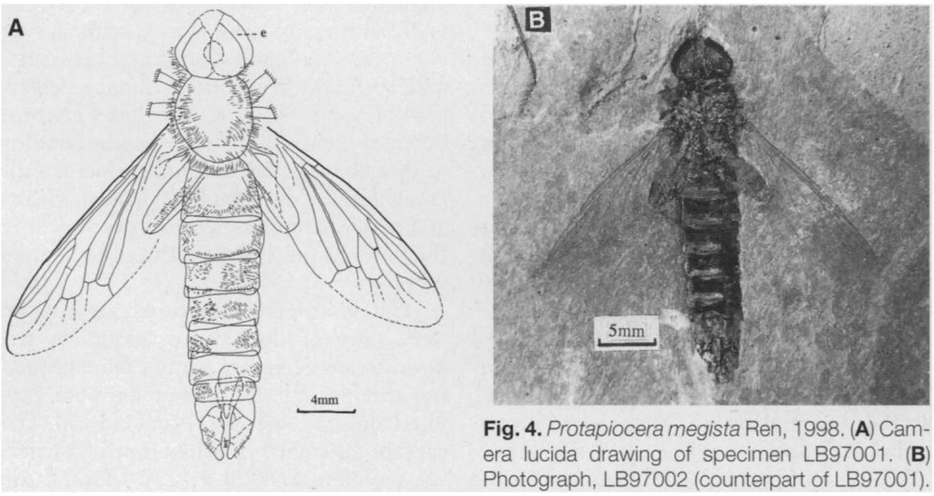

**Fig. 4.** *Protapiocera megista* Ren, 1998. (**A**) Camera lucida drawing of specimen LB97001. (**B**) Photograph, LB97002 (counterpart of LB97001).

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# Capture of Interplanetary and Interstellar Dust by the Jovian Magnetosphere

Joshua E. Colwell,* Mihály Horányi, Eberhard Grün

**Interplanetary and interstellar dust grains entering Jupiter's magnetosphere form a detectable diffuse faint ring of exogenic material. This ring is composed of particles in the size range of 0.5 to 1.5 micrometers on retrograde and prograde orbits in a 4:1 ratio, with semimajor axes $3 < a < 20$ jovian radii, eccentricities $0.1 < e < 0.3$, and inclinations $i \lesssim 20$ degrees or $i \gtrsim 160$ degrees. The size range and the orbital characteristics are consistent with in situ detections of micrometer-sized grains by the Galileo dust detector, and the measured rates match the number densities predicted from numerical trajectory integrations.**

The dust detector on the Galileo spacecraft (DDS) measures impacts of dust particles and gives estimates of the masses and the velocities of the grains (*1*). Grains were detected by the DDS inside about 20 Jovian radii ($R_J$; 1 $R_J$ = 7.1492 × $10^4$ km) on prograde and retrograde orbits around Jupiter (*2*). These grains are at least several tenths of a micrometer in radius.

During Galileo's second orbit, eight "large" dust grains were detected inside 20 $R_J$, and, based on the rotation angle of the detector and the impactor speeds, most of these particles follow retrograde orbits (Fig. 1). The impact rate of these particles on the detector was $I \approx 3 \times 10^{-5}$ s$^{-1}$. Similar numbers were seen on subsequent orbits. The number density of uniformly distributed particles on circular Keplerian orbits necessary to explain this impact rate is $n_{DDS} \approx I/\sigma(f_p/v_p + f_r/v_r)$, where $\sigma$ is the effective cross section of the DDS, $f_p$ and $f_r$ are the fraction of detected grains on prograde and retrograde orbits, respectively, and $v_p$ and $v_r$ are the relative velocities. We used the physical cross section $\sigma = 10^3$ cm$^2$ (*3*). Using circular Keplerian orbits for the dust at 15 $R_J$ (roughly the middle of the region where the large grains were detected), $n_{DDS} \approx 10^{-14}$ cm$^{-3}$, which implies a mean optical depth of $\tau_{dust} \lesssim 10^{-11}$. Captured interstellar and interplanetary grains and the jovian moons are potential sources of these grains.

To determine these sources, we integrated the trajectories of dust grains in Jupiter's magnetosphere, using the same numerical approach as in our earlier studies (*4*). The grains move under the influence of Jupiter's and the sun's gravity, solar radiation pressure, and the Lorentz force. The grain's charge is time-dependent and is calculated from the current balance equation $dQ_{dust}/dt = \Sigma_i I_i$, where $I_i$ is electron and ion thermal currents and secondary and photoelectron emission currents. The currents are all functions of the grain's velocity and position in the magnetospheric plasma and of the instantaneous charge on the grain which is assumed to have a density of 1.0 g cm$^{-3}$.

Our magnetospheric model uses Voyager plasma parameters (*5*–*6*) outside 5 $R_J$ and an "engineering" plasma model (*7*) inside 5 $R_J$. The magnetic field is the O6+ current sheet model, assuming rigid corotation up to a distance of $R = 50$ $R_J$ from Jupiter's center (*8*). Outside 50 $R_J$, we assumed solar wind conditions and reversed the azimuthal component of the magnetic field in 14-day intervals to imitate the sector structure of the interplanetary magnetic field (Fig. 2). There is no magnetotail or bow shock in this model. Grains were started with an initial potential of +5 V, the equilibrium value in the solar wind (*9*), at a distance of 100 $R_J$ from Jupiter. We followed the particles until they either hit Jupiter, were more than 300 $R_J$ from Jupiter, or 5 (Earth) years had passed. The fraction of captured grains and their orbital parameters enable us to estimate the number density of dust orbiting Jupiter from each of the possible sources.

Dust particles in the solar wind develop a positive charge and experience a retarding force entering Jupiter's magnetosphere because of the outward-pointing, corotating jovian electric field. On the outbound portion of their trajectory, dust grains regain some, but not all of their energy because of charging time delays. The grains' dynamical time scales are shorter than the charging time scales, so in general, they are not in charge equilibrium with the plasma in the jovian magnetosphere (*10*). Simultaneously, their angular momentum decreases. Similarly, grains within the jovian magnetosphere can also lose or gain energy and angular momentum leading to rapid changes of grain semimajor axis and eccentricity. The process is dependent on the size of the grains, which determines their charge-to-mass ratio and susceptibility to radiation pressure and the Lorentz force. Particles that experience this rapid loss of energy and angular momentum become captured in Jupiter's magnetosphere, where their lifetime is limited by sputtering, plasma drag, or collision with a moon or Jupiter (9).

Measurements of dust impacts by Galileo and Ulysses during interplanetary cruises showed that beyond about 3 astronomical units (1 AU = 1.49 × $10^{13}$ cm) the flux of submicrometer-sized dust particles is dominated by interstellar grains, with a flux of $F_{is} = 10^{-8}$ cm$^{-2}$ s$^{-1}$ in the same direction as the local interstellar wind (*11*). The mean mass of these particles is $10^{-12.5 \pm 1.5}$ g, and their approach speed to Jupiter varies from about 13 to 39 km s$^{-1}$ as Jupiter orbits the sun.

We computed the trajectories of grains with sizes of 0.4 to 1.0 μm in 0.1-μm increments, with 10,000 particles at each size (*12*). The grains were started with impact parameters randomly distributed between 0 and 10 $R_J$, with a uniform surface density (*13*). Trajectories were integrated at three different approach velocities corresponding to upstream (Jupiter's orbital velocity antiparallel to the dust velocities), downstream, and cross-stream geometries with respect to the flow of interstellar gas through the solar system.

The most grains captured at any size were nine of the 0.6-μm grains in the downstream geometry. In the same geometry, three of the 0.5-μm grains were captured and one each at 0.7 and 0.8 μm. The capture efficiency as a function of particle size therefore peaks at 9 × $10^{-4}$ for 0.6-μm

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J. E. Colwell and M. Horányi, Laboratory for Atmospheric and Space Physics, University of Colorado, Boulder, CO 80309-0392, USA.
E. Grün, Max Planck Institut für Kernphysik, 6900 Heidelberg, Germany.

*To whom correspondence should be addressed. E-mail: colwell@casper.colorado.edu