



# Middle Paleolithic complex technology and a Neandertal tar-backed tool from the Dutch North Sea

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We report the discovery of a 50,000-y-old birch tar-hafted flint tool found off the present-day coastline of The Netherlands. The production of adhesives and multicomponent tools is considered complex technology and has a prominent place in discussions about the evolution of human behavior. This find provides evidence on the technological capabilities of Neandertals and illuminates the currently debated conditions under which these technologies could be maintained. <sup>14</sup>C-accelerator mass spectrometry dating and the geological provenance of the artifact firmly associates it with a host of Middle Paleolithic stone tools and a Neandertal fossil. The find was analyzed using pyrolysis-gas chromatography-mass spectrometry, X-ray micro-computed tomography, and optical light microscopy. The object is a piece of birch tar, encompassing one-third of a flint flake. This find is from northwestern Europe and complements a small set of well-dated and chemically identified adhesives from Middle Paleolithic/Middle Stone Age contexts. Together with data from experiments and other Middle Paleolithic adhesives, it demonstrates that Neandertals mastered complex adhesive production strategies and composite tool use at the northern edge of their range. Thus, a large population size is not a necessary condition for complex behavior and technology. The mitigation of ecological risk, as demonstrated by the challenging conditions during Marine Isotope Stage 4 and 3, provides a better explanation for the transmission and maintenance of technological complexity.

Late Pleistocene | adhesive | birch bark tar | hafting | risk mitigation

We report the analysis of a flint flake embedded in a thick black residue discovered on the Zandmotor North Sea beach nourishment near The Hague, The Netherlands (Fig. 1A and *SI Appendix*, Fig. S1). The find has the same geological provenance as a Neandertal fossil discovered in 2009 (1). A direct accelerator mass spectrometry (AMS) radiocarbon date of ~50 ka cal BP confirms its Marine Isotope Stage (MIS) 3 Middle Paleolithic (MP) origin. Additional chemical analysis revealed that the flake was hafted with birch bark tar. As only 2 other MP sites have yielded chemically confirmed birch tar, the Zandmotor discovery represents a major increase in the number of Neandertal tar samples.

The production of birch tar is considered one expression of Neandertal and other Old World hominin complex technology (2) for which evidence is being increasingly documented (3). Examples are recent advances in our understanding of Neandertal pyrotechnology (4) and the use of multicomponent tools that rely on hafting and adhesives (5, 6). However, despite this mounting evidence, the degree of Neandertal technological innovation is still under debate (7, 8). This discussion is complicated, as it is not always specified why a certain behavior or technology is considered complex. Furthermore, the necessary conditions for the development and maintenance of complex technology, besides a large brain and a successful social transmission mechanism, are

unresolved. Proposed conditions include population size (9, 10), degree of residential mobility (11), degree of task specialization (12), and ecological risk (13).

Here we compare MP tar finds, including Zandmotor, to our experimental data. In doing so we are able to reconstruct the technological procedures used in birch tar production, allowing us to better identify complexity. The Neandertal tar finds provide evidence of a complex technology so engrained in their behavior that it was maintained at the limits of their ecological tolerance: glacial northwestern Europe. We evaluate factors driving the maintenance of complex technology, allowing us to draw conclusions as to the socioeconomic organization of Neandertals in particular but that are also applicable to other past human populations.

## Late Pleistocene Adhesives and the Relevance of Birch Tar

The high profile of adhesive technology and birch tar manufacture in discussions about Neandertals is problematic given the so

### Significance

We report the discovery of a 50,000-y-old Neandertal tar-hafted flint tool found off the present-day Dutch coastline. The production of birch tar adhesives was a major technological development, demonstrating complex Neandertal technology and advanced cognitive ability. The rarity of Middle Paleolithic adhesive finds makes each new discovery crucial for improving our understanding of Neandertal lifeways. We demonstrate that birch tar was a routine part of the Neandertal technological repertoire. In addition, the complex know-how required for adhesive production in northwestern Europe during Marine Isotope Stage 4 and 3 was maintained in small groups leading highly mobile lives. This suggests a degree of task specialization and supports the hypothesis that ecological risk drives the development of complex technology.

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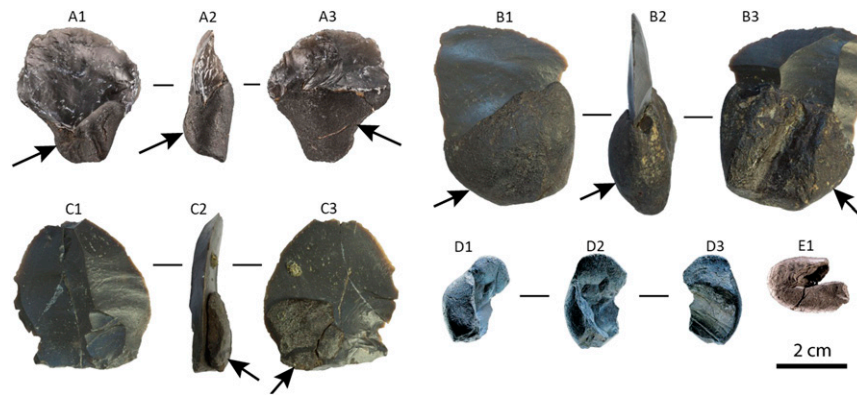
Data deposition: Our X-ray micro-CT scan data have been made public at the 4TU.Centre for Research Data, <https://doi.org/10.4121/uuid:0d7f284a-93ae-4d75-8361-984df49c2a4e>.

See Commentary on page 21966.

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**Fig. 1.** Images of all securely identified MP birch tar finds. (A) Zandmotor. (B and C) Campitello flakes. (D) Königsau A. (E) Königsau B. (A) Image courtesy of Frans de Vries (photographer). (B and C) Image courtesy of the Museum of Natural History, Università di Firenze (Specimen IGF 17520). (D and E) Image courtesy of the Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt/Juraj Lipták.

few well-characterized and dated archeological finds. The earliest known evidence of birch tar adhesives dates to a minimum age of 191 ka and consists of 2 unretouched flakes partly covered in birch bark tar from Campitello, Italy (14). At Königsau, Germany, 2 birch bark tar objects were found dating to >48 ka and >43 ka calBP (15). Other unambiguous MP adhesive evidence consists of bitumen in Syria and pine resin in Italy applied to stone tools for hafting (5, 16, 17) (Fig. 1 and Table 1).

Adhesives also developed in southern Africa. Here residues were observed on Middle Stone Age tools dating to at least 100 to 80 ka (22). They consist of conifer (*Podocarpus*) resin and tar (22, 23) (Table 1). Authorship of the African adhesives cannot be reliably determined because of the survival of late archaic forms and the limited number of associated taxonomically diagnostic fossils (25, 26). Nevertheless, adhesive technology was used in both Africa and Eurasia by varied hominin populations, and it may be a shared behavior among highly encephalized Pleistocene populations.

The production of adhesives is considered complex when the process is multisteped and requires forward planning, knowledge of materials, and abstraction (27, 28), such as when combining disparate ingredients or synthesizing a new material. For example, Neandertals mixed pine resin with beeswax (5) and bitumen with quartz and gypsum (16) and distilled tar from birch bark. Similarly, African humans combined resin with quartz and ochre (22, 29) and made *Podocarpus* tar (23). Whereas compound adhesives are made through an additive process, destructive distillation is transformative and concealed. The latter is only observed again with the invention of pottery and, later still, metallurgy. The complex procedural character of tar distillation, combined with recent experimental and archaeological finds, make birch tar a unique window into the development and maintenance of complex technology.

### The Zandmotor Find

**Geological Setting and Paleoenvironmental Context.** The artifact was found in 2016 by W. van Wingerden on the Zandmotor beach, The Netherlands (*SI Appendix*, Fig. S1). This beach was constructed in 2011 using dredged sands from 2 permit areas (Q16F and H), located 9 to 13 km offshore (Fig. 2). Here a wide range of archeological and paleontological remains from the Late Pleistocene and the Holocene were brought to the surface (30, 31). The provenance of the sands is documented in the dredging ships' logs and by the Dutch Ministry of Infrastructure and Water Management.

The Zandmotor dredging exploited medium- to coarse-grained sands, deposited on the Last Glacial Rhine-Meuse braid plain. Composing the majority of the dredged interval in permit area

Q16 are medium- to coarse-grained fluvial sands of the Rhine-Meuse valley, Units B2 and B4, dating to 70 to 30 ka (32). The full thickness of Unit B4 was mined, including reworked portions of Unit B2. The source bed stratigraphy is confirmed by the Zandmotor malacological and paleontological find assemblage (Fig. 2 and *SI Appendix*, Fig. S2; *SI Appendix* provides geological details).

Permit area Q16 is located at the northern rim of the MIS 3 Rhine-Meuse valley. Unit B4 stretches 40 km south (32, 33). Unit B4 is a source bed for Late Pleistocene mammal fauna and MP finds, including bifaces, and a Neandertal skull fragment (1, 30, 31, 34). The Zandmotor find is part of the same archaeological-paleontological complex, firmly situating it in an MP context (*SI Appendix*, Fig. S3).

**$^{14}\text{C}$ -AMS Dating.** Direct dating of the tar yielded a  $^{14}\text{C}$  date of  $47,100 \pm 500$  BP (GrA-69594). This date is close to the limit for the  $^{14}\text{C}$  method. By a tentative extrapolation of the calibration curve (35), we obtain an absolute age of  $\sim 50,000$  calBP, placing the find in early MIS 3. The date falls within the assemblage of optically stimulated luminescence (OSL) ages obtained for parent deposit Units B2 and B4 with median ages of 67 and 37 ka, respectively (32), confirming the find's MP attribution.

**Adhesive Identification.** Chemical identification of the black material adhering to the flake reveals a high content of triterpenoids betulin and lupeol, a biopolymeric waxy substance (36), and a series of long chain (dimethylated) dicarboxylic acids. This is directly comparable to the composition of known birch bark tars (15, 37), as illustrated by the chromatogram in *SI Appendix*, Fig. S4. This confirms that the material is birch bark tar.

**Description of the Find.** The find has maximum dimensions of  $39 \times 35 \times 14$  mm and weighs 12 g (Fig. 1 and *SI Appendix*, Fig. S5). The flake is made of a relatively fine-grained grayish flint. It originates from Saalian gravely outwashes, situated close to the findspot (Fig. 2 and *SI Appendix*, Fig. S2). The flake is unretouched and roughly oval in shape, with a sharp convex side. Located opposite the portion covered in adhesive, the convex side is interpreted as the tool's working edge. Approximately 40% of the dorsal surface is cortical. The cortex is almost completely covered by tar, possibly providing better adhesion owing to its rough texture (38). As a simple flake, the find cannot be assigned to a particular MP culture/industry.

No traces of extensive rounding are evident, and the surface of the flint appears relatively fresh, suggesting that the find derives from a primary context. The postdepositional microscopic polish that covers the flint surface obscures any wear traces, and

**Table 1. Overview of securely dated chemically and spectrometrically identified MP hafting adhesives currently known from Europe, the Levant, and contemporary southern African adhesives**

Country	Site	Material	Adhesive identification	Date	Dating method	Reference(s)
Italy	Campitello Quarry	2 flint flakes with birch tar	GC/MS	>191 ka	Biochronostratigraphic based on micromammals	(14)
Syria	Umm El Tlel	11 flint Levallois products with bitumen	GC/MS	~71 ka	Thermoluminescence of associated heated flints	(18, 19)
Syria	Hummal	1 Mousterian point, 1 (atypical) Levallois flake, and 1 broken Levallois point with bitumen	Scanning electron microscopy with energy dispersive X-ray, Fourier transform infrared spectroscopy, confocal Raman microscopy, GC/MS	50 to 80 ka	Associated with Tabun B-type Mousterian assemblage	(17, 20)
Germany	Königsau	2 lumps of birch tar	GC/MS	>43 and >48 ka	AMS on tar	(15, 21)
The Netherlands	Zandmotor	1 flint flake partially covered in birch tar	Thermally assisted hydrolysis-pyrolysis-GC/MS	~50 ka	AMS on tar	This study
Italy	Fossellone Cave	2 flint scrapers and 1 quartzite flake with pine resin, 1 flint scraper with pine resin and beeswax	GC/MS	55 to 40 ka	Maximum and minimum ages provided by luminescence and <sup>14</sup> C-dating of layers 21 and 26 (adhesives derive from layer 23 $\alpha$ )	(5)
Italy	Sant'Agostino Cave	5 flint scrapers, 1 Levallois flake with pine resin	GC/MS	~43 ka	Layer A1 dated by electron spin resonance	(5)
South Africa	Diepkloof Rock Shelter	1 Late Howiesons Poort quartz flake with <i>Podocarpus</i> resin	GC/MS	~60 to 55 ka	Level SU George dated by thermoluminescence and OSL	(22)
South Africa	Border Cave	2 chalcedony bladelet fragments, 1 scaled chalcedony piece with <i>Podocarpus</i> tar	GC/MS	~43 ka; ~40 ka	Layer 1BS Lower B + C charcoal dated by AMS; level 1BS LR pitch on microlith dated by AMS	(23)
South Africa	Sibudu	2 Howiesons Poort segments with <i>Podocarpus</i> resin	GC/MS	~65 to 62 ka	Layers GR and PGS dated by OSL	(24)

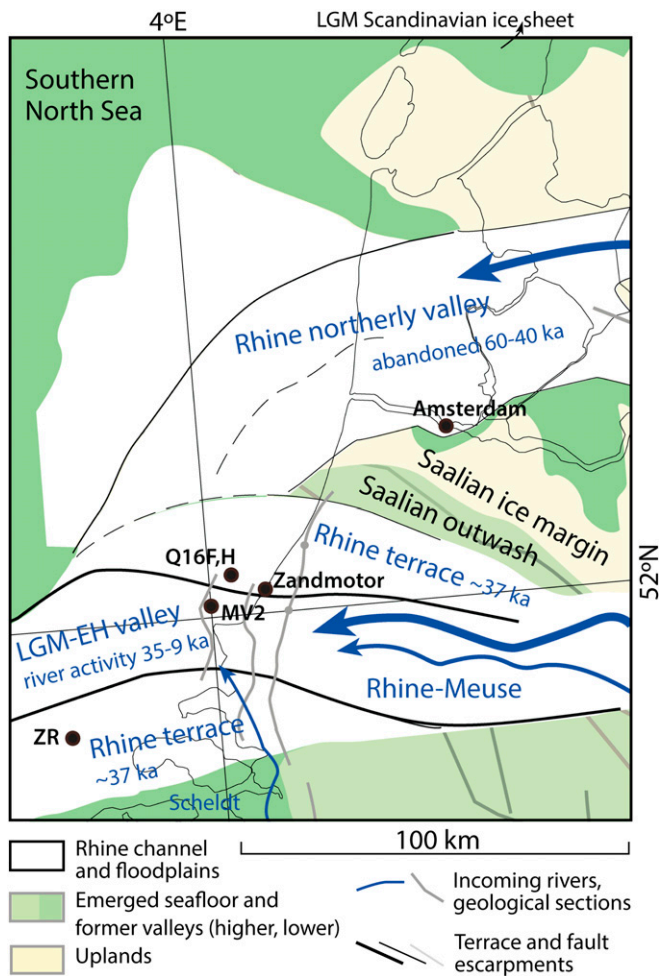
although the shape of the lateral edge is suitable for scraping and cutting, no conclusive use traces were found.

The adhesive has a total volume of 1,990 mm<sup>3</sup>. It has been folded and pressed over the dorsal side of the flake and the dull lateral edge (Figs. 1A and 3). The contact surface between the tar and the flake covers approximately one-third of the flint. The tar has a rough, rounded outer surface that protrudes 10.2 mm from the flake edge and shows a slight concavity. The protrusion might be the remainder of a simple tar handle.

The tar has a heterogeneous microstructure (39). Its outer surface consists of a layered coating 0.5 mm thick (Fig. 3A). The coating is tentatively attributed to weathering. Cracks through the tar present similar signs of weathering. Thin veins of highly attenuating material run along the interface of the flint and the tar and penetrate throughout the tar (Fig. 3B). Where the veins outcrop on the tar surface, they have an orange rust color, suggesting that they consist of iron oxide. The veins may result from preferential weathering along cracks and ancient flow lines from when the tar was in a molten state during production. A few dark elongated inclusions likely represent charcoal fragments (Fig. 3C).

### Middle Paleolithic Tar Production

To date, 4 methods of tar production, increasing in procedural complexity, have been successfully trialed: condensation, ash mound, pit and vessel, and a raised structure composed of an earthen mound containing a vessel and screen (8, 40). Increasing procedural complexity directly relates to increased tar yield efficiency (*SI Appendix, Table S1 and Fig. S6*). In single attempts, these experimental methods produced tar volumes of approximately 646, 877, 1,579, and 13,772 mm<sup>3</sup>, respectively. To make the amount of tar found at the Zandmotor is feasible with each method, but the simple methods would take considerably more time and energy. The simple methods, and the condensation method in particular (8), provide an excellent explanation for the origin and discovery of birch tar and offer suitable methods of producing small quantities of tar when birch resources are plentiful. However, the latter technique would require 40 times as much bark as the raised structure and would take roughly 10 h to produce the Zandmotor tar (8, 40). Similarly, in a Late Pleistocene open woodland (41), compared with the most complex method, the ash mound requires nearly twice as long to



**Fig. 2.** Paleogeography for the Rhine-Meuse-Scheldt Valley and surroundings during the Last Glacial (after ref. 33). Black dots indicate the relevant find locations: Zandmotor (tar find location, B4 depletion); Q16 F, H (dredging site for the Zandmotor beach); MV2 (Rotterdam Maasvlakte 2, find location MP artifacts, B4 sand depletion); ZR (Zeeland Ridges, find location Neandertal skull fragment, B4 outcrop).

collect the firewood and 10 times as much birch bark, which takes 10 times longer to distill (40, 42) (*SI Appendix, Table S1*). The size of the Zandmotor tar also falls within the range of the other Neandertal birch tar finds, which measure (maximum dimensions in mm, excluding flint)  $33 \times 21 \times 14$  (Zandmotor),  $42 \times 33 \times 18$  (Campitello Quarry),  $27 \times 20 \times 12$  (Königsau A), and  $23 \times 14 \times 6$  (Königsau B). Thus, the production of these amounts of MP tar represents a considerable technological investment in terms of resources.

Moreover, looking at production temperatures, it is likely that the most complex method was used. Temperatures inside the bark roll for the most successful ash mound experiment reached a maximum of  $\sim 260^\circ\text{C}$ . In the most successful raised structure experiment, temperatures reached between  $310^\circ\text{C}$  (inside the bark roll) and  $360^\circ\text{C}$  (inside the reaction chamber) (40). Based on the abundance of betulin and lupeol and the absence of degradation markers, the Zandmotor tar may have been produced in the range of  $350$  to  $400^\circ\text{C}$ . Similarly, the Königsau betulin content shows that it was also produced at temperatures below  $400^\circ\text{C}$  (15).

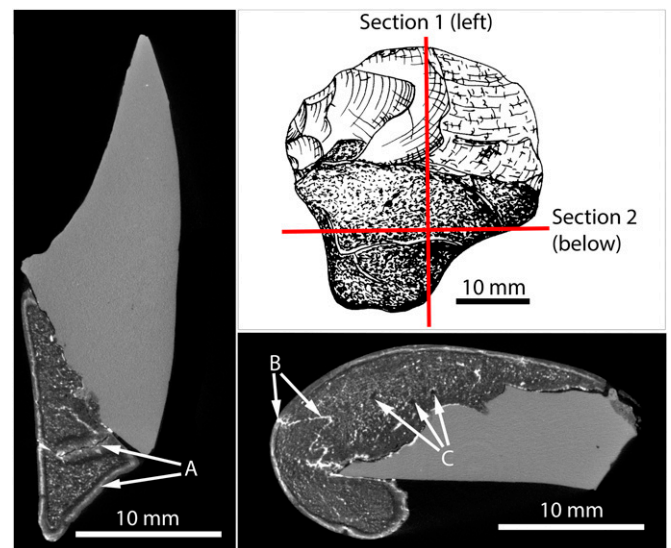
Contaminants can be a by-product of the production process, and the soil and bark products in the tar vary based on the production method (40). Micro-computed tomography (CT) scans

show a fine-grained contaminate of similar molecular weight to quartz sand or iron oxide, as well as some charcoal distributed throughout the adhesive matrix (Fig. 3C). The homogeneity of the fine-grained Zandmotor contaminants indicate that they were present when the tar was in a molten state and were mixed in thoroughly. Of the experimental production methods, only the intermediate and complex methods made a tar with sufficiently low viscosity to readily mix with contaminant particles. Tar produced by the simple methods has more charcoal and bark fibers and less sediment contaminants, while tar made by the complex production methods has higher concentrations of sand and lower concentrations of charcoal and bark fiber (40). The latter pattern is similar to what we see in the Zandmotor tar. The amount of time and energy required to collect the materials, the temperatures achieved during production, and the contaminants in the Zandmotor find all point to the use of a more complex high-yield tar production method.

### Procedural Complexity and Hafting Practices

The qualities that make a technology complex are often unspecified. Although Neandertal single-component tools sometimes exhibit elaborate production sequences (43), the most complex hunter-gatherer technology is represented by hierarchically organized composite facilities and tools and multiple-state tools (i.e., tools with moving parts). The development of composite technology is often seen as a hallmark of cognitive sophistication and demonstrates expert cognition, comparable to that in contemporary populations (28). Adhesive finds represent composite tools that require significantly more cognitive resources to produce and use than single-component tools (28, 44). Further to the use of tar in a multicomponent tool, the production of tar itself represents a 3-level hierarchically organized facility, with different components made to function together (40, 44) (*SI Appendix, Fig. S6*). In addition, the use of a separate object to collect the produced tar also reflects a degree of mechanical complexity.

Many ideas on the development of composite tool technologies are based on microscopic use-wear, macrofractures (6, 45), and the shape of tools (e.g., the presence of tangs, basal thinning). Yet the functional significance of such morphological features is not always clear (46). The exact hafting configurations and functioning of hafted tools are also debated (47, 48), while



**Fig. 3.** Micro-CT cross-section scans. (A) Weathered surface coating the tar and penetrating along an open crack. (B) Veins of highly attenuating matter following cracks in the tar. (C) Possible charcoal fragments.

variability in methods of hafting is almost completely unexplored (22, 27, 45, 49). Finds from Zandmotor, Campitello, and Fossellone demonstrate that Neandertals repeatedly hafted unmodified, typologically undiagnostic flakes (5, 14), not only Levallois products and retouched tools. This underscores that morphological tool features alone are not a good indication of the presence of hafting technology.

Hafted artifacts are generally envisaged as a stone tool connected to an organic handle (16, 47). The presence of folds, creases, and, in some instances, imprints indicate that all MP tar finds were thick and viscous when applied. The lumps are all folded and pressed over the prehensile portion of the flakes, opposite to the working edge. In addition, the Zandmotor and Campitello finds show no clear evidence of an organic handle (14). This suggests that the tar might not have affixed the flakes to a separate handle, but rather acted as a handle or backing material itself. Reconstructions of the lithic artifact originally embedded in the tar at Königsau A also suggest the lump was directly attached to a retouched bifacial knife (*SI Appendix, Fig. S7A*). This is comparable with the Levallois flakes from Syria, in which bitumen functions as a backing material (17). Similar objects are also found ethnographically, such as Australian aboriginal “leiliras” with *Spinifex* resin handles (50) (*SI Appendix, Fig. S7B*). This pattern demonstrates the need for nuanced thinking about the roles of adhesives in hafting in the Pleistocene.

We argue that the evidence for hafting and procedural complexity shown here represents a taphonomic exception that provides a window into Neandertal normality. We demonstrate that significant technological investment was expended even on the simple Zandmotor flake, mirroring the Campitello situation. This confirms the routine production of relatively large quantities of tar.

### Behavioral Implications

Evidence for Neandertal complex behavior is steadily accumulating. Potential indications for symbolic behavior include cave art (51, 52) and personal ornaments from >115 ka (52, 53). More frequent and continuously exhibited complex behaviors are technological in character, including adhesive production, multicomponent tool technology (5, 6), technological decisions based on a deep understanding of material properties (54), and pyrotechnology (3, 4). The shared nature of multicomponent tools and adhesive technology among Neandertals and African humans suggests that the propensity for such behaviors stems from a common ancestor.

The processes enabling the accumulation and maintenance of complex (technological) behaviors are undervalued, however. The use of complex technology has been proposed to depend on social group size (9) and to be negatively correlated with residential mobility (11). Archeological and genetic evidence demonstrates that Neandertals lived in very small social groups (55, 56). Due to their lower limb anatomy, these groups had relatively small territory sizes, likely exploited using a system of high residential mobility (57, 58). These modeled effects are supported by archaeological evidence, including limited site structures and shorter raw material transport distances compared with modern humans (59, 60), stable isotope evidence of relatively small territory size (61), and high femoral robusticity pointing to higher degrees of habitual mobility than seen in preindustrial hunter-gatherers (62). These effects must have been most pressing in the northern part of their range, where extreme residential mobility is expected (63). This means that small population size and high residential mobility did not constrain Neandertals from developing and maintaining highly complex (e.g., birch tar) technology. In a similar vein, the development and maintenance of complex behaviors in southern Africa has been attributed to an increased population density (10), but careful scrutiny of the evidence appears to not support this (64).

To warrant the considerable technological investment exhibited by tar production, the development and use of this technology had to confer fitness benefits on the users (65, 66). Complex tools and technological procedures are not exhibited under all conditions, not even by sufficiently cognitively equipped populations (44). Moreover, fitness benefits do not necessarily increase with increasing investment in complex behavior, and the technological investment must be worth the trouble (cf. ref. 67). Generally, as climates get colder, technological complexity increases (44, 68). During MIS 4 and 3, Neandertals at the northern edge of their distribution faced severe ecological risk (63, 66), and the North Sea fauna and vegetation confirm cold, inhospitable conditions for the Zandmotor find (1, 33, 41). The mitigation of ecological risk is one likely explanation for the development and use of complex procedures and technology. Neandertals who operated at the limits of their ecological tolerance (i.e., in conditions where they faced a high risk of resource failure) had to maintain highly complex technological routines. Similarly, in southern Africa, ecological risk also better explains behavioral changes than demography (69, 70). The maintenance of complex procedures can be aided through task specialization. There are ethnographic cases in which the maintenance of technology in general, and adhesive application in particular, are exclusively female domains (71, 72). Neandertal hafting of “domestic” undiagnostic flakes may suggest a higher degree of task specialization than previously considered (cf. refs. 12 and 73). The substantial technological investment into small domestic tools, as testified here, demonstrates that Neandertals used complex behavioral strategies to insulate themselves from the inclement conditions they experienced during MIS 4 and 3.

### Conclusions

The Zandmotor find is the first MP tar from The Netherlands and the North Sea and one of only a few directly dated archeological adhesive specimens globally. It is securely attributed to Neandertals, with an AMS date of ~50 ka and geological association with MP artifacts and a Neandertal fossil. The submerged landscape of the North Sea is therefore crucial for understanding Neandertals’ occupation of riverine lowlands in midlatitude Europe. This study represents a body of knowledge on the Late Pleistocene occupation of the North Sea formed by the collaboration of varied societal stakeholders, including amateur collectors, archeologists, paleontologists, geologists, and dredging partners.

Our analysis of Neandertal tar finds and the reconstruction of the production process introduces a method to study complex behaviors in the remote past. The birch tar finds demonstrate the use of compound tools by Neandertals, a trait shared by contemporary African humans. They also show that tar was produced and used in a similar hierarchical manner across Königsau, Campitello, and the Zandmotor, spanning 150 ka. Our analysis further confirms that Neandertals invested considerable time and resources in domestic tools and activities. The regular performance of logistically complex, cognitively demanding production processes provides important evidence on the evolution and transmission of complex technology.

We show that complex technological know-how was maintained in small groups leading highly mobile lives along the northern limits of their distribution. This contradicts 2 influential hypotheses on the necessary conditions for the development of technological complexity, namely large group size and low residential mobility. It supports the hypothesis that technological complexity is often used to mitigate ecological risk. It might also suggest a degree of task specialization, perhaps between genders. As such, the Zandmotor find, in conjunction with other Old World adhesives, has repercussions for our understanding of the entire history of technology and of the versatility and complex technological adaptation of Neandertals in particular.

## Methods

Dating was performed at the  $^{14}\text{C}$  laboratory of Groningen University, The Netherlands. AMS radiocarbon dating with AAA pretreatment was selected as the most appropriate method in view of previous experience with North Sea materials. Thermally assisted hydrolysis and pyrolysis-gas chromatography-mass spectrometry (GC/MS), with tetra methyl ammonium hydroxide for online hydrolysis and methylation, was used to identify the adhesive. The flint flake was analyzed to characterize its origin and typology. We studied the Zandmotor flint for potential use wear using optical and stereoscopic microscopy. X-ray micro-CT was used to analyze the internal structure of the adhesive and the

morphology of the part of the flake obscured by the tar (39). Further analytical details are provided in *SI Appendix*.

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