
STATED MEETING REPORT



Science as a Window into Wine History

Carole P. Meredith, Professor of Viticulture and Enology, University of California, Davis

The 1863rd Stated Meeting was hosted by the Academy's Western Center in Napa, California, on November 2, 2002. The meeting included tours of the Robert Mondavi Winery and COPIA: The American Center for Food, Wine & the Arts. President Patricia Meyer Spacks (University of Virginia), Western Center Vice President John Hogness (University of Washington), and Executive Officer Leslie Berlowitz welcomed Fellows and guests, as well as several newly elected members from the Western region.

Speaker Carole P. Meredith was introduced by Academy Fellow Walter Fitch, a professor in the Department of Ecology and Evolutionary Biology at UC Irvine. Meredith, a specialist in the DNA and genealogy of grapes, brings her insights as a wine maker to her work in academia. Her remarks follow.

My husband and I live in the hills on the west side of the Napa Valley. We have a vineyard, and we make wine under our own label, Lagier Meredith—a combination of our last names. Once we began growing grapes and making wine on our own, I developed a real understanding of the interests of my constituents—the grape growers and wine makers of California. Now that I also get my hands dirty, I think I do my job at the university a lot better.

Over the past ten years, my lab has been looking into the history of some of the classic wine grapes of the world. At first we thought we were simply working on variety identification. There are thousands of wine grape varieties in the world, and even more names that they go by. We thought we were developing a method to resolve some of the problems that result from using more than one name for the same wine grape. This becomes a technical



Speaker Carole P. Meredith (UC Davis)

issue, because people can't talk to each other if they don't know they're talking about the same grape variety. It also becomes an economic and regulatory issue with regard to wine labeling and the regulations of various governments about how beverages must be identified. We started out to use DNA typing simply as a method for objectively and irrefutably identifying grape varieties in order to reconcile some of the many problems and mistakes that exist around the world.

It rapidly became clear to us that this technology could also be a powerful tool for understanding genetic relationships among some of the classic wine grapes in the world and thereby resolving questions about their origins. I'm going to discuss our findings on four varieties: two classic grapes, Cabernet Sauvignon and Chardonnay, and two that are particularly important in California, Petite Sirah and Zinfandel. I will start with the Cabernet Sauvignon story, which represents the beginning of our work in this field, thanks to a serendipitous discovery.

First, however, it's important to explain how grapes are propagated, because that is key to understanding how a classic grape variety that is growing today in the Napa Valley—or in France or Australia or South Africa—is essentially unchanged from the first vine of that variety, which arose many centuries

ago. All the classic wine grapes are very, very old. They have been maintained by vegetative propagation, which means by using cuttings or buds, as you would with geraniums. Although some small genetic changes have taken place in the classic vines throughout history, they are essentially unchanged from the very first vines of those varieties.

All vines propagated by cuttings or buds from a preexisting vine are essentially clones. The first vine of a given variety is the only one that grew from a seed. That seed was the result of a sexual event that took place between two parents. In the case of grapevines, the two parents are always completely different genetically. Except for the propagation part—the cuttings and buds—this is completely analogous to human reproduction. Each person shares a lot of genetic material with both parents yet is completely dissimilar from each of them genetically. It's exactly the same with a grape variety. All the individual plants of that variety are genetically almost identical to each other, but they share only half their genetic information with each of the two parents that gave rise to the first vine of that variety. That's a key point to keep in mind.

Cultivated grape varieties can originate in a number of different ways. The very first cultivated grapes that existed were selections of wild vines. Bear in mind that all crops, including grapes, are derived from wild plants; they are not simply the products of human efforts.

Along the Napa River and the creeks in that area, grapevines with bright yellow leaves climb up the trees. They are *Vitis californica*—a wild vine, not cultivated. The wine grapes are all *Vitis vinifera*—a species native to Europe and western Asia. The first grape varieties were simply individual wild vines with fruit that people found attractive and eventually learned how to propagate. We cannot really learn anything about varieties that were selections from wild vines, because the wild genotypes that gave rise to those grapes no longer exist.

Another way that grape varieties can originate is by natural cross-pollination—either between wild

vines and the earliest of the cultivated varieties, or between the cultivated varieties themselves. All of the work that I'm going to talk about today takes advantage of what we can learn about these natural cross-pollinations. Over the past 160 years or so, modern grape breeders have performed controlled cross-pollinations between selected parents to develop new varieties. None of the classic wine grapes, however, have originated from a controlled cross; they are all so old as to predate deliberate cross-pollination between any kinds of plants, which did not begin until the eighteenth century.

To identify the genetic origins of a grapevine, we take a sample of that vine and chemically purify the DNA from the other components. We then target specific small segments of the DNA that we have previously identified as existing in multiple forms (called "alleles"), and we use a process called polymerase chain reaction (PCR) to make millions of copies of those small segments (called "markers"). We can then compare the alleles at a particular marker site in one variety with the alleles at that same site in another variety to establish whether they are the same or different. We follow this procedure for each marker we are analyzing. This is completely analogous to human DNA profiling. If



Left to right: George Olah (University of Southern California) and Gabor Somorjai (UC Berkeley)

you understand at all how human DNA profiling is performed in order to analyze genetic relationships among humans, then you won't have any trouble understanding what we do with grapes.

We look at the DNA profile of the variety we are curious about, along with the profiles of a pair of putative parent varieties. If we are indeed examining the actual parents, the progeny variety should share, at each marker site, one allele with one parent and one allele with the other parent. We analyze a large number of marker sites in order to deduce whether or not there is a probable parental relationship between two varieties and a third variety that we postulate to be the offspring.

Cabernet Sauvignon, as you probably know, is the most important red wine grape of the Bordeaux region of France. Wines labeled "Bordeaux" are typically made predominantly from Cabernet Sauvignon, along with Merlot and sometimes several other varieties. Cabernet Sauvignon, which is considered by many to be the most important and highest-quality red wine variety in the world, is widely grown in California and the New World countries. Because the name Sauvignon is derived from the old French word *sauvage*, meaning "wild," many people have speculated that Cabernet Sauvignon is a selection from a wild vine. We now know that it is not. Others have speculated that the Romans brought Cabernet Sauvignon into France from Albania, but we now know that was not the case. Still others have suggested that it was brought from Spain, but it wasn't. What we learned back in 1996 (this was our lab's first discovery, and it came as a big surprise) was that Cabernet Sauvignon is the offspring of Cabernet Franc, a red wine variety, and Sauvignon blanc, a white wine variety.

We went on to find that it's quite common for dark wine grapes to have one white parent. The color form is simply a dominant trait in the case of Cabernet Sauvignon. This was a discovery of a former graduate student of mine, John Bowers, who grew up in the Napa Valley in a family that has been involved with wine grapes for a long time. We were developing a database of the most important

wine grape varieties so that whenever we came across an unknown, we'd be able to identify it by matching the DNA profiles. At the time, we had only about fifty varieties in our database. One day John realized that his data showed that Cabernet Sauvignon shared half of its alleles with Cabernet Franc and half with Sauvignon blanc, which strongly suggested that those two varieties could be the parents of Cabernet Sauvignon. We then used some statistical methods that are used in human genetics to answer various questions: For each allele found in the offspring, how common is it in the whole population of grape varieties? What is the chance that Cabernet Sauvignon could share half of its alleles with Cabernet Franc and half with Sauvignon blanc simply by chance? What is the chance that Cabernet Sauvignon would have those alleles if those two varieties really were the parents? What we found, by fairly straightforward statistical analysis, is that it is vastly more likely that Cabernet Franc and Sauvignon blanc really are the parents of Cabernet Sauvignon.

This was the first time anyone had identified the origins of a classic wine grape. Up until then, wine writers had been free to speculate whatever they wanted about a variety's origins. There was never any way to examine their hypotheses until we realized that modern genetics gives us a way to learn about historical events that took place centuries or even millennia ago. By combining our new information with what we could glean from the French wine literature, we were able to deduce that Cabernet Sauvignon resulted from a natural cross in Bordeaux before 1700, because the first mention of Cabernet Sauvignon as being distinct from Cabernet Franc, with which it actually shares some physical characteristics, was made in the early 1700s.

Realizing that we had a powerful tool on our hands for learning about important wine grapes, we became more deliberate in our investigations. Another variety we have studied, Petite Sirah, has been grown in California for a very long time. It has never been a major grape, but it has had some



The garden at COPIA: The American Center for Food, Wine & the Arts (Napa, CA)

strong proponents. For a long time people thought that perhaps Petite Sirah was a form of Syrah, the noble grape of the Rhône valley in France. We knew that was probably not the case, because they were morphologically different, and so we began to investigate the origins of Petite Sirah. We obtained samples of some varieties that we thought would be relevant, including Peloursin and Durif, both from the south of France. We found that almost all of the Petite Sirah in California matched the DNA profile of Durif at every marker. Occasionally, however, we came across some Petite Sirah that matched the profile of Peloursin. When we investigated a bit further, we saw that Peloursin, although completely distinct from Durif, shares one allele with Durif at every marker, which suggested that Peloursin has a parental relationship with Durif.

We eventually determined that the French variety called Durif, which is the same as the California-grown grape known as Petite Sirah, is actually the offspring of Peloursin and true Syrah. This came as quite a surprise to people (even though the name used in California is Petite Sirah) because, having been told that Petite Sirah was definitely not the same variety as Syrah, people had begun to consider them as two completely different grapes. In fact, many regarded Petite Sirah with scorn, as if that grape were trying to pass as a relative of Syrah. When we discovered that Petite Sirah is Durif and confirmed that it is not Syrah, its detractors

thought, “Told you so. It has nothing to do with Syrah.” But then, shortly thereafter, we found out that Petite Syrah is the offspring of Syrah. So now Petite Sirah has taken on an elevated status because of the recognition that it is one-half Syrah, and people are noticing the similarities. Our discovery has been rather helpful to the people who produce Petite Sirah, because it has enabled them to gain inclusion in a trade organization called the Rhône Rangers, which promotes Rhône varieties grown in California.

Having found the parents of Cabernet Sauvignon and Petite Sirah, we decided to make a deliberate search for parents of other varieties by selecting a large number of candidates on the basis of certain criteria. We enlisted the collaboration of the world’s greatest living expert on French grapes, Dr. Jean-Michel Boursiquot, who at the time was a scientist and teacher in Montpellier. He was eager to participate in our project; after all, an American group had found the origin of a famous French grape, Cabernet Sauvignon, so our French colleagues were understandably interested in joining our efforts. We decided to focus on northeastern France, which is where Burgundy and Champagne are located. We chose about 300 candidates from the several thousand varieties at the French national grape variety collection in Montpellier, on the Mediterranean coast of France. Many of the varieties in that wonderful collection are no longer grown in France; they were rescued from remnant populations in vineyards destroyed by phylloxera. Some of these varieties were saved from extinction by being brought to the Montpellier site, where phylloxera cannot survive.

Mainly, we chose varieties that looked like those grown today in northeastern France, or varieties that had some historical tie to that part of France, or varieties that historical records speculated were related to varieties growing in the region. We also chose some varieties on a hunch, even though we didn’t have any concrete basis for including them.

We generated DNA profiles for those 300 varieties, at a relatively limited number of markers, so that

we could quickly eliminate those that were not closely related to the grapes of northeastern France. We analyzed the remaining varieties at a larger number of markers. John Bowers developed a computer program that would search among the DNA profiles of these varieties for parental relationships. We use numbers to record DNA data, and because the data are numerical, we can analyze them with a computer program; we don't have to rely on visual comparisons of DNA bands on a gel.

Among the 300 varieties analyzed, we found 26 pairs of parents for 26 varieties. Much to our surprise, however, those parents were not 26 different pairs. We found that 16 of the varieties had the same pair of parents: Pinot, which is the classic grape of northeastern France, and Gouais blanc, a variety I had never heard of before. All of the 16 different offspring most probably resulted from completely independent cross-pollination events that occurred in different places and at different times. Many of those offspring are varieties you've never heard of; some are no longer grown today. But one of those varieties is Chardonnay, which is probably the most important white wine grape grown in the world today. Some others are Melon, a quite important variety that produces the white Muscadet wines at the mouth of the Loire; Gamay noir, the grape from which the true Beaujolais is produced; and Aligote and Auxerrois, both important white wine grapes in northeastern France today. All of the 16 varieties with the same pair of parents are grown today, or were grown, in a corner of northeastern France, the area we were targeting.

It was a great advantage to have access to a collection like the one in Montpellier. If we had simply relied on commercial vineyards, we never would have discovered some of these genetic relationships. In fact, we never would have found Gouais, one of the parents, because it is not cultivated anywhere in France today; it exists only in the collection.

You may wonder why I'm saying Pinot when there is a Pinot noir, a Pinot gris, and a Pinot blanc. It's because these are simply three different color forms of the same variety; they all have the same DNA



Edward Feigenbaum of the Membership Committee (Stanford University), with Councilor Carolyn Shoemaker (Lowell Observatory)

profile. When we found that one of the parents of the 16 offspring was a Pinot, we did not know which of the color forms of Pinot it might have been in each of the 16 cases. (We would be able to figure that out, however, if we produced and tested some progeny from each of the 16.)

Pinot is known to be a very old variety. A Roman naturalist, writing about the things that were growing in Burgundy when the Romans arrived there about 2,000 years ago, described a variety that sounds just like Pinot noir. None of the grapes that were grown in the more southern parts of Europe resemble Pinot at all; it has a distinctive leaf shape. Gouais blanc, a reliable, sturdy grape, was once widely grown in northeastern France. In fact, Pinot and Gouais were the two most widely grown varieties in that region during the Middle Ages. However, whereas Pinot was grown by the nobility and the church on the best sites, usually on the slopes, Gouais was grown only by the peasants on the flat lands where they lived. Gouais was considered so mediocre that it was banned at least twice in Burgundy for being just too ordinary.

Using some old French books, we were able to deduce the probable distribution of both Gouais and Pinot in the Middle Ages. There would have

been ample opportunity for cross-pollination events between those two varieties, with Pinot growing on the slopes and Gouais growing on the nearby flats. Presumably, lots of individual seedlings sprung up over the years in different places and at different times, each the result of a cross-pollination between Gouais and Pinot.

We know that Pinot was already in northeastern France when the Romans arrived, but Gouais was not. Gouais blanc is actually a French synonym for an eastern European grape known as Heunisch weiss. How did it get to Burgundy? There seems to be some fairly strong evidence that Gouais was brought to France by Emperor Probus of Rome. Some previous emperors had become resentful of wine production in the provinces, because it was competing with wine production in Rome; for a time, Emperor Domitian actually prohibited grape growing in the provinces. But Probus, who had a great interest in agriculture, liked the provinces, and he especially liked the Gauls. He was from Dalmatia, which is part of present-day Croatia. It is written that he gave the Gauls a gift of a grapevine from his homeland. We have no proof, but we can speculate that perhaps that vine was Gouais blanc.

Why are Pinot and Gouais the parents of so many varieties? We have never found another pair of parents with offspring of more than one variety. We think it's quite likely that Pinot and Gouais make such a great combination because they arose from completely unrelated original wild populations. It's a classic example of heterosis—of genetically dissimilar parents producing very fit and adaptable offspring.

The most recent work my lab has been doing is probably the most satisfying for me because it has become so multidimensional: it's not only about genetics and history but also about people and collaboration.

Zinfandel is a very important and widely grown wine grape from California. It is used to make a number of outstanding wines, ranging from a rosé

that is called White Zinfandel to the very robust and dark-colored red Zinfandel wines that come from grapes grown in some of the cooler California regions. For a long time, Californians thought of Zinfandel as California's own grape, because no grape in Europe goes by that name. It was rather nice to think that for once we weren't emulating Europe by using another one of its classic grapes. Here we had a wine grape of our own, and it was a pretty good one too.

Nevertheless, it was obvious that Zinfandel was a member of *Vitis vinifera*, a European species. Because there is no *Vitis vinifera* native to the New World, Zinfandel must have originated somewhere in Europe—but we didn't know where. This mystery was the subject of books and a lot of speculation. Finding the answer was not only of historical interest; it also had some practical interest because today's growers of Cabernet Sauvignon or Syrah or Chardonnay often like to plant more than one subtype of that variety.

Subtypes within a variety are called “clones.” This is an unfortunate use of the word, because in wine, “clone” means something quite different from what it means in most biological contexts. The different subtypes of a variety are often adapted to slightly different conditions: they may ripen a bit earlier, or have a slightly different aroma, or have slightly larger or smaller berries. Growers and winemakers often have preferences, depending on the location of the vineyards or the kind of wine that they want to make. In California, all we had was a fairly uniform Zinfandel that had been grown here for a hundred years or so. If we wanted to get some more diversity into that variety, we had no idea where to go. If we wanted more subtypes of Chardonnay, we'd go to Burgundy. For subtypes of Cabernet Sauvignon, we'd go to Bordeaux. For subtypes of Syrah, we'd go to the Rhône. But for Zinfandel, we had no place to go.

In the 1970s, Austin Goheen, a retired colleague from UC Davis, was attending a conference in Apulia, on the heel of Italy. He tasted a local wine

with an Italian colleague and said, “This tastes like Zinfandel. Can you show me the vines?” Despite being told that the wine was nothing but an ordinary local red, Austin persisted and was shown the vines. They looked exactly like Zinfandel, and he thought that he might have finally found the home of that variety. The Italians called the grape Primitivo di Gioia. Eventually, when we did DNA comparisons, it became very clear that Primitivo and Zinfandel are simply synonyms for the same variety. But if you look into the history of Primitivo in Italy, it is referred to as an introduced grape, and it has not been grown there long at all. So Italy is not the home of Zinfandel.

The next place we became interested in was present-day Croatia, which used to be part of Yugoslavia before it separated into its component republics. The most distinguished red wine grape grown along the Dalmatian coast of Croatia, on the Adriatic Sea—as well as on many of the 1,100 islands off the coast—is Plavac Mali, long suspected to be the same as Zinfandel, or at least a relative. The Dalmatian coast is very close to the heel of Italy, so it’s entirely possible that a grape grown there might have found its way to Italy.

Miljenko Grgich, a Napa Valley winemaker who is originally from what is now Croatia, had been insisting for years that Plavac Mali was the original Zinfandel. He was very excited to learn of our



Councilor Peter Stansky (Stanford University) and President Patricia Meyer Spacks (University of Virginia) at the Robert Mondavi Winery

investigation and wanted to help in any way he could. Having left the former Yugoslavia a long time ago to seek his fortune in America, he felt that establishing a viticultural connection between his new home, California, and his old home, Croatia, would make his life complete.

In 1998, after having looked at a number of samples that we already had in Davis without reaching any satisfactory conclusions, I decided to go to Croatia, where I serendipitously made contact with two scientists at the University of Zagreb, Ivan Pejic and Edi Maletic. Even more serendipitously, I was able to enlist the help of Jasenka Piljac, a native of Croatia. We had first met when she was an undergraduate in biochemistry, washing dishes in my lab to earn some extra money (her parents had moved their large family to Davis when civil war broke out in Yugoslavia). Jasenka graduated from UC Davis with fantastic grades and had just returned to Croatia when I decided to embark upon my “Zinquest.” During my first trip to Croatia, she was my assistant, my translator, and my companion—an all-around great person to have at my side.

The four of us (Ivan, Edi, Jasenka, and I) traveled along the coast and to some islands, taking samples from various Plavac Mali vineyards, and then I brought them back to Davis to do the DNA analysis. My hypothesis at the time was that Plavac Mali was a genetically heterogeneous variety. We’d already looked at some samples of Plavac Mali vines maintained in Davis. They weren’t the same as Zinfandel, but I thought that perhaps if we looked at a larger range of samples from the Dalmatian Coast, we would find some that were Zinfandel. What we found, though, was that all 150 samples I brought back from Croatia were the same as what we already had in Davis, and none of them was Zinfandel.

Nevertheless, we did find a striking genetic relationship: Zinfandel turned out to be one of the parents of Plavac Mali. This came as a real surprise, because Plavac Mali is considered an old Dalmatian

grape, whereas Zinfandel has been viewed as a relatively young California upstart of unknown origins. It took us quite some time to find the other parent, but we eventually found it on an island off the coast. After my 1998 visit to Croatia, when it became clear that Plavac Mali was not Zinfandel, Ivan and Edi had continued to search. Every summer they visited more vineyards on more islands and talked to the growers in an effort to find every grape that could possibly be related to Zinfandel. Eventually, they found the variety called Dobricic, which turned out to be the other parent of Plavac Mali—the missing link in the Zinfandel–Plavac Mali relationship.

Although we had not found Zinfandel in Croatia, we had found its genetic footprints. We were beginning to suspect that Zinfandel was extinct in its homeland. When phylloxera went through Europe, it destroyed a lot of vineyards, and many varieties were lost. Unlike the French, the people of the Dalmatian Coast area did not have the resources or the foresight to establish a regional grape variety collection before all was lost. The damage done by phylloxera in Croatia, followed by the ravages of the Communist government and a couple of world wars, had all contributed to driving people off the land. We began to think we would never find Zinfandel in Croatia because it had probably succumbed to one of the many factors that had depleted the genetic resources of the Croatian vineyards.

Nonetheless, Ivan and Edi kept looking, and sending samples back to us, in 1999, 2000, and 2001. Their search was focused on the Dalmatian Coast between Dubrovnik, a UNESCO World Heritage city, and Split, an old Roman settlement, as well as a number of the major islands in the region. They always included little descriptions with the samples: “This one looks a lot like Zin,” or “Take a good look at this one; this has got to be Zin.” We kept analyzing them. None of them was Zinfandel, but many were its relatives. We were putting pieces of the puzzle together, but we were still missing Zinfandel itself.



Left to right: David Hogness (Stanford University) and Richard Herr (UC Berkeley)

At the end of 2001, I got an e-mail from Ivan that said, “This time we’ve really found it. We’ve really got Zin.” He had sent me the same sort of message several times before, so he was starting to sound like the boy who cried wolf. But by this time, Ivan had managed to equip his own lab to do some limited DNA analysis, even though it was very difficult for him to obtain the necessary chemicals. He said, “Listen, I’ve already looked at six markers. They match Zinfandel. We’ve found it. Mystery solved.” I told him I wouldn’t be convinced until we had analyzed more markers at Davis. He sent us the samples, and within a week or so of receiving them, we’d analyzed a lot more markers. This grape matched Zinfandel completely. In Croatia, it goes by the name Crljenak Kastelanski, which simply means “reddish grape from Kastela,” a coastal town just north of Split. So far we have confirmed the presence of this grape in only one vineyard, which has several thousand vines in it. Only nine of them are Zinfandel, and the rest are about a dozen other varieties. Had we waited a few more years, we might never have found it, because vineyards get replanted, and nobody recognized that there was anything special about this particular vineyard.

Ivan and Edi are continuing to look for more examples of Zinfandel in Croatia. I was there this past August and went with them to the vineyard where Crljenak Kastelanski is growing, so I could

see the vines for myself (and have my picture taken with them!). Ivan and Edi are hopeful that they will find this variety in more vineyards, and they will continue to look. During my most recent visit, we went to some vineyards on the islands of Solta and Ciovo and found some promising candidates on Ciovo.

We've now pieced together a possible history for the grape variety known as Zinfandel here, as Primitivo in Italy, and as Crljenak Kastelanski in Croatia (hence our own name for it: ZPC). This variety was born somewhere along the Dalmatian Coast and spread widely throughout the coast and the islands. We think that some monks who emigrated from Croatia to southern Italy in the eighteenth century to escape historically documented religious persecution brought the grape with them to Italy, where it became known as Primitivo and is now widely grown. At the same time, the grape also managed to make its way to the United States, but we're not certain how. One possibility is that it was established in the Vienna grape variety collection of Emperor Franz Josef, whose Austro-Hungarian empire included present-day Croatia, and then was imported from Vienna by a nurseryman on Long Island. Also, a lot of Croatians have made their way to California, and many are growing grapes here today. It's possible that some of them may have brought the variety with them.

We think that Zinfandel (a.k.a. Crljenak Kastelanski) was once widely grown in Croatia. Disease probably killed most of the vines, but not before a chance cross-pollination took place between Crljenak Kastelanski and Dobricic, giving rise to a seedling that became Plavac Mali. It probably was not noticed that Plavac Mali supplanted Crljenak Kastelanski, because they're very similar in appearance, but Plavac Mali was much better able to resist the disease pressure that had killed off the Crljenak Kastelanski, and thus it became well established as the most important red wine grape of Croatia today.

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AMERICAN ACADEMY OF ARTS AND SCIENCES

Main Office Norton's Woods
136 Irving Street
Cambridge, Massachusetts 02138
Telephone: 617-576-5000
Fax: 617-576-5050
E-mail: aaas@amacad.org
Website: <http://www.amacad.org>
Daedalus Telephone: 617-491-2600
Fax: 617-576-5088
E-mail: daedalus@amacad.org

Western Center 3000 Berkeley Place
University of California
Irvine, California 92697-7425
Telephone: 949-824-4553
Fax: 949-824-8022
E-mail: aaaswest@uci.edu

Midwest Center Lillie House, University of Chicago
5801 South Kenwood Avenue
Chicago, Illinois 60637
Telephone: 773-753-8162
Fax: 773-702-1115
E-mail: amacad@uchicago.edu

Bulletin Staff Alexandra Oleson, *Editor*
Carol Leach, *Associate Editor*

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