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PERSPECTIVES

Cybertaxonomy to accomplish big things in aphid systematics

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Abstract Biodiversity sciences have progressed at such a pace that the taxonomic community has been unable to grow concomitantly to keep up with the influx of biological data. This "taxonomic impediment" has led some to suggest that taxonomy is no longer pertinent and to the development of methodologies that circumvent the taxonomic process. This article does not seek to argue for the importance of taxonomy but rather is a call to the aphid taxonomy community to rise to the challenge by dramatically increasing the volume and comprehensiveness of its output without sacrificing quality. Recent informatics technology allows us to mobilize the 2 most important aphid taxonomy resources: experts and specimens, both distributed globally. "Cyberspecimens," museum specimens digitally rendered at a resolution sufficient for remote identification, and open "cybertaxonomic" tools will allow the international aphid taxonomic community to carry out large, ambitious, projects. The global aphid cybertaxonomy proposed here will serve not only the ends of research aphidologists, but also provide a model for other taxonomic communities to adapt and adopt as we confront both the taxonomic impediment and the taxonomic naysayers.

Key words Aphididae, collection, cyberspecimen, database, museum, specimen

Introduction

As the study of biodiversity gains recognition across the globe, conservation, ecology, molecular phylogeny, and other disciplines are investing in technology that bypasses alpha taxonomy (Pons *et al.*, 2006; Vernooy *et al.*, 2010; Maddison *et al.*, 2012). These disciplines, relatively well funded compared to taxonomy, are attempting to circumvent the "taxonomic impediment" as identified by the UN Secretariat of the Convention on Biological Diversity (2008). Simply put, biodiversity studies have created a renewed interest in taxonomic services, but there is a lack of readily available taxonomic expertise to supply those services. Rather than resulting in proportionally renewed funding opportunities for the taxonomy community, the potential funding has been diverted to other solutions that end up competing with the role of traditional taxonomy (Vogler & Monaghan, 2007; Grantham *et al.*, 2010; Padial *et al.*, 2010; Page, 2011). When funding is available to taxonomists, it is disproportionally invested in nonbiodiverse taxa (Leather, 2009, 2013). Paradoxically then, the increased emphasis on biodiversity studies has not led to resources becoming sufficiently available to tackle the critical issues facing taxonomists, the very discipline dedicated to describing in biological detail the biodiversity of the earth.

We must make clear to the entire scientific community, especially funding agencies, how taxonomic work is relevant and essential. We must be able to provide the coherent taxonomic framework expected of us in a robust and timely fashion, even as we defend alpha taxonomy for its own sake (Wheeler, 2008; Samyn & De Clerck, 2012). In short, taxonomists in general, and

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aphidologists in particular, must act to mobilize our greatest but most underappreciated resources: expert knowledge and museum specimens.

With both experts and specimens spread worldwide, globally comprehensive taxonomic work is a massive undertaking, but 3 key technological advances allow us to move forward. First, platforms such as Aphid Species File (Aphid.SpeciesFile.org) and Google Groups and Drive (groups.google.com and drive.google.com) allow us to collaborate in real time and across great distances. Second, the ability to digitally catalog complex imagery and ancillary data allows us to make specimens available online for virtual curation by experts irrespective of their physical address. Third, the ability to rapidly incorporate new information allows us to escape from the traditional pace of taxonomy and become more active participants in rapidly developing fields such as biodiversity conservation, border security, and global climate change.

We have the tools to mobilize our community's most valuable resources, structure our field to match the current scientific paradigm, and position ourselves to gain the resources we need to move forward. The key lies in linking the aphid taxonomy community with the breadth of aphid biological diversity represented by our museum specimens.

The current state of aphid taxonomy

With the publication of *Aphidura iranensis* (Nieto Nafría *et al.*, 2013), the total number of extant aphid species reached 5 000 (Aphididae, Hemiptera, sensu Remaudière & Remaudière 1997; Favret 2013 is the source of taxonomic statistics here and elsewhere). With 520 genera, this would make for a reasonable 10 species per genus, but the reality is stark: fully one third of aphid genera are monotypic, half of all genera belong to a single subfamily (235 to a single tribe, Macrosiphini), and a 4th of all aphid species belong to 1 of only 4 genera (*Aphis*, 559 species; *Cinara*, 244; *Macrosiphum*, 233; *Uroleucon*, 244).

In 2012, we lost one of the great aphidologists of our time, Victor Eastop. Quotations from his obituaries are relevant here. "[Eastop] took some pride in NOT having described numerous new species. Indeed by recognizing many synonymies he probably removed more names from the described aphid fauna than he added" (Martin, 2012). "In 1976 he produced (with D. Hille Ris Lambers) a *Survey of the World's Aphids*, the 1st publication to catalogue aphids on the world scale. Until then all taxonomic work on aphids had been restricted to particular regions of the world, but many pest aphids distribute themselves around the world on crops and ornamental plants, so publications that cover the whole world are most appropriate. Vic was convinced that this was the way to proceed . . . " (Blackman, 2012).

I invoke the memory of Eastop to underscore that the way forward in aphid taxonomy lies less in the description of new species of *Aphis* and new genera of Macrosiphini, as important as that may be, and more in the systematic revision and synthesis of these and other large aphid groups, and that on a global scale. Almost all aphid taxonomic work continues to be geographically restricted, and currently no one has the resources to undertake alone the comprehensive revision of a large group such as the species of *Aphis* or the genera of Macrosiphini. However, we can address these large and problematic aphid groups by using informatics tools, linking our expertise and specimens across time and space using cybertaxonomy.

Cybertaxonomy

At its heart, "cybertaxonomy" is little more than simple "taxonomy," but it aims to mobilize taxonomy through digital networks of people, products, and data. Wheeler's (2007) aims of cybertaxonomy are here modified and adapted to aphids:

(i) Search for and describe species across the globe using as broad a dataset as possible (i.e., not just morphology and host association alone).
(ii) Classify species phylogenetically, providing Linnaean classifications and names.
(iii) Connect everything that is known about each species to its name.
(iv) Link specimens and experts efficiently and effectively.
(v) Organize and actively exchange data and literature.
(vi) Mobilize taxonomic knowledge communities and coordinate resources across them.

The quadrennial International Symposium on Aphids, most recently held in 2013 in Beijing, China, is a gathering of aphid specialists of all disciplines. A European francophone network, the "*Réseau de Biologie adaptive des Pucerons et des Organismes associés*," includes over a hundred members and meets annually to hold workshops and exchange ideas related to aphid evolution research. The "Aphid Special Interest Group" of the Royal Entomological Society meets regularly and the "International Aphid Genomics Consortium" is very active. The aphidology community may be networked generally, but the aphid "international taxon knowledge community," is not yet fully "coordinated" (Wheeler, 2007) and has not produced a major collaborative taxonomic product (but see

Nieto Nafría *et al.*, 2011). The "Aphid Systematics Group" (groups.google.com/forum/#!forum/systemaphid), a "Google Group" of aphid systematists worldwide, serves as the nucleus for an ambitious global collaborative project, welcoming all aphidologists and their associates to join.

Aphid taxonomy's "virtual species observatory" (Wheeler, 2007) consists of a collection of digital tools that facilitate and accelerate systematic research and collaboration, with a firm emphasis on specimens and specimen data.

Networked specimen data

Aphid Species File (ASF) serves bibliographic, nomenclatural, and taxonomic data on the aphids of the world (Favret & Eades, 2009) and is the principal source of such data for third-party aggregators such as the Catalogue of Life (www.catalogueoflife.org), the Encyclopedia of Life (eol.org), and the Global Biodiversity Information Facility (GBIF, www.gbif.org). It currently includes ~60 000 individual citations, linking aphid taxa to their treatments in published references. Along with tracking taxonomic citations, ASF can record changes in taxon concepts (e.g., Franz & Cardona-Duque, 2013). Importantly, ASF can serve aphid specimen data linked to its taxonomic records.

Currently, GBIF (data.gbif.org) serves ~22 000 aphid specimen records with latitude and longitude coordinates, almost all from the Illinois Natural History Survey (Champaign, IL, USA). The US NSF Advancing Digitization of Biological Collections program is funding aphid specimen digitization (tcn.amnh.org) but no aphid taxonomist is directly involved in the project. The paucity of digitized aphid specimen data is perhaps due to the difficulty of establishing the necessary informatics infrastructure such as databases and servers. ASF has the capacity to serve specimen data, both on its own site and to GBIF. It is open to any aphidologist who wishes to share data. Individual collections can share their aphid data on ASF, and taxon revisers can publish specimen data from multiple collections.

By prepopulating a relational desktop specimen database with aphid names from ASF, plant names from the USDA Plants database (USDA, NRCS, 2013) and others, and geographic localities from the GEOnet Names Server (NGA, 2013) and others, specimen data entry can be relatively rapid. The author has developed a database and workflow that fully digitizes 88 aphid slides per person-hour, including: (i) sorting slides, (ii) labeling each with a sticker-style unique identifier label, (iii) scanning them into image files unique for each slide, and (iv) capturing the key label data of aphid species, plant host, collection locality, and collection date. Given limited resources, data capture should prioritize the quality specimens that are the subject of ongoing research.

A database of specimens can be used to populate distribution maps and dynamically generate geographic checklists and host plant catalogs. Unlike traditional catalogs based on literature citations (e.g., Holman, 2009), dynamic specimen-based catalogs are free to the user, they are easily kept up to date, and identifications remain confirmable. Spurious host records are also easily identified. Aphids are tightly associated with their hosts and accurate host identity is critical to most aphid research, so records for singleton alatae may be filtered out, or only those host records found for a certain number of independently collected colonies could be counted. Aphidologists do not routinely retain vouchers of host plants for confirmed identification, so a metric of host identity confidence based on the number of aphid specimen records would be particularly valuable. Digital specimen records can also autopopulate "material examined" sections of taxonomic manuscripts.

Whereas ASF serves dynamic data subject to edits such as reidentifications, static versions of certain specimen data may be useful. The "material examined" portion of taxonomic articles could take the reader directly to a downloadable dataset that would reflect the data exactly as they were presented in the publication. For example, Sheffield (2013) simultaneously published a description of a new bee species and the digitized specimen data associated with his description. The published article and the specimen data reference each other via digital object identifiers (DOI) (doi:10.3897/zookeys.283.4674 and doi:10.5886/txsd3at3, respectively). Entering either DOI into a resolver (www.doi.org) is sufficient to find the original.

For projects in progress, taxonomically defined sections of ASF can be cloned and made private, available online to authorized users only (Cigliano & Eades, 2010). Thus, collaborators can enter and update data for the focus taxon and release the data publicly only once the pertinent article is published. Each collaborative group of aphid taxonomists thus works on a private clone of their project's taxon. The cloned database serves as the focal point for the collaboration and significantly contributes to global aphid knowledge when it is released to the public. ASF has received significant investment from aphidologists in 5 countries (see Acknowledgments, below) and is seeking taxonomic group leaders to accelerate its growth and functionality for our scientific community and others.

Cyberspecimens

Unlike most other insect groups, aphids are generally preserved on microscope slides for examination and museum storage. Compared to pinning insects, clearing and preparing slide-mounted aphids incurs great cost in time and material (Hille Ris Lambers, 1950). However, slide-mounted specimens are examined from 1 direction, directly above, making aphids relatively easy to image. Purpose-built microscope slide scanners have long been on the market, used by medical researchers to digitize medical pathology slides. A survey of several such models proved disappointing for insect slides, however: even those that could image several focal planes in the vertical-depth or *Z*-axis dimension, proved inadequate to image relatively thick insect slides. The instruments best fitted to the task were actual compound microscopes outfitted with motorized stages and specialized imaging software. The major microscope manufacturers now sell software packages capable of assembling tiled and *Z*-stacked, high-magnification and high-resolution images that can be served online. The assembled images thus permit the viewer to navigate a digital rendition of a specimen in 3 virtual dimensions. One can focus up and down through the *Z*-axis of any number of images of a cleared specimen at predefined intervals; one can move the assembled images in an *X*–*Y* plane to find and examine microscopic detail of any part of the specimen. Essentially, the digital imagery creates a virtual rendition of the specimen that is almost as informative as the specimen itself. Made available online with its ancillary data, this digital imagery becomes a "cyberspecimen" (Fig. 1).

Cyberspecimens have the potential to dramatically accelerate aphid systematics. Perhaps the biggest obstacle to learning aphid taxonomy and identifying aphids is the lack of reference material. Only a small handful of aphidologists work in a significant aphid repository, and the world's 2 largest and most important aphid collections, the Natural History Museum (London) and the Muséum national d'Histoire naturelle (Paris), themselves no longer have full-time aphid curators on staff. Cyberspecimens can be served online as a reference collection available to anyone with a computer and an Internet connection (Ang *et al.*, 2013).

Cyberspecimens would obviate the need to send fragile material on loan. Since real specimens are endangered

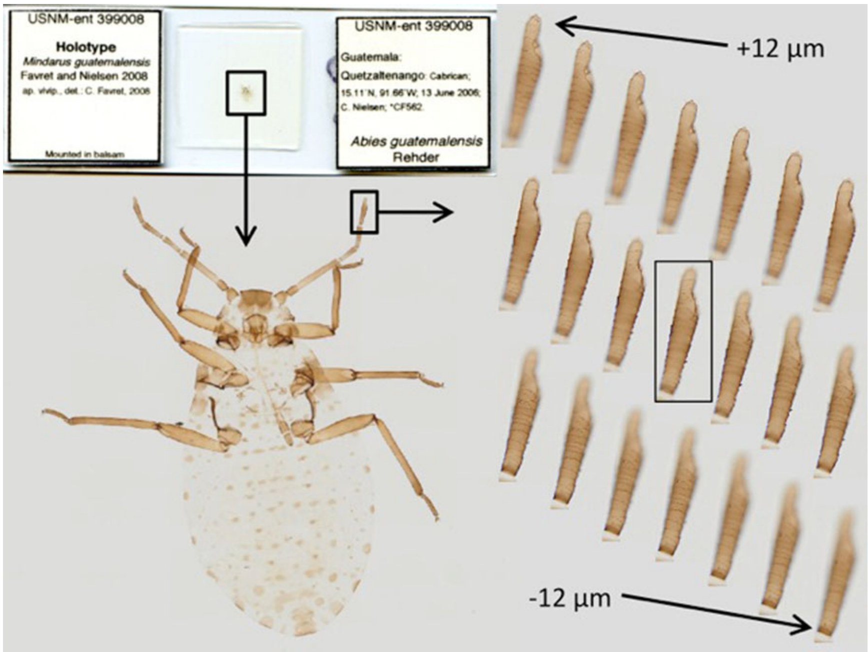

Fig. 1 Representation of a cyberspecimen. The labels of the microscope slide were printed directly from a specimen database and the labeled slide was imaged with a flatbed scanner. The 21 stacked images of the 6th flagellomere are each 1.2 μm apart, vertically, spanning a vertical range of 24 μm. The framed image is the central image slice (reference slice 0 μm). The specimen was imaged with an Olympus® VS120 microscope and cellSens® software. The cyberspecimen can be examined with free OliVIA® software. The composite imagery of the specimen, at 20×, includes 1 260 individual images that span *X*–*Y* dimensions of 3.0 mm × 3.5 mm and a vertical *Z*-axis of 40 μm.

when they leave their host institution, some museums do not loan primary types as a matter of policy. Unlike the current state with pinned insects (e.g., Ang *et al.*, 2013) aphid cyberspecimens are digitized in total, so the user can examine the entire specimen, not just those characters that were selected *a priori* by the imager. Cyberspecimens can also be shared with collaborators or colleagues from whom identifications, confirmations, or other help are requested.

Cyberspecimens can serve as molecular vouchers, permitting others to efficiently confirm, annotate, or change the original determinations based on molecular techniques. DNA sequence databases have too many mis- or unidentified sequences (Bridge *et al.*, 2003; Kwong *et al.*, 2012) and even those sequences that are tied to a specimen are not identifiable without a loan or a trip to the specimen's repository. Cyberspecimen vouchers could be made available to the entire aphid community for identification and validation.

Most molecular aphid systematics and barcoding endeavors destroy the specimen during DNA extraction. Some researchers preserve a colony-mate of the destroyed specimen for identification purposes, but colonies are often mixed (Vantaux *et al.*, 2011), so unless 1 specimen was observed giving birth to the other, there is no way to ensure that the 2 specimens were genetic clones. Given the prevalence of mixed colonies, the unwary may even have 2 different species. Nondestructive DNA extraction methods can simultaneously extract DNA and clear the specimen for slide mounting (Favret, 2005). Most modern DNA extraction kits can be used nondestructively: the aphid, its venter sliced open, is simply left overnight in extraction buffer and removed the next day with sterile forceps. The DNA purification process then continues with the extracted DNA in the buffer solution. Such methods permit unequivocal association of DNA sequences and specimens, including newly established primary types (Favret, 2009; Favret & Miller, 2011), and are safe for the specimen. As an aside, this technique can be used to clear specimens independently of DNA extraction, and avoids the risk of over-clearing the specimen often encountered with KOH-based clearing methods–for this latter application, the author uses the method described by Hillis *et al.* (1996, p 342).

Distributed morphological observations

Every aphid taxonomist makes qualitative and quantitative observations of the specimens examined and identified. Species descriptions always include such specimen observation data, as do many identification keys. These data usually become disassociated from their source specimens, however, leaving the next taxonomist to rescore the very same specimens for the very same characters, and missing the opportunity to incrementally improve our taxonomic resolution. Databased specimens should be kept associated with their observational data and vice versa, and these linked data should be inputted into a coordinated, community-run and community-accessible database.

Just as specimen collection data can be compiled and automatically exported for "material examined" portions of taxonomic manuscripts, so compiled morphological data can be automatically exported for taxon descriptions. A species description thus becomes the compiled data of all the observations of all the specimens of that species. These data can be exported as static descriptions for establishing new taxa, but descriptions can also remain dynamic, each newly examined specimen adding to and refining the description available online. If a specimen were later reidentified as a different species, the data for that specimen would be removed automatically from the composite description of 1 species and added to the other.

Aggregated specimen data can also be used to automatically populate interactive identification keys. The quantitative measurements and qualitative character coding used for AphID, an online interactive key to polyphagous and cosmopolitan aphid species (Favret & Miller, 2012), were exported from a specimen database and reimported into the Lucid® software (Queensland Biological Information Technology, Brisbane, Australia) that runs the identification key. As additional specimens are examined, newer data help refine the key. Conversely, if a certain character seems spurious, it will remain possible to reexamine the source specimens and reevaluate the character or confirm the determination. This feature has already proven itself useful for AphID (see Acknowledgments).

Morphological examination is often a subjective task and even certain anatomical measurements can differ between observers. For example, Noordam's (1991) body length for most species included the cauda, whereas Blackman and Eastop (2006) excluded it. AphID (Favret & Miller, 2012) features a glossary with detailed pictures of anatomical characters and descriptions of how quantitative characters should be measured, but a more thorough standardization of aphid morphological terminology can help assure that data from different observers are cross-compatible. Among other benefits, an ontology (a network of relationships of concepts) of aphid anatomy would establish the foundation for morphological nomenclature; it would ensure that two people are discussing the same anatomical concept (e.g., "unguis" has two completely different meanings:

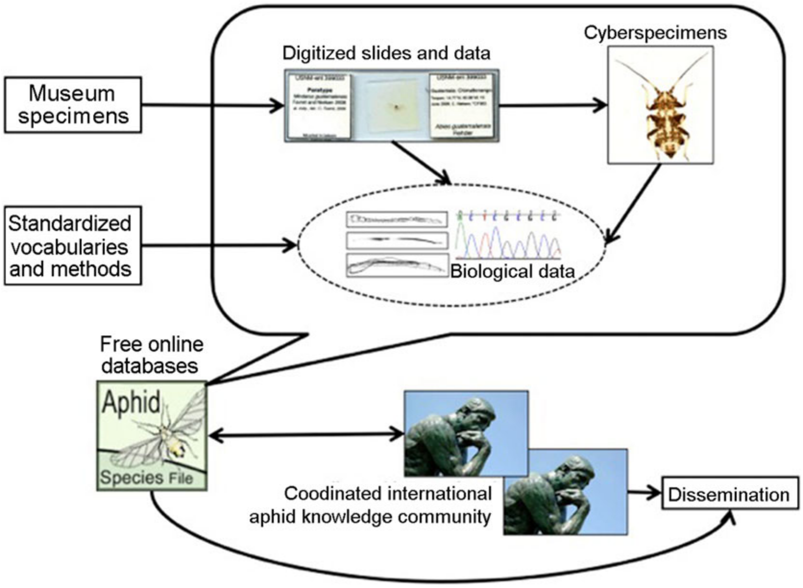

Fig. 2 Conceptual cybertaxonomic workflow, starting with physical museum objects and ending with published scientific products. Photograph of Auguste Rodin's "The Thinker" in Kansas City, MO, USA, is by Brian Hillegas (www.flickr.com).

AphID.AphidNet.org/glossary.php#unguis). An aphid ontology would also help render human observations into a machine-friendly, computable format (Yoder *et al.*, 2010), and would be based on discreet observations tied directly to specific specimens as discussed above (Deans *et al.*, 2012).

AphidAtlas is a nascent project initiated by the International Aphid Genomics Consortium to develop an ontology for aphids, primarily as a means to map the connections between genes, transcripts, and proteins. The goals of AphidAtlas primarily address the needs of molecular biologists, but also explicitly include aphid anatomy. The inclusion of anatomy will be of great interest to taxonomists, and taxonomist involvement will help ensure the representation of species other than those whose genomes are sequenced.

Rising to the challenge

This article serves as a plea to the aphid taxonomic community to tackle larger and more ambitious projects. Massively multiauthored publications are de rigueur in certain disciplines but almost nonexistent in taxonomy. However, addressing the taxonomy of intractably large aphid groups will require active international collaboration of the sort that readily leads to multiauthored papers. If each participant (i) databased and (ii) examined a set of specimens, (iii) recorded their observations following standardized methods using standardized vocabulary, (iv) selected high-quality representatives and primary type specimens for cyberspecimen rendering, and (v) worked iteratively with their colleagues to refine the taxon concept, the "coordinated international aphid knowledge community" (Wheeler, 2007) could efficiently produce durable, updatable, high-quality taxonomic products (Fig. 2).

There are, of course, obstacles to overcome. Perhaps the most significant is political in nature. Especially given the current funding challenges, taxonomists may feel the need to compete against each other rather than cooperate. It is clear that any major venture will have to establish clear understandings regarding data ownership and sharing, publication and authorship, and other sensitive matters. Certain resource-intensive tasks such as DNA sequencing and 3-dimensional digital imaging would best be centralized in one or a few laboratories. Ultimately, however, by collaborating to reduce the taxonomic impediment, increase the access of the scientific community to our unique and critical contributions, and banding together to renew the relevance of our field, funding and resource availability for our discipline stands to gain in comparison to our current situation. Given the ubiquity of the Internet and accessibility to a myriad of online tools, there is opportunity in cybertaxonomy for all aphidologists to make a significant and lasting contribution to our science. We have the tools available to make a start, and the future of our field will benefit from the combined contributions of every one of us.

Acknowledgments

This article seeks to promote the tools to put primary, reviewable, and confirmable aphid data onto taxonomists' desktops. However, it should be noted that the Internet also provides the medium to publish and maintain up to date summary and review works. Roger Blackman (retired, the Natural History Museum, London) maintains, updates, and provides for free, an extraordinary aphid knowledge synthesis and identification tool, Aphids on the World's Plants (AphidsOnWorldsPlants.info). I would like to thank the contributors to Aphid Species File for their active participation: Masakazu Sano (Okinawa City Municipal Museum), Andrey Stekolshchikov (Russian Academy of Sciences, St. Petersburg), Ge-Xia Qiao and Li-Yun Jiang (Chinese Academy of Sciences, Institute of Zoology, Beijing), Gary Miller and Andrew Carmichael (US Department of Agriculture, Systematic Entomology Laboratory, Beltsville, Maryland), and Andrew Jensen (Washington State University, Pullman). Susan Halbert (Florida Department of Agriculture and Consumer Services, Gainesville) found some questionable characters in AphID; they were re-evaluated in the source specimens and the key was updated. Yvan Rahbé (Institut National de la Recherche Agronomique, Lyon, France) is the chief coordinator of AphidAtlas. Xiao-Lei Huang (Chinese Academy of Sciences, Institute of Zoology, Beijing) provided helpful conversational insight and encouragement. Karen Favret (University of Montreal) edited and contributed valuable comments to the manuscript. I also express my sincere thanks to 2 reviewers, unremunerated and recognized only anonymously, for providing expert opinions regarding a previous version of this manuscript.

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