Bourguignon Unit

Associate Professor Tom Bourguignon

Back row, from left to right: Catherine Gatt, Esra Kaymak, Ales Bucek, Tracy Audisio, Simon Hellemans, Kensei Kikuchi, Anna Prokhorova.
Front row, from left to right: Zhuli Cheng, Gelyn Bourguignon, Kazuko Toyoda, Kalleshwara Swamy, Lauro Bourguignon, Nobuaki Mizumoto, Tadanami Mizumoto, Thomas Bourguignon, Eiji Bourguignon.

Abstract

During the financial year 2023, we kept on working on the genomes of the 45 termites and two cockroaches we started sequencing during FY2020 and FY2021. We finished many comparative genomics analyses on these genomes and started writing several papers. As every financial year, we sequenced >1000 termite and cockroach samples for phylogenetic purposes. We also sequenced a dozen cockroach and termitophylous beetle genomes for comparative genomics analyses. We published 14 peer-reviewed papers, two of which were in Nature Index journals.

1. Staff

- Thomas Bourguignon, Associate Professor
- Ales Bucek, Postdoctoral Scholar (Until May 2023)
- Anna Prokhorova, Postdoctoral Scholar (Until August 2023)
- Simon Hellemans, Postdoctoral Scholar
- Nobuaki Mizumoto, Postdoctoral Scholar (Until December 2023)
- Kalleshwara Swamy Chicknayakanahalli Marulasiddappa, Postdoctoral Scholar (Since July 2023)
- Yi-Ming Weng, Postdoctoral Scholar (Since January 2024)

- Esra Kaymak, Technical Staff
- Aoi Mizumoto, Technical Staff (June – December 2023)
- Kensei Kikuchi, Ph.D. Student
- Tracy Audisio, Ph.D. Student
- Cong Liu, Ph.D. Student
- Zhuli Cheng, Ph.D. Student
- Tereza Berankova, Visiting Research Student
- Catherine Gatt, Visiting Research Student (September – December 2023, March 2023-)
- Kazuko Toyoda, Research Unit Administrator, Administrative Assistant

2. Collaborations

2.1 Historical biogeography of termites

- Type of collaboration: Joint research
- Researchers:
    - Professor Yves Roisin, University of Brussels
    - Professor Nathan Lo, University of Sydney
    - Professor Rudolf A. Scheffrahn, University of Florida
    - Professor Eliana Cancello, University of Sao Paulo
    - Professor Jan Sobotnik, Czech University of Life Sciences
    - Associate Professor Theodore A. Evans, University of Western Australia
    - Associate Professor David Sillam-Dussès, University of Paris 13

2.2 Functional evolution of termite gut microbes

- Type of collaboration: Joint research
- Researchers:
    - Professor Nathan Lo, University of Sydney
    - Professor Gaku Tokuda, University of the Ryukyus
    - Professor Jan Sobotnik, Czech University of Life Sciences

2.3 Functional evolution of termite genomes

- Type of collaboration: Joint research
- Researchers:
    - Associate Professor Dino McMahon, Free University of Berlin
    - Professor Jan Sobotnik, Czech University of Life Sciences
    - Dr. Mark Harrison, University of Münster

3. Activities and Findings

3.1 Molecular phylogeny and historical biogeography of termites

We continued working on the molecular phylogeny and historical biogeography of termites during FY2023. Our most significant achievement was on the termite fauna from Madagascar, a region of the world that was seldom sampled in the past.

The historical biogeography of termites has been studied in detail using ancestral range reconstructions on molecular phylogenetic trees. While past studies provided a clear picture of the historical biogeography of termites, they largely overlooked the termite fauna of Madagascar, a continental island renowned for the uniqueness of its endemic fauna. We reconstructed time-calibrated phylogenetic trees using 601 termite mitochondrial genomes, including 92 mitochondrial genomes of termites from Madagascar (Figure 1). Our analyses indicate that termites colonized Madagascar between seven and ten times independently during the second half of the Miocene, between 8.4-16.6 Ma (95% HPD: 6.1-19.9 Ma). Therefore, termites colonized Madagascar by means of long-distance over-water dispersals more than 70 million years after the separation of Madagascar and India. Our study provides additional evidence that the fauna of Madagascar originated from dispersal events rather than vicariance through continental drift. Notably, the timing of the termite colonization of Madagascar matches that of Australia and took place during the global expansion of grasslands. Furthermore, the taxonomic composition of the Neoisopteran fauna of Madagascar and Australia are strikingly similar, providing new evidence that the rise of termites as the dominant animal decomposers in terrestrial tropical biomes was fostered by new ecological opportunities arising from the spread of new biomes.

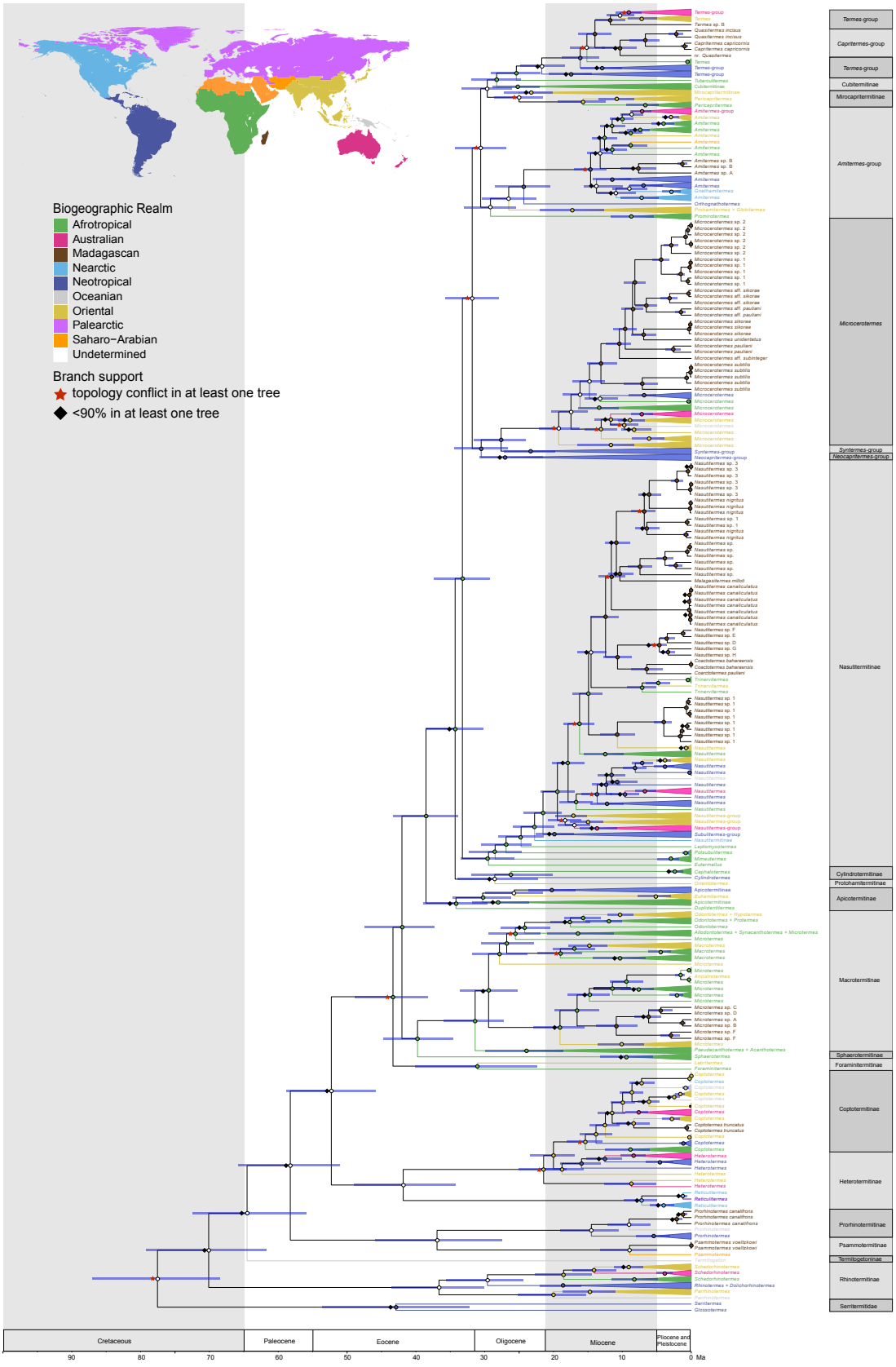

Figure 1. Time-calibrated Bayesian phylogeny inferred from 601 mitochondrial genomes. Node labels provide a summary of node supports across the six phylogenetic analyses: red stars indicate topology conflicts for at least one analysis, and black diamonds indicate support value <90% for at least one analysis. Nodes without labels have support values >90% for all analyses. Node bars indicate the 95% HPD intervals estimated with BEAST 2. Tips and node circles are color-coded to indicate biogeographic realms. White circles indicate undetermined ancestral distribution. Clades containing species collected in the same biogeographic realm are collapsed, except for species collected in the Madagascan realm. The tree was reproduced from Wang et al. (2023).

3.2 Functional evolution of termite gut microbes

We have been investigating the functional evolution of the gut microbiome of termites using the gut metagenomes of 221 termite samples. The first paper based on this dataset was published during FY2022 (Arora et al. 2022). We published a second paper during FY2023 in which we described the cophylogeny between termites and their gut microbes.

Termites are classical models for studying gut microbiomes. They host unique communities of lignocellulolytic bacteria, including many bacteria found nowhere else than in termite guts. These endemic gut bacteria are believed to be acquired by a combination of horizontal transfers between termite species and vertical transfers from parents to offspring. We built bacterial phylogenetic trees using marker genes derived from 202 termite gut metagenomes and showed that the cophylogenetic patterns found between termites and their endemic gut bacteria can be explained by a model involving vertical transfers only (Figure 2). Therefore, horizontal transfers between termite species are not needed to explain the cophylogenetic patterns between termites and their endemic gut bacteria. Our results indicate that the symbiotic system composed of termites and their gut bacteria is potentially the oldest case of an animal strictly cospeciating with some gut bacterial lineages.

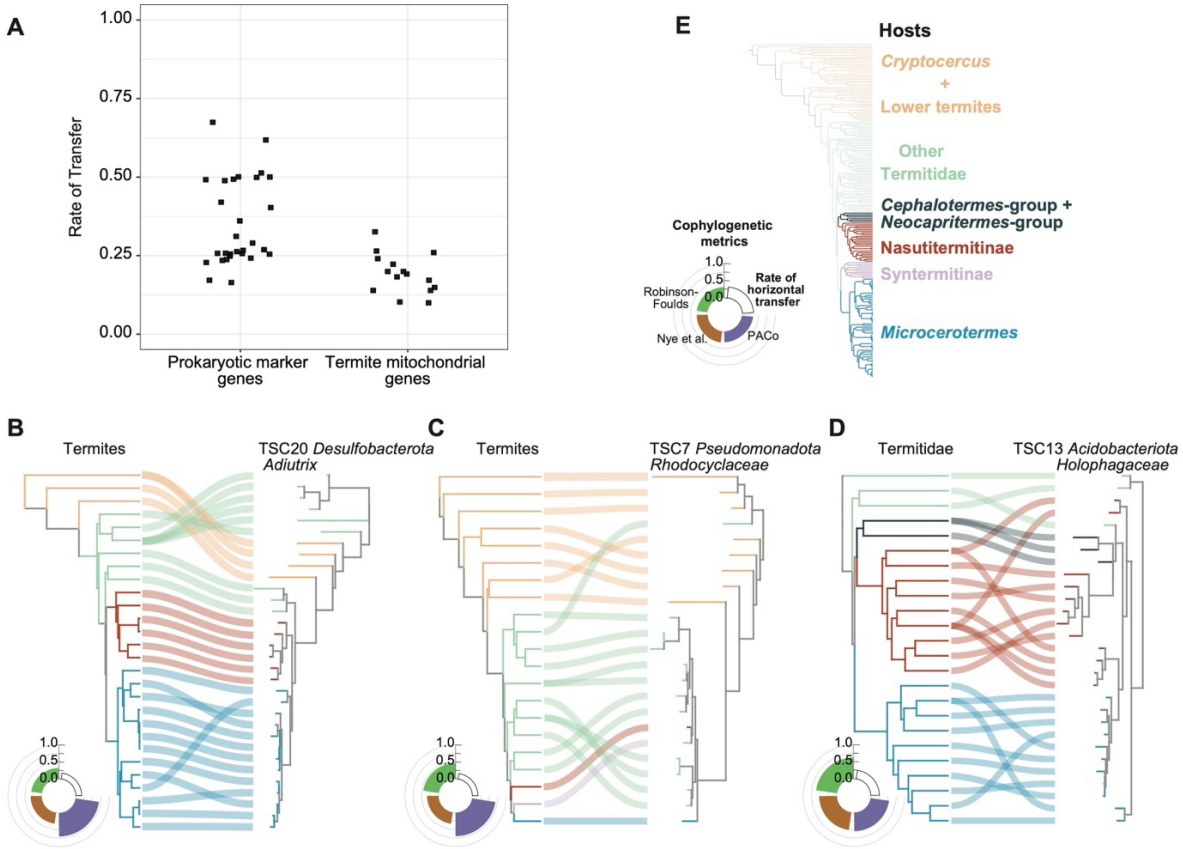

Figure 2. Rate of transfer and phylogenetic trees of some termite-specific bacterial clades (TSCs) showing strong cophylogenetic signals with termites. (A) Rates of horizontal transfer estimated using the maximum likelihood method implemented in the GeneRax software. Tanglegrams between termites and (B) the *Desulfobacterota Adiutrix* TSC20, (C) the *Pseudomonadota Rhodocyclaceae* TSC7, and (E) the *Acidobacteriota Holophagaceae* TSC13. (E) Phylogenetic tree of termites inferred from mitochondrial genomes. Bacterial phylogenies were reconstructed using the marker gene COG0552. The diagrams below the phylogenetic trees indicate the results of the cophylogenetic analyses and the estimation of the horizontal transfer rate. The figure was reproduced from Arora et al. (2023).

4. Publications

4.1 Journals

1. Arora J., Bucek A., Hellemans S., Beránková T., Romero Arias J., Fisher B., Clitheroe C., Brune A., Kinjo Y., Šobotník J., & Bourguignon T. (2023) Evidence of cospeciation between termites and their gut bacteria on a geological time scale. *Proceedings of the Royal Society B: Biological Sciences*, 290, 20230619.
2. Carrijo T.F., Castro D., Wang M., Constantini J.P., Bourguignon T., Cancello E.M., Roisin Y., & Scheffrahn R.H. (2023) Diminishing the taxonomic gap in the neotropical soldierless termites: descriptions of four new genera and a new *Anoplotermes* species (Isoptera, Termitidae, Apicotermitinae). *ZooKeys*, 1167, 317-352.
3. Chakraborty A., Šobotník J., Votypkova K., Hradecky J., Stiblik P., Synek J., Bourguignon T., Baldrian P., Engel M.S., Novotny V., Odriozola I. & Vetrovsky T. (2023) Impact of wood age on termite microbial assemblages. *Applied and Environmental Microbiology*, 89, e00361-23.1.
4. Mizumoto N., Hellemans S., Engel M.S., Bourguignon T., Buček A. 2024. Extinct and extant termites reveal the fidelity of behavior fossilization in amber. *Proceedings of the National Academy of Sciences*, 121, e2308922121. doi: 10.1073/pnas.2308922121
5. Wang Y.S., Zhang J.W., Lo N., Bourguignon T., Guo L., Li B.L., Che Y.L., & Wang Z.Q. (2023) Phylogenetic analysis of Blaberoidea reveals non-monophyly of taxa and supports the creation of multiple new subfamilies. *Cladistics*, 39, 198-214.
6. Kovacs T.G.L, Walker J., Hellemans S., Bourguignon T., Tatarnic N.J., McRae J.M., Ho S.Y.W, Lo N. 2024. Dating in the dark: elevated substitution rates in cave cockroaches (Blattodea: Nocticolidae) have negative impacts on molecular date estimates. *Systematic Biology*, 73, 532-545. doi: 10.1093/sysbio/syae002
7. Hellemans S., Hanus R. 2024. Termite primary queen — ancestral, but highly specialized eusocial phenotype. *Current Opinion in Insect Science*, 61, 101157. doi: 10.1016/j.cois.2023.101157
8. Romero Arias J., Hellemans S., Kaymak E., Akama P. D., Bourguignon T., Roisin Y., Scheffrahn R. H., Šobotník J. 2024. Mitochondrial phylogenetics position a new Afrotropical termite species into its own subfamily, the Engelitermitinae (Blattodea: Termitidae). *Systematic Entomology*, 49, 72-83. doi: 10.1111/syen.12607
9. Wang M., Hellemans S., Buček A., Kanao T., Arora J., Clitheroe C., Rafanomezantsoa J.-J., Fisher B.L., Scheffrahn R., Sillam-Dussès D., Roisin Y., Šobotník J., Bourguignon T. 2023. Neoisoptera repetitively colonised Madagascar after the Middle Miocene climatic optimum. *Ecography*, 2023: e06463. doi: 10.1111/ecog.06463
10. Sillam-Dussès D., Jandák V., Stiblik P., Delattre O., Chouvenc T., Balvín O., Cvačka J., Soulet D., Synek J., Brothánek M., Jiřiček O., Engel M., Bourguignon T., Šobotník J. 2023. Alarm communication predates eusociality in termites. *Communication Biology*, 6, 83, doi: 10.1038/s42003-023-04438-5
11. Araujo N.S., Hellemans S., Roisin Y., Fournier D. 2023. Transcriptomic profiling of castes and of sexually and parthenogenetically produced reproductive females in the termite *Cavitermes tuberosus*. *Entomologia Experimentalis et Applicata*, 171, 350-360, doi: 10.1111/eea.13285

12. Tanaka Y., Valentini G., Pratt. C. S., Shimoji H., Mizumoto N. (2023) Obtaining long movement trajectories of leaders and followers in ant tandem runs. *STAR Protocols*, 4, 102769, DOI: 10.1016/j.xpro.2023.102769
13. Mizumoto N. (2023) TManual: Assistant for manually measuring length development in structures built by animals. *Ecology and Evolution*, 13, e10394, DOI: 10.1002/ece3.10394
14. Mizumoto N., Tanaka Y., Valentini G., Richardson O. T., Annagiri S., Pratt. C. S., Shimoji H. (2023) Functional and mechanistic diversity in ant tandem runs. *iScience*, 26, 106418, DOI: 10.1016/j.isci.2023.106418

4.2 Books and other one-time publications

Nothing to report

4.3 Oral and Poster Presentations

1. Bourguignon, T. 2024. Evolution of termites and their gut microbiota. International Symposium on termites and scale insects. Central Mindanao University, Philippines
2. Bourguignon, T. 2023. Evolution of termites and cockroaches with their bacterial symbionts. ERATO Evolving Symbiosis Project International Seminar Series #27. Tsukuba, Japan
3. Bourguignon, T. 2023. Evolution of termites and cockroaches with their bacterial symbionts. International Conference of Blattodea Research (ICBR), Münster, Germany
4. Bourguignon, T. 2024. Investigating the metabolism of dominant termite gut bacteria. Biology and Genomics of Social Insects. Social Insects Meeting at Cold Spring Harbor, USA
5. Hellemans, S., 2024. Genome phylogenetic signal and sex chromosomes in termites. 2nd Termite Genomics Workshop. BAM Federal Institute for Materials Research and Testing, Berlin, Germany
6. Mizumoto N., Kikuchi K., Hellemans S., Bourguignon T., Bailey N. 2023. Evolution of leader-follower role in termite tandem runs. Entomology 2023 (Entomological Society of America). National Harbor (Maryland), USA
7. Fontaine, N., Hellemans, S., Roisin, Y. 2023. Un complexe d'espèces cryptiques dans le premier genre de termites décrit (Termes Linné 1758). 31ème congrès de l'Union Internationale pour l'Etude des Insectes Sociaux – Section Française (UIEIS-SF). Toulouse, France
8. Timmermans, J., Hellemans, S., Fontaine, N., Roisin, Y. 2023. Comment l'inquilinisme façonne les systèmes de reproduction au sein d'une relation inquiline-hôte chez les termites. 31ème congrès de l'Union Internationale pour l'Etude des Insectes Sociaux – Section Française (UIEIS-SF). Toulouse, France
9. Mizumoto N., Evolution of termite tandem runs: How Formosan termite differs and is similar to other lineages. 3rd International Conference of the Subterranean Termite: Dr. Minoru Tamashiro Memorial Symposium, Honolulu, USA
10. Mizumoto N., Kikuchi K, Hellemans, Bourguignon T., Bailey N., Evolution of leader-follower role in termite tandem runs. Entomology 2023, Nov 2023, National harbor, MD, USA
11. Gazdick K., Lee S.B., Mizumoto N., Chouvenc T., Su N. Y., Foraging behavior of Coptotermes formosanus and its ability to intercept in-ground bait. Entomology 2023, Nov 2023, National harbor, MD, USA

12. Gazdick K., Lee S.B., Mizumoto N., Chouvenc T., Su N. Y., 104th annual meeting of the Florida Entomological Society, USA
13. Kikuchi K. and Mizumoto N., Individual termite movements reflect nest complexity evolution. The 25th Annual Meeting of the Society of Evolutionary Studies, Japan
14. Taniguchi J., Inoue T., Hung J-F., Hirai A., Mizumoto N., Takeshita F., Kawabata Y., Evolution of movement directions in crabs: restructuring the ancestral state from the behavioral traits of extant species. The 42th Annual Meeting of the Japan Ethological Society (Kyoto), Japan
15. Kikuchi K. and Mizumoto N.，巣構造（自己組織化）の違いとシロアリ行動パターンの進化 The 94th Annual Meeting of the Zoological Society of Japan (Yamagata), Japan
16. Taniguchi J., Inoue T., Hung J-F., Hirai A., Mizumoto N., Takeshita F., Kawabata Y., Evolution of movement directions in crabs: restructuring the ancestral state from the behavioral traits of extant species. The 25th Annual Meeting of the Society of Evolutionary Studies, Japan
17. Mizumoto N., The University of Tokyo, Komaba seminar, Japan.
18. Mizumoto N., University of Sydney, School of Life and Environmental Sciences, Seminar, Australia
19. Mizumoto N., How do you balance your focus on conceptual questions with focus on questions motivated by the organisms you study? The 25th Annual Meeting of the Society of Evolutionary Studies, Japan
20. Mizumoto N., Kyoto University, Laboratory of Insect Ecology, Kakuchi-seminar, Japan
21. Cong L., 2nd Termite Genomics Workshop (15-19th, January 2024, BAM, Berlin).
22. Kalleshwara Swamy. C, Status of termite taxonomy in India, 2024 at Central Mindanao University, Philippines
23. Audisio T., Near chromosome-level assemblies reveal that genome structure is not highly conserved in termites. 2nd Termite Genomics Workshop in Berlin, Germany
24. Audisio T., Near chromosome-level assemblies reveal that genome structure is highly conserved in termites. The International Society for Blattodea Research in Münster, Germany
25. Kalleshwara Swamy. C., Functional role of termites and microbes in wood degradation and carbon recycling in different forests and climatic gradients of India, Delhi at Ministry of Environment, Forest and Climate change, India
26. Kensei K., Comparative Study of Termites' Nesting Strategies and Individual Movement Patterns, Central Mindanao University, Philippines
27. Kalleshwara Swamy, C., Revision of Indian termite taxonomy based on mitogenome data, Tohoku University, Japan

5. Intellectual Property Rights and Other Specific Achievements

Mizumoto N., TManual: Assistance for manually measuring length development of animal structures, https://github.com/nobuaki-mzmt/tmanual

6. Meetings and Events

6.1 EGU Seminar by visitors

- Insights into the onset of African Miombo woodlands: Phylogenomics of the keystone genus *Brachystegia* (Fabaceae, Detarioideae) by Dr. Arthur F. Boom from the Royal Museum for Central Africa (Biology Department, Section Vertebrates, Tervuren, Belgium)
- Exploring diversification tempos and evolutionary histories from African rain to montane forests by Dr. Jérémy Migliore from the Muséum départemental du Var, Toulon, France
- Functional heterogeneity: relationship between group performance and individual behavioural differences By Dr. Isaac Planas-Sitjà from the Department of Biological Sciences, Tokyo Metropolitan University (https://www.researchgate.net/profile/Isaac-Planas), Japan
- From alpine beetle populations to Cretaceous moth radiation: can we connect the dots between microevolution and macroevolution? By Dr. Yi-Ming Weng from the University of Florida, USA
- Cichlid fishes as a model for evolution of altruism in vertebrates by Dr. Shun Satoh from Kyoto University, Japan

7. Other

Nothing to report.