ORIGINAL ARTICLE

Micro CT approach applied in taxonomy: An example on the species *Melanopopillia hainanensis* (Coleoptera: Scarabaeidae)

Yuanyuan Lu, Haidong Yang, Ming Bai*

Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
**Corresponding author, E-mail: baim@ioz.ac.cn*

Abstract Three dimensional morphology of *Melanopopillia hainanensis* Lin, 1980 is reported firstly by using Micro CT technology, including internal and external structures. The male of *M. hainanensis* is described for the first time. A key to the species of *Melanopopillia* is given. This study shows an example of the potential application on the 3D morphology in invertebrate taxonomy, especially in the comparison of important structures with complicated 3D morphology, *e.g.* aedeagus, muscles.

Key words Rutelinae, *Melanopopillia hainanensis*, China, 3D morphology.

1 Introduction

For traditional taxonomy, text descriptions, line drawings and photographs are the main information that can be obtained from the literature. However, brief descriptions and inaccurate line drawings can lead to incorrect interpretations (Godfray, 2002). In those situations, the type specimens and/or determined specimens are relied on by taxonomists (Faulwetter *et al*., 2013). With the development of photographic technology, 2D photographs are now more used in taxonomic studies than line drawings, due to their more detailed and authentic information (Brecko *et al*., 2014). It is easier than before for the readers to make a morphological comparison between different species. Nevertheless, natural organisms like insects are three-dimensional, therefore 2D images still provide limited information as they don't show characters in every angle.

For taxonomy of scarab beetles, the male genitalia are very important in the identification (Richmond *et al*., 2016). However, the fact is that the genitalia of beetles are characterized in three-dimensional space. The traditional line drawings or 2D photographs are not always enough to show the all characters in every angle.

X-ray micro computed tomography (Micro CT, μ-CT) or synchrotron radiation microtomography (SR-μCT) and 3D reconstruction technology have been introduced into several extant and extinct insect groups recently (Faulwetter *et al*., 2013; Steinhoff & Uhl, 2015; Bai *et al*., 2016, 2017; Schmidt *et al*., 2016; Ashe-Jepson *et al*., 2019; Luo *et al*., 2019). And the use of Micro CT greatly enhances the efficiency of obtaining detailed anatomical data and allows morphological characters to be shown in greater detail, which enhanced next-generation-morphology (Garcia *et al*., 2017a; Staab *et al*., 2018; Gorb *et al*., 2019). Researches in taxonomy of extinct insect like Formicidae accelerate the application of this technology (Agavekar *et al*., 2017; Garcia *et al*., 2017a, b; Staab *et al*., 2018; Sharaf *et al*., 2019). Here we use the Micro CT technology in the taxonomic work on a scarab genus (*Melanopopillia*), which will add a research example of animal taxonomy.

The genus *Melanopopillia* was proposed by Lin, 1980 and includes three species from China, *M. dinghuensis* Lin, 1980, *M. hainanensis* Lin, 1980 and *M. praefica* (Machatschke, 1971). Since then, no more species are described in this genus. Among them, *M. hainanensis* was described based on only two female specimens from Hainan. In the recent collections

Received 4 July 2019, accepted 20 October 2019
Executive editor: Fuqiang Chen

originating from Hainan Province, a series of specimens of *Melanopopillia* was found including both male and female, which are identified as *M. hainanensis* according to the characters of scutellum and pygidium. Here we describe the male of *M. hainanensis* for the first time and provide the 3D morphology of the male specimen and genitalia. The revised key to the genus is provided.

2 Materials and methods

2.1 Materials

The materials examined are deposited in the following collections (curators in parenthesis):
IZCAS—Institute of Zoology, Chinese Academy of Sciences, Beijing, China (Ming Bai);
NMPC—National Museum, Praha, Czech Republic (Jiří Hájek).
Figures 1–17, and 21 all generated based on specimen IOZ(E) 1913270.

2.2 Observation and 2D images

Morphological terminology follows Lu *et al.* (2018).

The body length was measured from the apex of the clypeus to the apex of the elytra. The length of pronotum was measured in the middle in dorsal view and its width at the place of greatest width. The ratio of interocular width to head width was measured in dorsal view at greatest width of head and nearest interocular distance.

For observation of morphological structures, specimens were softened by putting them into water for 3–4 hours. Observations and dissections were carried out under an Olympus SZ61 stereomicroscope. The digital images were created with a Canon 5D digital camera in conjunction with a Canon MP-E 65mm f/2.8 1-5X Macro Lens, then stacked by Helicon Focus 5.3.10® based on specimen IOZ(E) 1913270. All images were edited and adjusted in Adobe Photoshop CC®.

2.3 Micro computed tomography and 3D images

The body and dissected aedeagus of *M. hainanensis* (specimen IOZ(E) 1913270) were imaged using propagation phase-contrast synchrotron radiation microtomography (PPC-SR-μCT) on the beamline 13W at the Shanghai Synchrotron Radiation Facility (SSRF). The isotropic voxel size is 3.25 μm. The beam was monochromatized at an energy of 14 keV using the double crystal monochromator. To obtain a phase-contrast effect, we used a sample-detector distance (propagation distance) of 300 mm and 900 projections on 180°. The phase retrieval and slice reconstruction were performed using PITRE software. Based on the obtained image stacks, three-dimensional structures of the specimen were reconstructed and virtually dissected with Amira 5.4 (Visage Imaging, San Diego, USA). Three-dimensional model in pdf. format was generated by Geomagic Studio 12.0.0. All images were edited and adjusted in Adobe Photoshop CC®.

3 Results

3.1 Three-dimensional reconstruction in habitus and male genitalia

The 3D model of *M. hainanensis* was generated by Amira. Figures 9–11 are the screenshots from the 3D model in common angle. Figures 12–14 are the screenshots from the 3D model in specific angle which can provide more detail than 2D photographs. Figures 13–14 show the internal structures from the 3D model.

The 3D model of aedeagus of *M. hainanensis* was generated by Amira. Figures 15–17 are the screenshots from the 3D model in specific angle. The related 3D model in PDF file can be found from Figure 21 generated by Geomagic Studio.

3.2 Taxonomy

***Melanopopillia hainanensis* Lin, 1980** (Figs 1–17)

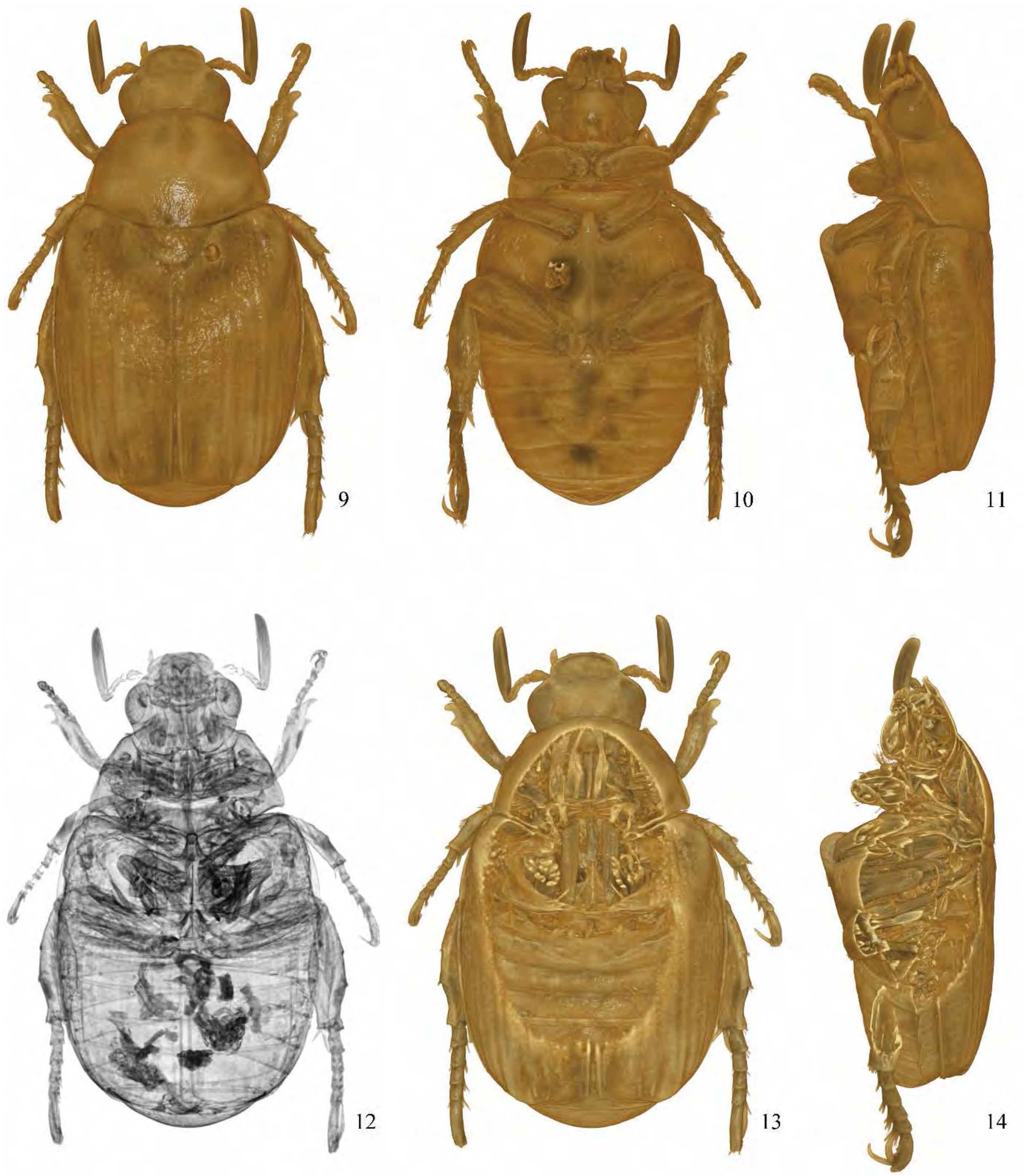
Melanopopillia hainanensis Lin, 1980: 293, 301, fig. 2 (original description); Zorn, 2006: 267 (catalogue); Krajčík, 2007: 83 (catalogue); Krajčík, 2012: 158 (catalogue); Zorn & Bezděk, 2016: 343 (catalogue).

Figures 1–8. Male of *Melanopopillia hainanensis*. 1–3. Habitus. 1. Dorsal view. 2. Ventral view. 3. Lateral view from left. 4. Head and pronotum. 5. Propygidium and pygidium. 6–8. Aedeagus. 6. Dorsal view. 7. Lateral view from right. 8. Ventral view. Scale bars: 1–5 = 5 mm; 6–8 = 1 mm.

Type locality. 'Hainan, Jianfengling'.

Material examined (15♂26♀). CHINA: Hainan Prov.: 2♂5♀ (NMPC), Baotie, Bawangling Mts, Hainan, China, 19.09°N, 109.12°E, 415–800 m, 7–8.V.2011, leg. M. Fikáček, V. Kubeček & L. Li; 1♂1♀ (IZCAS), Tianchi, Jianfengling

Mts, Hainan, China, 900 m, 12.IV.1980, light trap, leg. Fuji Pu (IOZ(E)1966874, 1966875); 1♀ (IZCAS), Jianfengling Mts, Hainan, China, 21.V.1997, leg. Wenzhu Li (IOZ(E)1966877); 1♀ (IZCAS), Tianchi, Jianfengling Mts, Hainan, China, 18.74°N, 108.86°E, 808 m, 20.V.2009, leg. Keqing Song (IOZ(E)1966876); 1♀ (IZCAS), Diaoluo Mts, Lingshui County, Hainan, China, 960 m, 8.V.2011, leg. Wenxin Lin (IOZ(E)1947170); 2♂1♀ (IZCAS), Yinggeling Mts, Baisha, Hainan, China, 600–780 m, 27–30.IV.2011, leg. Wenxin Lin (IOZ(E)1946900, 1946885, 1946886); 1♂ (IZCAS), Guzhandao, Wuzhishan Mts, Hainan, China, 18.86°N, 109.68°E, 638 m, 11.IV.2010, leg. Meiying Lin (IOZ(E)1946881); 1♂ (IZCAS), Diaodengling, Limushan Mts, Qiongzhong, Hainan, China, 19.19°N, 109.74°E, 555 m, 4.IV.2010, leg. Kuiyan Zhang (IOZ(E)1946876); 1♂1♀ (IZCAS), Diaodengling, Limushan Mts, Qiongzhong, Hainan, China, 19.15°N, 109.74°E, 555 m, 4.VI.2010, leg. Meiying Lin (IOZ(E)1946887, 1946882); 3♂3♀ (IZCAS), Diaodengling, Limushan Mts, Qiongzhong, Hainan, China,



Figures 9–14. 3D model for habitus of *Melanopopillia hainanensis*. 9. Dorsal view. 10. Ventral view. 11. Lateral view from left. 12. Phantom view. 13. Frontal plane. 14. Sagittal plane. These photos are screen shots of the 3D model of habitus.

19.15°N, 109.74°E, 555 m, 4.IV.2010, leg. Tianyang Jiao (IOZ(E)1913270, 1913275, 1913273, 1913271, 1913272, 1913274); 1♂2♀ (IZCAS), Tianchi, Jianfeng, Hainan, China, 800 m, 10.IV.1980, leg. Fuji Pu (IOZ(E)1966244, 1966245, 1966246); 1♀ (IZCAS), Bawangling Mts, Changjiang County, Hainan, China, 635 m, 14.V.2007 (IOZ(E) 1946883); 1♀ (IZCAS), Binlanghu Lake, Limushan Mts, Qiongzhong County, Hainan, China, 19.20°N, 109.72°E, 562 m, 7.IV.2010, leg. Meiying Lin (IOZ(E)1946880); 1♀ (IZCAS), Yinhe Hulinzhan, Limushan Mts, Qiongzhong County, Hainan, China, 19.19°N, 109.74°E, 727 m, 5.IV.2010, leg. Kuiyan Zhang (IOZ(E)1946879); 1♀ (IZCAS), Tianchi, Jianfengling Mts, Ledong, Hainan, China, 18.74°N, 108.86°E, 828 m, 20.V.2009, leg. Xinlei Huang (IOZ(E)1946884); 1♀ (IZCAS), Jianfengling Mts, Hainan, China, 700–900 m, 10.IV.1980, leg. Shuzhi Ren (IOZ(E)1966127); 3♂5♀ (IZCAS), Yulingu, Jianfengling Mts, Hainan, China, 18.75°N, 108.93°E, 656 m, 12.IV.2019, leg. Yandong Chen (IOZ(E)2080296 –2080303).

Description of male. Body shape. Elongate ovoid, weakly convex.

Color. Ground color dark brown with strong metallic luster.

Head. Clypeus subrectangular, disc very densely, transversely and confluently punctate; anterior corners rounded; anterior margin weakly reflexed; frons very shallowly impressed medially, densely punctate; vertex sparsely punctate; ratio of interocular width/width of head approximately 0.59; antennal club longer than antennomeres 2–6 combined.

Pronotum approximately 1.7 times wider than long; disc finely and densely punctate, punctures becoming gradually larger and denser laterally, partly confluently; sparse erect setae present near anterior angles and along lateral margin; anterior angles subrectangular; posterior angles obtuse; sides of pronotum very weakly converging anteriad in posterior two thirds, then strongly curved, strongly converging; without basal marginal line; all other marginal lines complete.

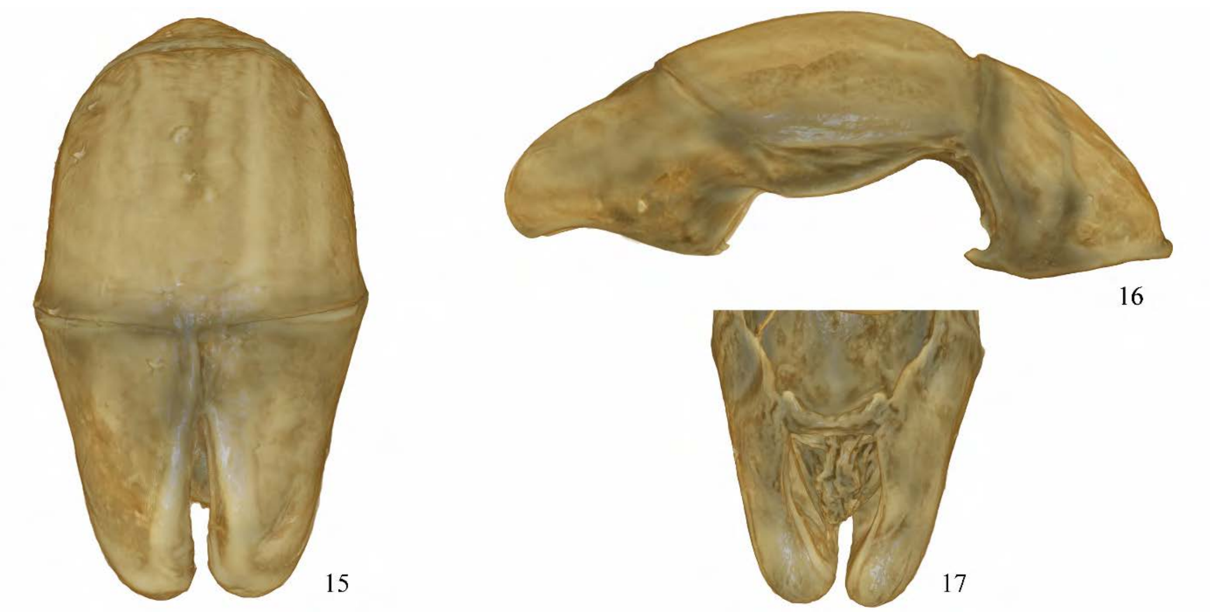
Scutellum nearly semicircular, width about twice as long as the length, finely and sparsely punctate.

Elytra near scutellum with strong impressions; regularly striate; costal intervals more convex than interstices; strial punctures distinct; subsutural interstice with 2 to 4 vague secondary striae being irregularly anteriorly and some of them disappearing in posterior third; vague duplicated secondary striae also present in interstices 2 and 3; elytral surface with sparse micropunctation; humeral umbone and apical protuberance prominent; opaque area at apical curvature very narrow, laterally ending at apical protuberance; lateral margin with moderately wide flat paramarginal extension between humerus and middle of elytron; epipleuron broad near humerus, ending slightly posteriorly of elytral midlength; posterior margin evenly rounded.

Propygidium glabrous. Pygidium weakly convex; apex broadly rounded; punctation dense, transverse; apex with several long, erect brownish setae.

Ventral thoracic surface densely covered with soft, long, brown setae.

Meso-metaventral process short, compressed between mesocoxae, projecting slightly downwards in lateral view, anteriorly vertical and straight; apex subcircular; bulbiform in ventral view.



Figures 15–17. 3D model for aedeagus of *Melanopopillia hainanensis*. 15. Dorsal view. 16. Ventral view. 17. Lateral view from right. These photos are screen shots of the 3D model of aedeagus.

Figures 18–20. Natural habitats of the *Melanopopillia hainanensis* Lin, 1980. 18. The flowers of Melastomataceae. 19. *M. hainanensis* visiting the flowers of Melastomataceae. 20. Surroundings. Photoed by Yandong Chen from Yulingu, Jianfengling Mts., Hainan, China in 12. IV. 2019.

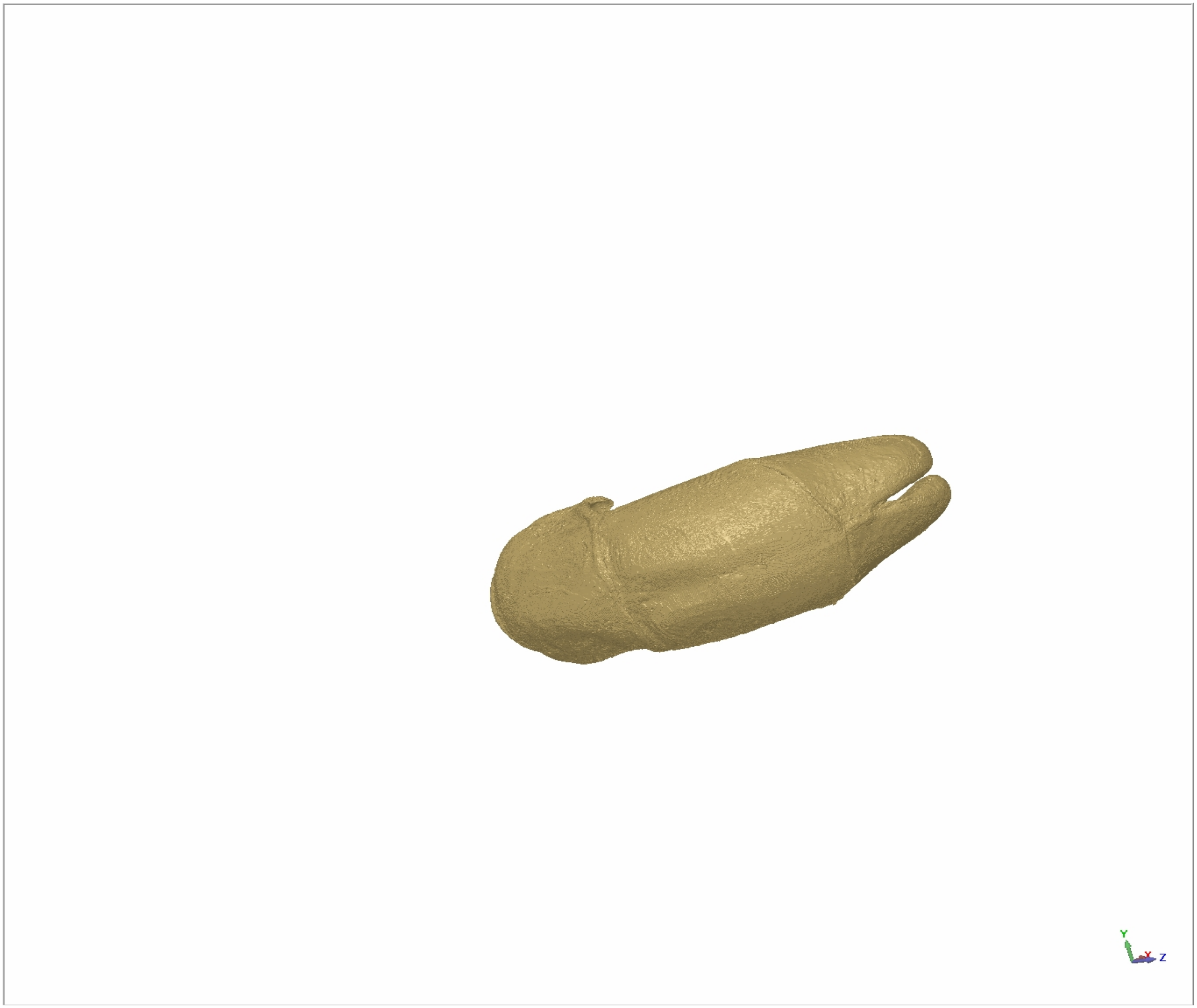


Figure 21. 3D model for aedeagus of *Melanopopillia hainanensis* Lin, 1980. Click on the image to activate the 3D Model.

Abdominal ventrites with transverse band of sparse, long, white setae in posterior half (broadly interrupted in middle); ventrites 1–5 carinate laterally.

Legs. Meso- and metafemur with several irregular bands of long brown setae. Protibia bidentate, broadened; proximal tooth short, situated close to the rather short, curved apical tooth; inner spur short, at level of space between proximal and apical tooth. Metatibia strongly fusiform; protarsus slightly thickened; protarsomere 5 (without claws) longer than tarsomeres 2–4 combined; inner protarsal claw approximately 2/3 as long as protarsomere 5, deeply incised apically, upper branch spiniform, lower branch rectangular; outer mesotarsal claw as long as mesotarsomere 5, incised at apex, upper branch spiniform; metatarsal claws unequal, outer claw approximately twice as thick and 1/3 longer than inner claw.

Aedeagus as in Figures 15–17.

Female. Protibia slender, apical tooth of protibia long and spatulate; protarsus articulated slightly basally of level of proximal tooth; inner spur long, positioned between 1/2 and 2/3 of tibial length; modified claws of pro- and mesotarsi shorter, two apical branches more equal than in males; antennal club slightly longer than antennomeres 2–6 combined.

Measurements. Total body length 10.7–13.4 mm, total body width 6.6–8.4 mm.

Morphological variability. Punctures in head, pronotum and pygidium sparser or denser, more or less confluent with each other; abdominal ventrites 5 weakly or strongly carinate laterally. Shape of parameres very constant.

Diagnosis. This species is peculiar and differs from the other species of this genus by the following combined characters: scutellum punctate; pygidium punctation dense, transverse; ventrites 1–5 carinate laterally. Moreover, the general shape of the aedeagus differs from the shape found in all other species: parameres gradually narrower from the beginning; the end is round, with apex inwardly curved (Figs 15–17).

Collecting data. Specimens collected in the Yulingu (IOZ(E)2080296–2080303) were collected from the flowers of Melastomataceae (Figs 18–20).

Distribution. China (Hainan).

Key to the *Melanopopillia* species (revised from Lin, 1980).

1. Abdominal ventrites strongly carinate laterally (Fig. 3); pygidium punctate (Fig. 5) 2
   Abdominal ventrites rounded or angulately rounded laterally; pygidium sculptured; parameres almost parallel, tips broad in both lateral and dorsal view .... ***Melanopopillia praefica* (Machatschke, 1971)**
2. Outer costal intervals (4 to 6) more convex than interstices, partly rugose; scutellum punctate (Fig. 4); parameres gradually narrower anteriad, tips rounded in dorsal view, inwardly curved in lateral view .... ***Melanopopillia hainanensis* Lin, 1980**
   Outer costal intervals (4 to 6) slightly convex than interstices, smooth; scutellum smooth; parameres subtriangle, tips slightly sharp, inwardly curved in lateral view .... ***Melanopopillia dinghuensis* Lin, 1980**

4 Discussion

The male of *Melanopopillia hainanensis* was firstly described here, which enrich the knowledge of the small genus *Melanopopillia*. Furthermore, by using micro computed tomography technology, we obtained high-resolution 3D images and generated the 3D models of *M. hainanensis*. By comparing figures 1–8 with 9–17, it is sure that this 3D model reflects the real characters. Compared with the traditional taxonomy methods, *e.g.* line drawings, 2D photographs, μ-CT technology can provide more detailed morphological information from every angle. Moreover, the 3D model of male genitalia is specific and can be saved as small sized pdf. format files which allow the readers to handle and examine relevant structures interactively (van de Kamp *et al*., 2014). In other words, one can compare the male genitalia directly with the models in PDF files, removing the need to handle big data in complex software. These 3D data can be used in the future for quantitative analysis like 3D geometric morphometrics. In addition, it can also enrich the online specimens' 3D model database in future (Godfray, 2007; Ziegler *et al*., 2010; Wheeler *et al*., 2012).

Funding This research was supported by the National Natural Science Foundation of China (31672345, 31961143002).

Acknowledgments The authors wish to express their sincere gratitude to Carsten Zorn for providing useful suggestions for this study. Moreover, we are very grateful to the collection managers and curators Jianxiong Li, Ping Yang and Richou Han (GIABR), Martin Fikáček, Jiří Hájek and Matthias Seidel (NMPC) for preparing loans of unidentified ruteline material for examination.

References

Agavekar, G., Garcia, F.H., Economo, E.P. 2017. Taxonomic overview of the hyperdiverse ant genus Tetramorium Mayr (Hymenoptera, Formicidae) in India with descriptions and X-ray microtomography of two new species from the Andaman Islands. *PeerJ*, 5: e3800. doi: 10.7717/peerj.3800.

Ashe-Jepson, E., Garbout, A., Ouvrard, D. 2019. Phylogeny of the Eocene Aphalarinae (Hemiptera: Psylloidea) from Baltic amber, with description of a new species using X-ray micro-computed tomography scanning, and a new genus synonymy, *Journal of Systematic Palaeontology*, 17(14): 1233–1244. doi: 10.1080/14772019.2018.1518345.

Bai, M., Beutel, R.G., Klass, K.D., Zhang, W.W., Yang, X.K., Wipfler, B. 2016. †Alienoptera—a new insect order in the roach-mantodean twilight zone. *Gondwana Research*, 39: 317–326. doi: 10.1016/j.gr.2016.02.002.

Bai, M., Nie, R.E., Zhang, W.W., Ren, D., Shih, C.K., Yang, X.K. 2017. The first fossil Athyreini beetle (Coleoptera: Geotrupidae). *Organisms Diversity and Evolution*, 17: 157–162. doi: 10.1007/s13127-016-0292-4.

Brecko, J., Mathys, A., Dekoninck, W., Leponce, M., VandenSpiegel, D., Semal, P. 2014. Focus stacking: Comparing commercial top-end set-ups with a semi-automatic low budget approach. A possible solution for mass digitization of type specimens. *ZooKeys*, 464: 1–23. doi: 10.3897/zookeys.464.8615.

Faulwetter, S., Vasileiadou, A., Kouratoras, M., Dailianis, T., Arvanitidis, C. 2013. Micro-computed tomography: Introducing new dimensions to taxonomy. *ZooKeys*, 263: 1–45. doi: 10.3897/zookeys.263.4261.

Garcia, F.H., Fischer, G., Liu, C., Audisio, T.L., Economo, E.P. 2017a. Next-generation morphological character discovery and evaluation: an X-ray micro-CT enhanced revision of the ant genus *Zasphinctus* Wheeler (Hymenoptera, Formicidae, Dorylinae) in the Afrotropics. *ZooKeys*, 693: 33–93. doi: 10.3897/zookeys.693.13012.

Garcia, F.H., Fischer, G., Liu, C., Audisio, T.L., Alpert, G.D., Fisher, B.L., Economo, E.P. 2017b. X-Ray microtomography for ant taxonomy: An exploration and case study with two new Terataner (Hymenoptera, Formicidae, Myrmicinae) species from Madagascar. *PLoS ONE*, 12(3): e0172641. doi:10.1371/journal.pone.0172641.

Godfray, H.C.J. 2002. Challenges for taxonomy - The discipline will have to reinvent itself if it is to survive and flourish. *Nature*, 417: 17–19. doi: 10.1038/417017a.

Godfray, H.C.J. 2007. Linnaeus in the information age. *Nature*, 446: 259–260. doi: 10.1038/446259a.

Gorb, S.N., Pullwitt, T., Kleinteich, T., Busshardt, P. 2019. The insect unguitractor plate in action: Force transmission and the micro CT visualizations of inner structures. *Journal of Insect Physiology*, 117: 103908. doi: 10.1016/j.jinsphys.2019.103908.

Krajčík, M. 2007. Checklist of Scarabaeoidea of the World. 2. Rutelinae (Coleoptera: Scarabaeidae: Rutelinae), *Animma. X*. suppl., 4: 1–139.

Krajčík, M. 2012. Checklist of the world Scarabaeoidea. *Animma. X*. suppl., 5: 1–278.

Lin, P. 1980. A new genus, *Melanopopillia*, from China (Coleoptera: Rutelidae). *Entomotaxonomia*, 2: 297–301.

Lu, Y.Y., Zorn, C., Kŕal, D., Bai, M., Yang, X.K. 2018. Taxonomic revision of the genus *Glenopopillia* (Coleoptera: Scarabaeidae: Rutelinae). *Acta Entomologica Musei Nationalis Pragae*, 58(2): 297–320. doi: 10.2478/aemnp-2018-0026.

Luo, X.Z., Antunes-Carvalho, C., Wipfler, B., Ribera, I., Beutel, R.G. 2019. The cephalic morphology of the troglobiontic cholevine species *Troglocharinus ferreri* (Coleoptera, Leiodidae). *Journal of Morphology*, 280: 1207–1221. doi: 10.1002/jmor.21025.

Richmond, M.P., Park, J., Henry, C.S. 2016. The function and evolution of male and female genitalia in Phyllophaga Harris scarab beetles (Coleoptera: Scarabaeidae). *Journal of Evolutionary Biology*, 29: 2276–2288. doi: 10.1111/jeb.12955.

Schmidt, J., Belousov, I., Michalik, P. 2016. X-ray microscopy reveals endophallic structures in a new species of the ground beetle genus Trechus Clairville, 1806 from Baltic amber (Coleoptera, Carabidae, Trechini). *ZooKeys*, 614: 113–127. doi: 10.3897/zookeys.614.9283.

Sharaf, M.R., Aldawood, A.S., Economo, E.P., Wachkoo, A.A., Garcia, F.H. 2019. Taxonomy of Arabian Temnothorax Mayr (Formicidae: Myrmicinae) with description of a new species enhanced by x-ray microtomography. *Scientific Reports*, 9: 11009. doi: 10.1038/s41598-019-47260-y.

Staab, M., Garcia, F.H., Liu, C., Xu, Z.H., Economo, E.P. 2018. Systematics of the ant genus Proceratium Roger (Hymenoptera, Formicidae, Proceratiinae) in China - with descriptions of three new species based on micro-CT enhanced next-generation-morphology. *ZooKeys*, 770: 137–192. doi: 10.3897/zookeys.770.24908.

Steinhoff, P.O.M., Uhl, G. 2015. Taxonomy and nomenclature of some mainland SE-Asian Coeliccia species (Odonata, Platycnemididae) using micro-CT analysis. *Zootaxa*, 4059: 257–276. doi: 10.11646/zootaxa.4059.2.2.

van de Kamp, T., Rolo, T.D., Vagovic, P., Baumbach, T., Riedel, A. 2014. Three-Dimensional Reconstructions Come to Life - Interactive 3D PDF Animations in Functional Morphology. *PLoS ONE*, 9(7): e102355. doi: 10.1371/journal.pone.0102355.

Wheeler, Q., Bourgoin, T., Coddington, J., Gostony, T., Hamilton, A., Larimer, R., Polaszek, A., Schauff, M., Solis, M.A. 2012. Nomenclatural benchmarking: the roles of digital typification and telemicroscopy. *ZooKeys*, 209: 193–202. doi: 10.3897/zookeys.209.3486.

Ziegler, A., Ogurreck, M., Steinke, T., Beckmann, F., Prohaska, S., Ziegler, A. 2010. Opportunities and challenges for digital morphology. *Biology Direct*, 5:45. doi: 10.1186/1745-6150-5-45.

Zorn, C. 2006. Anomalini. *In*: Löbl, I., Smetana, A. (eds), *Catalogue of Palaearctic Coleoptera, Vol. 3*. Apollo Books, Stenstrup. pp. 251–276.

Zorn, C., Bezděk, A. 2016. Rutelinae. *In*: Löbl, I., Löbl, D. (eds), *Catalogue of Palaearctic Coleoptera, Vol. 3, Revised and updated edition*. Brill, Leiden-Boston. pp. 317–358.