Description of six new species of the subgenus Panophrys within the genus Megophrys (Anura, Megophryidae) from southeastern China based on molecular and morphological data

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Abstract
The diversity of the subgenus Panophrys within the genus Megophrys has been revealed to be extremely underestimated from southeastern China. Herpetological surveys coupled with extensive sampling in a longitudinal mountain belt located in southeastern China resulted in the discoveries of six new species of the subgenus Panophrys. Furthermore, the new discoveries support the findings of “micro-endemism”, “sympatric phenomenon” and “sympatric but distant phylogenetically” which appear to be common among Panophrys species, and also indicates that the Asian horned toads would be good candidates for studies on speciation and biogeography, and additionally emphasizes the conservation difficulties of these toads.

Keywords
Conservation, Megophrys, southeastern China, species diversity, subgenus Panophrys, speciation, biogeography

Introduction
The Asian horned toads (Megophrys) comprise 85 recognized species which were previously classified in the subfamily Megophryinae (Frost 2019). They are widespread in montane forest area in tropical and subtropical Asia, including southern mainland...
China, southern and eastern Himalayas, across Indochina to Malay, to the islands of the Sunda Shelf and the Philippines (Chen et al. 2017; Deuti et al. 2017; Mahony et al. 2017; Mahony et al. 2018; Li et al. 2018; Liu et al. 2018; Munir et al. 2018; Messenger et al. 2019; Tapley et al. 2018; Frost 2019). As a consequence of both morphological similarity among species and the complex patterns of genetic divergence, the taxonomy of these toads always has been controversial. Although several researchers have proposed different taxonomic schemes in recent decades (Dubois 1987; Rao and Yang 1997; Dubois and Ohler 1998; Jiang et al. 2003; Zheng et al. 2004; Frost et al. 2006; Li and Wang 2008; Fei et al. 2009; Fei and Ye 2016; Chen et al. 2017; Mahony et al. 2017), the debate remains. Based on a large-scale molecular analysis, Chen et al. (2017) considered that subfamily Megophryinae is composed of five genera, namely Atympanophrys Tian & Hu, 1983, Brachytarsophrys Tian & Hu, 1983, Megophrys Kuhl & Van Hasselt, 1822, Ophryophryne Boulenger, 1903 and Xenophrys Günther, 1864. Almost at the same time, based on the integrative analysis with phylogeny and morphological examination, Mahony et al. (2017) treated the entire subfamily Megophryinae as a single genus Megophrys and divided it into seven subgenera, i.e. Atympanophrys, Brachytarsophrys, Megophrys, Ophryophryne, Panophrys Rao & Yang, 1997, Pelobatrachus Beddard, 1908 and Xenophrys, and 25 known species were placed in the subgenus Panophrys. Subsequently, Liu et al. (2018) partially agreed with this taxonomic system based on a substantial study on phylogenetic similarity, and revealed unusually high levels of species diversity in the subgenus Panophrys with a total number of 60 species, 2.4 times of previously known, including 41 unnamed cryptic species and 39 of which were from southeastern China. Therefore, Panophrys species diversity from southeastern China is extremely underestimated.

In the past years, we have carried out continual herpetological surveys coupled with extensive sampling in a longitudinal mountain belt with a west-east width of 100 km, north-south length of 800 km in the middle of southeastern China, from Hong Kong and Shenzhen in the Pearl River Delta, across the Jiulian Mountains and Luoxiao Mountains, north to the Yangtze River (Fig. 1). The surveys resulted in the discovery of 15 unnamed Panophrys species (Liu et al. 2018) and descriptions of 14 new species of amphibians and reptiles, namely Leptobrachella laui (Sung, Yang & Wang, 2014), Megophrys (Brachytarsophrys) popei (Zhao, Yang, Chen, Chen & Wang, 2014), M. (Panophrys) cheni (Wang & Liu, 2014), M. (Pa.) lini (Wang & Yang, 2014), Megophrys (Pa.) jinggangensis (Wang, 2012), Nidirana nankunensis Lyu, Zeng, Wang, Lin, Liu & Wang, 2017, Amolops albispinus Sung, Hu, Wang, Liu & Wang, 2016, Gracixalus jinggangensis Zeng, Zhao, Chen, Zhang & Wang, 2017 and Gr. guangdongensis Wang, Zeng, Lyu, Liu & Wang, 2018; Goniurosaurus yingdeensis Wang, Yang & Cui, 2010, Go. zhelongi Wang, Jin, Li & Grismer, 2014, Takydromus albomaculosus Wang, Gong, Liu & Wang, 2017, Rhabdophis guangdongensis Zhu, Wang, Takeuchi & Zhao, 2014 and Ophisthotropis shenzhenensis Wang, Guo, Liu, Lyu, Wang, Luo, Sun & Zhang, 2017.

In the present study, we re-reviewed several species defined by Liu et al. (2018) from this mountain belt based on molecular and morphological data and formally described six new species of Megophrys.
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Material and methods

Sampling

For molecular analysis, a total of 42 samples (17 were attained from GenBank and 25 were new materials in this study) from the collection of unnamed specimens of the subgenus Panophrys, together with 39 samples (37 from GenBank and two new materials) from 21 recognized species of Panophrys were used as in-groups in this study. In addition, four samples (all from GenBank) from two recognized species of the subgenus Atympanophrys, four samples (three from GenBank and one new materials) from two recognized species of the subgenus Brachytarsophrys, three samples (one from GenBank and two new materials) from two recognized species of the subgenus Ophryophryne, two samples (all from GenBank) from two recognized species of the subgenus Pelobatrachus, and six samples (five from GenBank and one new materials) of three recognized species of the subgenus Xenophrys were incorporated into our dataset and used as out-groups. Details see Table 1. All muscle samples were preserved in 95% ethanol and stored at -40 °C.
### Table 1. Localities, voucher information, and GenBank accession numbers for all specimens used in this study.

| Subgenus of *Megophrys* s. l. | ID | Species name      | Locality                                      | Specimen voucher no. | Genbank Accession No. | 16S  | CO1  |
|-------------------------------|----|-------------------|-----------------------------------------------|----------------------|-----------------------|------|------|
| *Panophrys*                   | 1  | *M. dongguanensis* sp. nov. | China: Mt. Yinping, Dongguan City, Guangdong | SYS a001971/ CIB110006 | MK524097             | MK524128 |
|                               | 2  | *M. dongguanensis* sp. nov. | China: Mt. Yinping, Dongguan City, Guangdong | SYS a001972          | MK524098             | MK524129 |
|                               | 3  | *M. dongguanensis* sp. nov. | China: Mt. Yinping, Dongguan City, Guangdong | SYS a001973          | MH406647             | MH406083 |
|                               | 4  | *M. dongguanensis* sp. nov. | China: Mt. Yinping, Dongguan City, Guangdong | SYS a001974          | MH406648             | MH406084 |
|                               | 5  | *M. dongguanensis* sp. nov. | China: Mt. Yinping, Dongguan City, Guangdong | SYS a001975          | MH406649             | MH406085 |
|                               | 6  | *M. dongguanensis* sp. nov. | China: Mt. Yinping, Dongguan City, Guangdong | SYS a002007          | MH406654             | MH406090 |
|                               | 7  | *M. jiulianensis* sp. nov. | China: Mt. Jiulian, Ganzhou City, Jiangxi    | SYS a002107          | MK524099             | MK524130 |
|                               | 8  | *M. jiulianensis* sp. nov. | China: Mt. Jiulian, Ganzhou City, Jiangxi    | SYS a002108          | MK524100             | MK524131 |
|                               | 9  | *M. jiulianensis* sp. nov. | China: Mt. Jiulian, Ganzhou City, Jiangxi    | SYS a002109          | MK524101             | MK524132 |
|                               | 10 | *M. jiulianensis* sp. nov. | China: Mt. Jiulian, Ganzhou City, Jiangxi    | SYS a004219          | MH406791             | MH406253 |
|                               | 11 | *M. jiulianensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a003622          | MK524102             | MK524133 |
|                               | 12 | *M. jiulianensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a003623          | MK524103             | MK524134 |
|                               | 13 | *M. mufumontana* sp. nov. | China: Mt. Mufu, Pingjiang County, Hunan    | SYS a006390/ CIB110012 | MK524104           | MK524135 |
|                               | 14 | *M. mufumontana* sp. nov. | China: Mt. Mufu, Pingjiang County, Hunan    | SYS a006391          | MK524105             | MK524136 |
|                               | 15 | *M. mufumontana* sp. nov. | China: Mt. Mufu, Pingjiang County, Hunan    | SYS a006392          | MK524106             | MK524137 |
|                               | 16 | *M. mufumontana* sp. nov. | China: Mt. Mufu, Pingjiang County, Hunan    | SYS a006419          | MK524107             | MK524138 |
|                               | 17 | *M. nankunensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a004498          | MK524108             | MK524139 |
|                               | 18 | *M. nankunensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a004499          | MK524109             | MK524140 |
|                               | 19 | *M. nankunensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a004500          | MK524110             | MK524141 |
|                               | 20 | *M. nankunensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a004501          | MH406822             | MH406284 |
|                               | 21 | *M. nankunensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a004502          | MH406823             | MH406285 |
|                               | 22 | *M. nankunensis* sp. nov. | China: Mt. Nankun, Huizhou City, Guangdong  | SYS a004503          | MH406824             | MH406286 |
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| Subgenus of Megophrys s. l. | ID | Species name | Locality | Specimen voucher no. | Genbank Accession No. |
|-----------------------------|----|--------------|----------|----------------------|----------------------|
| Panophrys                  |    |              |          |                      |                      |
|                            | 23 | *M. nanlingensis* sp. nov. | China: Nanling Nature Reserve, Shaoguan City, Guangdong | SYS a001959 | MK524111  MK524142 |
|                            | 24 | *M. nanlingensis* sp. nov. | China: Nanling Nature Reserve, Shaoguan City, Guangdong | SYS a001960 | MK524112  MK524143 |
|                            | 25 | *M. nanlingensis* sp. nov. | China: Nanling Nature Reserve, Shaoguan City, Guangdong | SYS a001964 | MH406646  MH406082 |
|                            | 26 | *M. nanlingensis* sp. nov. | China: Mt. Qiyun, Chongyi County, Jiangxi | SYS a002334 | MH406686  MH406132 |
|                            | 27 | *M. nanlingensis* sp. nov. | China: Mt. Qiyun, Chongyi County, Jiangxi | SYS a002356 | MK524113  MK524144 |
|                            | 28 | *M. nanlingensis* sp. nov. | China: Mt. Qiyun, Chongyi County, Jiangxi | SYS a002357 | MH406687  MH406133 |
|                            | 29 | *M. nanlingensis* sp. nov. | China: Mt. Qiyun, Chongyi County, Jiangxi | SYS a002358 | MH406688  MH406134 |
|                            | 30 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a002610 | MK524114  MK524145 |
|                            | 31 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a002611 | MK524115  MK524146 |
|                            | 32 | *M. wugongensis* sp. nov. | China: Yangshimu Scenic Area, Pingxiang City, Jiangxi | SYS a002625 | MK524116  MK524147 |
|                            | 33 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004777/ CIB110011 | MK524117  MK524148 |
|                            | 34 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004796 | MK524118  MK524149 |
|                            | 35 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004797 | MK524119  MK524150 |
|                            | 36 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004798 | MK524120  MK524151 |
|                            | 37 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004799 | MH406852  MH406314 |
|                            | 38 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004800 | MH406853  MH406315 |
|                            | 39 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004801 | MH406854  MH406316 |
|                            | 40 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004802 | MH406855  MH406317 |
|                            | 41 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004803 | MH406856  MH406318 |
|                            | 42 | *M. wugongensis* sp. nov. | China: Wugongshan Scenic Area, Anfu County, Jiangxi | SYS a004804 | MK524121  MK524152 |
|                            | 43 | *M. acuta* | China: Heishiding Nature Reserve, Zhaoqing City, Guangdong | SYS a001957 | KJ579118  MF667898 |
|                            | 44 | *M. acuta* | China: Heishiding Nature Reserve, Zhaoqing City, Guangdong | SYS a002159 | MF667869  MF667899 |
| ID | Species name   | Locality                                           | Specimen voucher no.          | Genbank Accession No.          |
|----|----------------|----------------------------------------------------|-------------------------------|-------------------------------|
| 45 | M. bielinski   | China: Mt. Wawu, Meishan City, Sichuan            | SYS a005313                   | MH406892 MH406354             |
| 46 | M. bielinski   | China: Mt. Wawu, Meishan City, Sichuan            | SYS a005314                   | MH406893 MH406355             |
| 47 | M. boettiger   | China: Longhu Forest Station, Shaowu City, Fujian  | SYS a004126                   | MH406785 MH406245             |
| 48 | M. boettiger   | China: Mt. Wuyi, Fujian                           | SYS a004150                   | MF667879 MF667914             |
| 49 | M. brachypholis| China: Hongkong                                    | SYS a005563                   | MK324122 MK324153             |
| 50 | M. brachypholis| China: Hongkong                                    | SYS a005564                   | MK324123 MK324154             |
| 51 | M. caudoprocta | China: Mt. Badagongshan, Zhangjiajie City, Hunan   | SYS a004281                   | MH406795 MH406257             |
| 52 | M. caudoprocta | China: Mt. Badagongshan, Zhangjiajie City, Hunan   | SYS a004293                   | MH406796 MH406258             |
| 53 | M. cheni       | China: Taoyuanhong Nature Reserve, Zhuzhou City, Hunan | SYS a002123 | KJ560396 MF667904 |
| 54 | M. cheni       | China: Taoyuanhong Nature Reserve, Zhuzhou City, Hunan | SYS a002140 | MF667872 MF667905 |
| 55 | M. huangshani  | China: Mt. Huangshan, Anhui                        | SYS a002702                   | MF667882 MF667919             |
| 56 | M. huangshani  | China: Mt. Huangshan, Anhui                        | SYS a002703                   | MF667883 MF667920             |
| 57 | M. insularis   | China: Nan’ao Island, Guangdong                    | SYS a002169 (Holotype)        | MF667887 MF667924             |
| 58 | M. insularis   | China: Nan’ao Island, Guangdong                    | SYS a002170                   | MF667888 MF667925             |
| 59 | M. jingdongensis| China: Mt. Wuliang, Yunnan                        | SYS a003928                   | MH406773 MH406232             |
| 60 | M. jingdongensis| China: Mt. Wuliang, Yunnan                        | SYS a003929                   | MH406774 MH406233             |
| 61 | M. jinggangensis| China: Mt. Jinggang, Jiangxi                       | SYS a004028                   | MH406780 MH406239             |
| 62 | M. jinggangensis| China: Mt. Sifang, Hengdong County, Hunan          | SYS a004825                   | MH406858 MH406320             |
| 63 | M. kuatunensis | China: Mt. Wuyi, Jiangxi                           | SYS a003449                   | MF667881 MF667916             |
| 64 | M. lini        | China: Nanfengmian Nature Reserve, Jiangxi         | SYS a002128                   | KJ560416 MF667907             |
| 65 | M. lini        | China: Nanfengmian Nature Reserve, Jiangxi         | SYS a002381                   | MF667874 MF667908             |
| 66 | M. minor       | China: Duijiangyang City, Sichuan                 | SYS a003209                   | MF667862 MF667891             |
| 67 | M. minor       | China: Duijiangyang City, Sichuan                 | SYS a003210                   | MF667863 MF667892             |
| 68 | M. obesa       | China: Heishiding Nature Reserve, Guangdong       | SYS a002271                   | KJ579121 MH406123             |
| 69 | M. obesa       | China: Heishiding Nature Reserve, Guangdong       | SYS a005025                   | MH406868 MH406330             |
| 70 | M. ombrophila  | China: Mt. Wuyi, Fujian                           | WUY12015101                   | KX856397 /                     |
| 71 | M. omeimontis  | China: Mt. Laojunshan, Yibin City, Sichuan        | SYS a002741                   | MH406710 MH406162             |
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#### Subgenus of Megophrys s. l.

| ID | Species name       | Locality                              | Specimen voucher no. | Genbank Accession No. |
|----|--------------------|---------------------------------------|-----------------------|-----------------------|
| 72 | *M. omeimontis*    | China: Hejiang County, Sichuan         | SYS a004916           | MH406864 MH406326     |
| 73 | *M. sangzhienis*   | China: Mt. Badagongshan, Hunan         | SYS a004307           | MH406798 MH406260     |
| 74 | *M. sangzhienis*   | China: Mt. Badagongshan, Hunan         | SYS a004313           | MH406802 MH406264     |
| 75 | *M. spinata*       | China: Mt. Leigong, Guizhou            | SYS a002226           | MH406675 MH406115     |
| 76 | *M. spinata*       | China: Mt. Leigong, Guizhou            | SYS a002227           | MH406676 MH406116     |
| 77 | *M. tubergranulatus* | China: Mt. Badagongshan, Hunan       | SYS a004310           | MH406801 MH406263     |
| 78 | *M. wushanensis*   | China: Shennongjia Forestry District, Hubei | SYS a003008     | MH406732 MH406184     |
| 79 | *M. wushanensis*   | China: Shennongjia Forestry District, Hubei | SYS a003009     | MH406733 MH406185     |
| 80 | *M. wuliangshanensis* | China: Mt. Wuliang, Yunnan      | SYS a003924           | MH406771 MH406230     |
| 81 | *M. wuliangshanensis* | China: Mt. Wuliang, Yunnan      | SYS a003925           | MH406772 MH406231     |
| 82 | *M. gigantica*     | China: Mt. Ailao, Yunnan              | SYS a003883           | MH406766 MH406225     |
| 83 | *M. gigantica*     | China: Mt. Wuliang, Yunnan            | SYS a003933           | MH406775 MH406234     |
| 84 | *M. shapingensis*  | China: Mt. Wasu, Sichuan              | SYS a005310           | MH406890 MH406352     |
| 85 | *M. shapingensis*  | China: Zhaosui County, Sichuan        | SYS a005339           | MH406897 MH406359     |
| 86 | *M. chuananensis*  | China: Hejiang County, Sichuan         | SYS a004926           | MH406901 MH406364     |
| 87 | *M. chuananensis*  | China: Hejiang County, Sichuan         | SYS a004927           | MH406902 MH406365     |
| 88 | *M. popei*         | China: Taoyuan District, Hubei         | SYS a001864           | MH406361 KM504256     |
| 89 | *M. popei*         | China: Mt. Jinggang, Jiangxi           | SYS a004209           | MK524124 MK524155     |

#### Atympanophrys

| 90 | *M. hansi*         | Vietnam: Quang Nam, Tra My District    | AMNH 163680           | KY022203 /          |
| 91 | *M. microstoma*    | China: Mt. Wuhuang, Pubei County, Guangxi | SYS a003492   | MK524125 MK524156   |
| 92 | *M. microstoma*    | China: Mt. Wuhuang, Pubei County, Guangxi | SYS a003493   | MK524126 MK524157   |

#### Brachytarsophrys

| 93 | *M. nasuta*        | Malaysia: Sabab, Lahad Datu District   | FMNH 231281           | KY022186 /          |
| 94 | *M. stejnegeri*    | Philippines: Mindanao, Bukidnon Province | FMNH 250842   | KY022190 /          |

#### Ophryophyne

| 95 | *M. glandulosa*    | China: Mt. Gaoligong, Yunnan           | SYS a003758           | MH406755 MH406214   |
| 96 | *M. glandulosa*    | China: Mt. Gaoligong, Yunnan           | SYS a003794           | MH406759 MH406218   |
| 97 | *M. mangshanensis* | China: Mt. Longtou, Guangdong          | SYS a002750           | MF667866 MF667895   |
| 98 | *M. mangshanensis* | China: Mt. Dayao, Guangxi               | SYS a004870           | MH406861 MH406323   |
| 99 | *M. medogensis*    | China: Medog County, Tibet              | SYS a002932           | MH406725 MH406177   |
|100 | *M. medogensis*    | China: Medog County, Tibet              | SYS a002933           | MK524127 MK524158   |
DNA Extraction, PCR and sequencing

Genomic DNA was extracted from muscular tissue using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. All samples were sequenced for two mitochondrial genes, i.e., partial 16S ribosomal RNA gene (16S) and complete cytochrome C oxidase 1 gene (CO1). Primers used for 16S were L3975 (5’-CGCCTGTTTACCAAAAACAT-3’) and H4551 (5’-CCGGTCTGAACTCAGATCACGT-3’) following Simon et al. (1994), and for CO1 were Chmf4 (5’-TYTCWACWAAYCAYAAAGAYATCGG-3’) and Chmr4 (5’-ACYTCRGGRTGRCCRAARAATCA-3’) following Meyer et al. (2005). PCR amplifications were processed in a 20-reaction volume with the cycling conditions that initial denaturing step at 95 °C for 4 min, 35 cycles of denaturing at 94 °C for 40 s, annealing at 53 °C for 40 s and extending at 72 °C for 1 min, and final extending step of 72 °C for 10 min. PCR products were purified with spin columns. The purified products were sequenced with both forward and reverse primers using BigDye Terminator Cycle Sequencing Kit per the guidelines, on an ABI Prism 3730 automated DNA sequencer by Shanghai Majorbio Bio-pharm Technology Co., Ltd and Beijing Genomics Institute. All sequences have been deposited in GenBank (Table 1).

Phylogenetic analyses

DNA sequences were aligned in MEGA 6 (Tamura et al. 2013) by the Clustal W algorithm with default parameters (Thompson et al. 1997). Two gene segments, 535 base pairs (bp) of 16S and 645 bp of CO1, were concatenated seriatim into a 1180-bp single sequence. The dataset was partitioned according to the genes and codon positions, and then tested respectively in jmodeltest v2.1.2 with Akaike and Bayesian information criteria, all resulting in the best-fitting nucleotide substitution models of GTR + I + G. Sequenced data was analyzed using Bayesian inference (BI) in MrBayes 3.2.4 (Ronquist et al. 2012). Three independent runs were conducted in BI analysis, each of which was performed for 2,000,000 generations and sampled every 1000 generations with the first 25% samples were discarded as burn-in, resulting a potential scale reduction factor (PSRF) of < 0.01. Pairwise distances (p-distance) were calculated in MEGA 6 using the uncorrected p-distance model.

Morphometrics

All specimens were fixed in 10 % buffered formalin and later transferred to 70% ethanol for preservation, and deposited at the Museum of Biology, Sun Yat-sen University (SYS) and Chengdu Institute of Biology, the Chinese Academy of Sciences (CIB), China. Measurements follow Fei et al. (2009), and were taken with digital calipers to the nearest 0.1 mm. These measurements were as follows:
SVL  snout–vent length (from tip of snout to vent);
HDL  head length (from tip of snout to rear of jaws);
HDW  head width (head width at commissure of jaws);
SNT  snout length (from tip of snout to anterior corner of eye);
ED   eye diameter (diameter of exposed portion of eyeball);
IOD  interorbital distance (minimum distance between upper eyelids);
IND  internasal distance (distance between nares);
TD   tympanum diameter (horizontal diameter of tympanum);
TED  tympanum–eye distance (distance from anterior edge of tympanum to posterior corner of eye);
HND  hand length (distance from distal end of radioulna to tip of phalanx of finger III);
RAD  radioulna length;
TIB  tibia length (distance from knee to heel);
FTL  foot length (distance from distal end of tibia to tip of distal phalanx of toe IV).

Sex was determined by direct observation of calls, the presence of internal vocal sac openings and the presence of testicles observed through dissection for males, as well as the presence of eggs and ovaries on the abdomen through anatomise for females. Presence or absence of nuptial pads/spines was examined with a microscope.

Comparative morphological data of *Megophrys* species allocated to the subgenus *Panophrys* (currently contains 32 species) (Mahony et al. 2017; Tapley et al. 2017; Wang et al. 2017a; Wang et al. 2017b; Zhang et al. 2017; Li et al. 2018; Tapley et al. 2018), and a small-sized species *M. feii* (incertae sedis), were obtained from examination of museum specimens (see Appendix 1) and from the literature (Table 2). The order of the new species accounts follows the distributions of the new species that located in the longitudinal mountain belt from the south to the north.

**Results**

**Phylogenetics**

The Bayesian inference (BI) phylogenetic tree was integrated in Figure 2; the $p$-distances at the mitochondrial 16S rRNA gene fragment among all samples of the subgenus *Panophrys* were given in Table 3.

In our phylogenetic tree, all sequences of the genus *Megophrys* grouped into six clades with strong node support values, which were consistent with the results from Mahony et al. (2017) and Liu et al. (2018), and corresponded to the six subgenera: *Panophrys, Ophryophryne, Xenophrys, Atympanophrys, Brachytarsophrys* and *Pelobatrachus*. The subgenus *Panophrys* is further divided into three subclades, named western subclade A, western subclade B and eastern subclade.
Figure 2. Bayesian inference tree derived from partial DNA sequences of the mitochondrial 16S rRNA + CO1 genes.
Table 2. References for morphological characters for congeners of the subgenus Panophrys and Megophrys feii (incertae sedis).

| ID | Subgenus Panophrys | Literature obtained |
|----|--------------------|---------------------|
| 1  | M. acuta Wang, Li & Jin, 2014 | Li et al. 2014 |
| 2  | M. baolongensis Ye, Fei & Xie, 2007 | Ye et al. 2007 |
| 3  | M. cinchuanensis Ye & Fei, 1995 | Ye and Fei 1995 |
| 4  | M. binlingensis Jiang, Fei & Ye, 2009 | Fei et al. 2009 |
| 5  | M. boettgeri (Boulenger, 1899) | Fei et al. 2012 |
| 6  | M. brachykolos Inger & Romer, 1961 | Inger and Romer 1961 |
| 7  | M. caudoprocta Shen, 1994 | Fei et al. 2012 |
| 8  | M. cheni (Wang & Liu, 2014) | Wang et al. 2014 |
| 9  | M. daweimontis Rao & Yang, 1997 | Fei et al. 2012 |
| 10 | M. fansipanensis Tapley, Cutajar, Mahony, Nguyen, Dau, Luong, Le, Nguyen, Nguyen, Portway, Luong & Rowley, 2018 | Tapley et al. 2018 |
| 11 | M. huangshanensis Fei & Ye, 2005 | Fei et al. 2012 |
| 12 | M. hoanglienensis Tapley, Cutajar, Mahony, Nguyen, Dau, Luong, Le, Nguyen, Nguyen, Portway, Luong & &, 2018 | Tapley et al. 2018 |
| 13 | M. insularis (Wang, Liu, Lyu, Zeng & Wang, 2017) | Wang et al. 2017b |
| 14 | M. jingdongensis Fei & Ye, 1983 | Fei et al. 2012 |
| 15 | M. jinggangensis (Wang, 2012) | Wang et al. 2012 |
| 16 | M. kuatunensis Pope, 1929 | Fei et al. 2012 |
| 17 | M. latidactyla Orlov, Poyarkov & Nguyen, 2015 | Orlov et al. 2015 |
| 18 | M. leishanensis Li, Xu, Liu, Jiang, Wei & Wang, 2018 | Li et al. 2018 |
| 19 | M. liboensis (Zhang, Li, Xiao, Li, Pan, Wang, Zhang & Zhou, 2017) | Zhang et al. 2017 |
| 20 | M. lini (Wang & Yang, 2014) | Wang et al. 2014 |
| 21 | M. lishuiensis (Wang, Liu & Jiang, 2017) | Wang et al. 2017a |
| 22 | M. minor Stejneger, 1926 | Wang et al. 2017b |
| 23 | M. ombrophila Messenger & Dahn, 2019 | Messenger et al. 2019 |
| 24 | M. omeimontis Liu, 1950 | Fei et al. 2009 |
| 25 | M. palpebralespinosa Bourret, 1937 | Fei et al. 2012 |
| 26 | M. rubrinerana Tapley, Cutajar, Mahony, Chung, Dau, Nguyen, Luong & Rowley, 2017 | Tapley et al. 2017 |
| 27 | M. sangzhiensis Jiang, Ye & Fei, 2008 | Jiang et al. 2008 |
| 28 | M. shuichengensis Tian & Sun, 1995 | Tian et al. 2000 |
| 29 | M. spinata Liu & Hu, 1973 | Fei et al. 2012 |
| 30 | M. tuberogranulatus Shen, Mo & Li, 2010 | Mo et al. 2010 |
| 31 | M. wushanensis Ye & Fei, 1995 | Ye and Fei 1995 |
| 32 | M. wushanensis Ye & Fei, 1995 | Ye and Fei 1995 |

**Incertae sedis**

| ID | Subgenus Panophrys | Literature obtained |
|----|--------------------|---------------------|
| 1  | M. feii Yang, Wang & Wang, 2018 | Yang et al. 2018 |

The western subclade A is composed of Megophrys omeimontis, M. binglingensis, M. sangzhiensis, M. spinata, M. wushanensis and M. jingdongensis, and the western subclade B is composed of M. minor, all of which are distributed in southwestern China.

The eastern subclade contains 14 known species from southeastern China, i.e. M. boettgeri, M. huangshanensis, M. kuatunensis, M. brachykolos, M. insularis, M. cheni, M. lini, M. jinggangensis, M. ombrophila, M. acuta, M. sangzhiensis, M. caudoprocta, M. tuberogranulatus and wushanensis, and other six lineages made up of samples from the aforementioned longitudinal mountain belt in the middle of southeastern China with significant genetic differences (Table 3).
Table 3. Uncorrected \( p \)-distances among *Megophrys* species of the subgenus *Panophrys* in this study, based on mitochondrial 16S r RNA genes.

| Species & ID No. | (1)–(6) | (7)–(12) | (13)–(16) | (17)–(22) | (23)–(29) | (30)–(42) | (43)–(44) | (45)–(46) | (47)–(48) | (49)–(50) | (51)–(52) | (53)–(54) | (55)–(56) | (57)–(58) |
|-----------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| *M. dongguanensis* sp. nov. (1)–(6) | 0.0–0.2 |
| *M. jiulianensis* sp. nov. (7)–(12) | 5.3–5.8 |
| *M. mufumontana* sp. nov. (13)–(16) | 6.3 |
| *M. nankunensis* sp. nov. (17)–(22) | 5.3–6.1 |
| *M. nanlingensis* sp. nov. (23)–(29) | 5.3–5.4 |
| *M. wugongensis* sp. nov. (30)–(42) | 4.4–4.2 |
| *M. acuta* (43)–(44) | 4.7–4.9 |
| *M. binlingensis* (45)–(46) | 4.6 |
| *M. boettgeri* (47)–(48) | 4.2–4.7 |
| *M. brachykolos* (49)–(50) | 4.7–4.9 |
| *M. caudoproctus* (51)–(52) | 5.4 |
| *M. cheni* (53)–(54) | 4.4–4.7 |
| *M. huangshanensis* (55)–(56) | 5.1 |
| *M. inulensis* (57)–(58) | 4.2 |
| *M. jingdongensis* (59)–(60) | 5.6–6.4 |
| *M. jiangdongensis* (61)–(62) | 4.2 |
| *M. kwangtunensis* (63) | 5.4 |
| *M. lini* (64)–(65) | 4.2 |
| *M. minor* (66)–(67) | 5.7 |
| *M. oba* (68)–(69) | 4.7 |
| *M. onprobhila* (70) | 5.7 |
| *M. osteonotus* (71)–(72) | 4.3 |
| *M. tangshanensis* (73)–(74) | 5.1 |
| *M. spinata* (75)–(76) | 4.8 |
| *M. tuberogranulatus* (77) | 4.7 |
| *M. wuhuensi* (78)–(79) | 4.9–5.4 |
| *M. wuxiangshanensis* (80)–(81) | 7.2 |
Table 3. (Continued) Uncorrected $p$-distances among *Megophrys* species of the subgenus *Panophrys* in this study, based on mitochondrial 16S rRNA genes.

| Species & ID No.          | (59)–(60) | (61)–(62) | (63) | (64)–(65) | (66)–(67) | (68)–(69) | (70) | (71)–(72) | (73)–(74) | (75)–(76) | (77) | (78)–(79) | (80)–(81) |
|--------------------------|-----------|-----------|------|-----------|-----------|-----------|------|-----------|-----------|-----------|------|-----------|-----------|
| *M. jingdongensis* (59)–(60) | 0         |           |      |           |           |           |      |           |           |           |      |           |           |
| *M. jinggangensis* (61)–(62) | 5.3       | 0–0.5     |      |           |           |           |      |           |           |           |      |           |           |
| *M. kuantunensis* (63)     | 5.8       | 4.4       | 0    |           |           |           |      |           |           |           |      |           |           |
| *M. lini* (64)–(65)        | 6.3       | 4.4       | 3.7  | 0         |           |           |      |           |           |           |      |           |           |
| *M. minor* (66)–(67)       | 7.2–7.5   | 6.8–7.5   | 6.5–6.8 | 7.7–7.9 | 0–0.2     |           |      |           |           |           |      |           |           |
| *M. ohsu* (68)–(69)        | 6.3       | 4.9–5.3   | 4.2  | 4.2       | 7.2–7.5   | 0         |      |           |           |           |      |           |           |
| *M. ombrophila* (70)       | 6.7       | 5.3–5.8   | 4.9  | 5.8       | 8.2–8.4   | 3         | 0    |           |           |           |      |           |           |
| *M. omeimontis* (71)–(72)  | 3         | 4.4–4.9   | 4.7  | 5.1       | 5.8–6.1   | 5.6       | 5.6  | 0         |           |           |      |           |           |
| *M. sangzhiensis* (73)–(74)| 3.9       | 5.6       | 5.8  | 6.3       | 7.2–7.5   | 7.2       | 6.5  | 4         | 0         |           |      |           |           |
| *M. spinata* (75)–(76)     | 3.9       | 5.8       | 6    | 5.6       | 6.5–6.8   | 7         | 6.7  | 3         | 2         | 0         |      |           |           |
| *M. tuberogranulatus* (77) | 4         | 3         | 3    | 4.7       | 5.8–6.1   | 4.7–5.8   | 4.4  | 3.7       | 3.7       | 3.7       | 0    |           |           |
| *M. wushanensis* (78)–(79) | 5.4–5.6   | 3.7–4.7   | 3.7–4.7 | 5.6–5.8 | 7.2–7.5   | 5.4–5.8   | 4.7–4.9 | 3.7–4.7   | 5.1–5.4   | 5.1–5.4   | 2.1  | 0         |           |
| *M. wuliangshanensis* (80)–(81) | 3.7       | 5.8       | 5.1  | 6.7       | 6.5–6.8   | 5.8       | 6.5  | 3.5       | 4.9       | 4.4       | 4.2  | 4.7–5.1  | 0–0.5     |
Among them, all samples from Mt. Mufu, Hunan (samples 13–16 in Table 1) clustered into a basal lineage of an eastern subclade with strong node supports and almost have no molecular differences; further, this population can be distinguished from all known species and other undescribed lineages by distinctive morphological characters and significant molecular differences with a lowest $p$-distance of 2.8%. Therefore, the population from Mt. Mufu represented a separately evolving lineage, and is described as a new species, *Megophrys* (*Panophrys*) *mufumontana* sp. nov., below.

All samples from Mt. Wugong, Jiangxi (samples 30–42 from Yangshimu Scenic Area and Wugongshan Scenic Area) clustered into a lineage with strong node supporting values and almost no genetic differences, which was defined as a species and recognized as *M*. sp12 by Liu et al. (2018); further, the population from Mt. Wugong can be distinguished from all known species and other undescribed lineages by distinctive morphological differences and significant molecular differences with a lowest $p$-distance of 4%. Therefore, the population from Mt. Wugong represented a separately evolving lineage and is described as a new species, *Megophrys* (*Panophrys*) *wugongensis* sp. nov., below.

All samples from Mt. Yinping, Guangdong (samples 1–6) clustered into a lineage with strong node support values and small genetic differences (highest $p$-distance 0.2%), which was defined as a species and recognized as *M*. sp11 by Liu et al. (2018); samples 17–22 from Mt. Nankun, Guangdong clustered into a lineage with strong node support values and small genetic differences (highest $p$-distance 0.7%), which was defined as a species and recognized as *M*. sp10 by Liu et al. (2018); these two populations are sister taxa to each other with significant genetic differences ($p$-distances 2.6–2.8%), and can be further distinguished from all known species and other undescribed lineages by distinctive morphological differences and significant molecular differences. Therefore, the populations from Mt. Yinping and Mt. Nankun represented two separately evolving lineages, and are described as new species, *Megophrys* (*Panophrys*) *dongguanensis* sp. nov. and *Megophrys* (*Panophrys*) *nankunensis* sp. nov., below.

Samples 7–10 from Mt. Jiulian, Jiangxi and samples 11–12 from Mt. Nankun, Guangdong clustered into a lineage with small genetic differences (highest $p$-distance 0.7%), which is a sister subclade to *M. boettgeri* and *M. huangshanensis* with large genetic differences (lowest $p$-distance 2.3%); therefore, these samples represented a separately evolving lineage, which was defined as a species and recognized as *M*. sp30 by Liu et al. (2018), and is described as a new species, *Megophrys* (*Panophrys*) *jiulianensis* sp. nov., below.

Samples 26–29 from Mt. Qiyun, Jiangxi were defined as a species and recognized as *M*. sp6 by Liu et al. (2018) and the samples 23–25 from Nanling Nature Reserve, Guangdong were defined as a species and recognized as *M*. sp7 by Liu et al. (2018). Although the populations from two locations are divided into two branches, the highest $p$-distance is only 0.7%. Moreover, there are no distinct morphological characters that can distinguish them from each other. Herein, we considered these two populations as one taxon, which is the sister taxon to *M. lini* with large genetic differences ($p$-distances 3.7–4.4%), representing a new species and described as, *Megophrys* (*Panophrys*) *nanlingensis* sp. nov., below.
**Taxonomic accounts**

*Megophrys (Panophrys) dongguanensis* J. Wang & Y.Y. Wang, sp. nov.

http://zoobank.org/94DBE153-5A7C-4820-8E27-E9BE41C3A764

Fig. 3, Table 4

**Holotype.** SYS a001973, adult male, collected by Run-Lin Li on 13 December 2012 from Mt. Yinping, Xiegang County (22°54’17.20"N, 114°13’23.88"E; 132 m a.s.l.), Dongguan City, Guangdong Province, China.

**Paratypes (10 males).** SYS a002007, adult male, collected on 17 March 2013 by Run-Lin Li from Mt. Yinping, Qingxi County (22°53’26.21"N, 114°10’14.82"E; 277 m a.s.l.), Dongguan City, China; adult males, SYS a001971/CIB110006, SYS a001972, 1974–1975, collected on 12–13 December 2012, SYS a001492–1495, collected on 23 December 2012 by Run-Lin Li from the same locality as the holotype (100–300 m a.s.l.).

**Diagnosis.** (1) Body size small to moderate, SVL 30.2–39.3 mm in 11 adult male specimens; (2) head width slightly larger than head length, HDW/HDL ratio 1.04–1.09; (3) snout pointed in dorsal view; (4) tympanum distinct, moderate-sized, TD/ED ratio 0.42–0.60; (5) strong vomerine ridge bearing vomerine teeth; (6) margin of tongue not notched behind; (7) hindlimbs short, heels not meeting, tibio-tarsal articulation reaching the region between tympanum and eye; (8) presence of subarticular tubercles and absence of lateral fringes on fingers, relative finger lengths II < I ≤ IV < III; (9) toes with rudiment of webbing at their bases and without lateral fringes, subarticular tubercles only present at the base of each toe; (10) numerous granules present on dorsal surface of body, several large tubercles present on surface of flanks; (11) presence of a barely visible reddish horn-like tubercle at the edge of the upper eyelid; (12) supratympanic fold distinct, whitish; (13) yellowish brown dorsally, with an incomplete dark triangular marking between eyes and usually an X-shaped marking on back of trunk; (14) ventral surface black brown, with white spots on posterior surface of abdomen; (15) males with a single subgular vocal sac; (16) presence of nuptial pads with darker nuptial spines on dorsal surface of the first and second fingers in adult males during breeding season, respectively.

**Comparisons.** Comparative data of *Megophrys dongguanensis* sp. nov. with *M. feii* and the 33 recognized members of *Megophrys* s.l. allocated to the subgenus *Panophrys* are listed in Table 5.

With significantly smaller body size, SVL 30.2–39.3 mm in males, *Megophrys dongguanensis* sp. nov. differs from the eight members with larger SVL values: *M. baolongensis* (42.0–45.0 mm in males), *M. binlingensis* (45.1–51.0 mm in males), *M. caudoprocta* (81.3 mm in male), *M. jingdongensis* (53.0–56.5 mm in males), *M. omei-montis* (56.0–59.5 mm in males), *M. sangziensis* (54.7 mm in single male), *M. spinata* (47.2–54.4 mm in males) and *M. shuichengensis* (102.0–118.3 mm in males).

*Megophrys dongguanensis* sp. nov. differs from 12 species occurring in eastern and southern China (*M. acuta, M. brachykolos, M. boettgeri, M. cheni, M. huangshanensis,
M. insularis, M. jinggangensis, M. kuatunensis, M. lini, M. lishuiensis, M. obesa and M. ombrophila) by the following combination of characters: presence of vomerine teeth (vs. absent in M. acuta, M. boettgeri, M. brachykolos, M. cheni, M. huangshanensis, M. kuatunensis, M. lini, M. lishuiensis, M. obesa and M. ombrophila), margin of tongue not notched posteriorly (vs. notched in M. boettgeri, M. cheni, M. huangshanensis, M. insularis and M. kuatunensis), absence of lateral fringes on toes (vs. presence of narrow lateral fringes on toes in M. acuta, M. jinggangensis and M. kuatunensis; presence of wide lateral fringes on toes in M. boettgeri, M. cheni and M. lini), toes with rudimentary webbing (vs. toes without webbing in M. lishuiensis, M. kuatunensis and M. ombrophila), hindlimbs short, with heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. hindlimbs comparatively longer, with heels meeting or overlapping in M. cheni, M. boettgeri, M. kuatunensis, M. jinggangensis and M. lini), tibio-tarsal articulation reaching the region between tympanum and eye when hindlimb is stretched along the side of the body (vs. reaching forward to the shoulder in M. brachykolos and to the posterior edge of tympanum in M. insularis).
Description of six new species of the subgenus Panophrys within the genus Megophrys...  

**Table 5.** Diagnostic characters separating the seven new species described in this study from *Megophrys feii* (incertae sedis) and 33 recognizing species of the *Megophrys* s.l. allocated to the subgenus *Panophrys.*

| Species                  | SVL | Horn-like tubercle at edge of upper eyelid | Vomeronal teeth | Tongue | Lateral fringes on toes | Toes | TD/ED | TIB/SVL |
|--------------------------|-----|-------------------------------------------|-----------------|--------|------------------------|-----|-------|---------|
| M. dongguanensis         | 30.2–39.3 (9) | /                                          | +               | −      | −                       | +   | 0.42–0.60 | 0.41–0.46 |
| M. nankunensis           | 29.9–34.9 (11) | 39.4–41.9 (2)                              | +               | −      | −                       | −   | 0.43–0.61 | 0.35–0.42 |
| M. jiulianensis          | 30.4–33.9 (9) | 34.1–37.5 (2)                              | +               | +      | −                       | +   | 0.50–0.59 | 0.44–0.48 |
| M. nanlingensis          | 30.5–37.3 (10) | /                                          | +               | +      | +                       | +   | 0.43–0.57 | 0.45–0.51 |
| M. wugongensis           | 31.0–34.1 (4) | 38.5–42.8 (9)                              | +               | −      | −                       | −   | 0.45–0.53 | 0.37–0.44 |
| M. mufumontana           | 30.1–30.8 (2) | 36.3 (2)                                   | +               | −      | −                       | +   | 0.51–0.58 | 0.47–0.53 |
| M. acuta                 | 27.1–33.0 (10) | 28.1–33.6 (4)                              | ++              | −      | +                       | +   | 0.57–0.71 | 0.38–0.45 |
| M. baolinensis           | 42.0–45.0 (5) | /                                          | +               | −      | +                       | −   | 0.41       | 0.46       |
| M. bicusinensis          | 32.0–36.0 (4) | 40.2–42.5 (2)                              | −               | −      | + or −                  | +   | 0.33–0.50 | 0.46–0.48 |
| M. baolinensis           | 45.1–51.0 (3) | /                                          | −               | +      | +                       | /   | 0.47–0.52 | 0.52–0.53 |
| M. boeticzeri            | 34.5–37.3 (20) | 39.7–46.8 (10)                             | +               | −      | +                       | +   | 0.40–0.67 | 0.45–0.49 |
| M. brachybelos           | 33.7–39.3 (5) | 33.9–45.9 (2)                              | +               | −      | −                       | +   | > 0.50     | 0.37–0.42 |
| M. caudopicta            | 81.3 (1)      | /                                          | ++              | −      | +                       | +   | 0.50       | 0.51       |
| M. cheni                 | 26.2–29.5 (15) | 31.8–34.1 (3)                              | +               | −      | ++                      | ++  | 0.41–0.54 | 0.50–0.54 |
| M. dauweimontsi          | 34.0–37.0 (18) | 40.0–46.0 (3)                              | +               | +      | +                       | /   | 0.54       |            |
| M. fanaespanensis        | 30.9–44.3 (13) | 41.7–42.5 (2)                              | +               | +      | +                       | −   | 0.53–0.80 | 0.49–0.59 |
| M. feii                  | 24.3–25.1 (4) | 28.2–28.2 (9)                              | +               | −      | +                       | ++  | 0.51–0.58 | 0.48–0.55 |
| M. huangliencens         | 37.4–47.6 (11) | 59.6 (1)                                   | +               | +      | +                       | −   | 0.54–0.75 | 0.44–0.63 |
| M. huangshanensis        | 36.0–41.6 (4) | 44.2 (1)                                   | +               | −      | −                       | −   | < 0.50     | 0.42–0.45 |
| M. insularellus          | 38.8–42.2 (5) | 47.3 (1)                                   | +               | −      | +                       | +   | 0.46–0.57 | 0.40–0.43 |
| M. jingdongensis         | 53.0–56.5 (3) | 63.5 (1)                                   | +               | +      | ++                      | +++ | 0.58–0.59 |
| M. jinggangensis         | 35.1–36.7 (2) | 38.4–41.6 (3)                              | ++              | −      | −                       | +   | 0.73–0.88 | 0.47–0.50 |
| M. kuatunensis           | 26.2–29.6 (13) | 37.4 (1)                                   | +               | −      | +                       | +   | 0.44       | 0.38–0.48 |
| M. latidactyla           | 38.9 (1)      | /                                          | ++              | −      | +                       | ++  | 0.85       | 0.52       |
| M. leishanensis          | 30.4–38.7 (10) | 42.3 (2)                                   | +               | −      | −                       | −   | +         | /         |
| M. libensis              | 34.7–67.7 (5) | 60.8–70.6 (8)                              | +++             | +      | +                       | ++  | 0.48–0.78 | 0.44–0.61 |
| M. lini                  | 34.1–37.9 (20) | 37.9–39.0 (4)                              | +               | −      | −                       | −   | 0.40–0.60 | 0.46–0.53 |
| M. libensis              | 30.7–34.7 (13) | 36.9–40.4 (3)                              | +               | −      | −                       | −   | /         | /         |
| M. minus                 | 34.5–41.4 (2) | /                                          | −               | −      | +                       | +   | 0.8–0.83   | 0.46–0.48 |
| M. obesa                 | 35.6 (1)      | 37.5–41.2 (6)                              | +               | −      | −                       | −   | 0.51–0.66 | 0.41–0.47 |
| M. umbrophila            | 27.4–34.5 (5) | 32.8–35.0 (4)                              | +               | −      | −                       | −   | 0.52–0.69 | 0.32–0.41 |
| M. omelaroides           | 56.0–59.5 (10) | 60.7–72.5 (3)                              | +               | +      | +                       | +   | 0.52–0.56 |            |
| M. palpabrachybelos      | 36.2–38.0 (2) | /                                          | ++              | −      | −                       | ++  | /         | 0.55       |
| M. rubrimeris            | 26.7–30.5 (8) | /                                          | ++              | +      | +                       | −   | 0.58–0.76 | 0.48–0.56 |
| M. sanghiensis           | 54.7 (1)      | /                                          | ++              | +      | +                       | +   | 0.62       | 0.59       |
| M. shuichengensis        | 102.0–118.3 (7) | 99.8–115.6 (6)                             | ++              | −      | −                       | ++  | 0.67       | 0.43–0.47 |
| M. spinata               | 47.2–54.4 (18) | 54.0–55.0 (2)                              | −               | −      | +                       | ++  | 0.43       | 0.56–0.58 |
| M. tubergranulatus       | 33.2–39.6 (9) | 50.5 (1)                                   | + or −          | −      | −                       | −   | 0.50       | 0.45–0.51 |
| M. wulaishanensis        | 27.3–31.6 (10) | 41.0–41.5 (2)                              | −               | −      | + or −                  | −   | 0.50       | 0.50–0.51 |
| M. weihanensis           | 30.4–35.5 (10) | 38.4 (1)                                   | −               | −      | −                       | (in female), + (in male) | +     | 0.50       | 0.47–0.48 |

1 long point (+++); slightly large (++), small (+), absent or indistinct (−); 2 present (+), or absent (−); 3 notched (++), feebly notched (+), or not notched (−); 4 wide (++), narrow (+), lacking (−); 5 at least one-fourth webbed (+++), at most one-fourth webbed (++), with rudimentary webbing (+), or without webbing (−).
From the remaining 10 species occurring in China, *Megophrys dongguanensis* sp. nov. can be distinguished by the presence of vomerine teeth (vs. absent in *M. binchuanensis*, *M. leishanensis*, *M. minor*, *M. tuberogranulatus*, *M. wuliangshanensis* and *M. wushanensis*), by the unnotched tongue (vs. tongue notched in *M. daweimontis*, *M. liboensis*, *M. minor* and *M. rubrimera*), by the absence of lateral fringes on toes (vs. wide in *M. binchuanensis*, *M. liboensis*, *M. palpebralespinosa* and *M. wushanensis* (in males); narrow in *M. rubrimera*), by the rudimentary webbing on toes (vs. toes without webbing in *M. rubrimera* and *M. wuliangshanensis*; at least one-fourth webbed in *M. palpebralespinosa*), by the heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. heels meeting in *M. binchuanensis* and *M. tuberogranulatus*; heels meeting or overlapping in *M. minor* and *M. wushanensis*; heels overlapping in *M. leishanensis*, *M. liboensis*, *M. palpebralespinosa* and *M. wuliangshanensis*).

*Megophrys dongguanensis* sp. nov. differs from the remaining species, *M. fansipanensis*, *M. hoanglienensis* and *M. latidactyla*, by the small horn-like tubercle at edge of upper eyelid (vs. slightly large in *M. latidactyla*), by the unnotched tongue (vs. tongue notched in *M. fansipanensis*, *M. hoanglienensis* and *M. latidactyla*), by the absence of lateral fringes on toes (vs. wide in *M. latidactyla*), by the presence of rudimentary webbing on toes (vs. webbing indistinct or absent in *M. fansipanensis* and *M. hoanglienensis*).

*Megophrys dongguanensis* sp. nov. further differs from *M. feii*, for which molecular data are lacking and cannot be allocated to any subgenus base on morphology only (Yang et al. 2018) by the larger body size, SVL 30.2–39.3 mm in males (VS. 24.3–25.1 mm in males), presence of nuptial pad with nuptial spines in males during breeding season (vs. absent), presence of vomerine teeth (vs. absent), unnotched tongue (vs. slightly notched), absence of lateral fringes on toes (vs. moderate or wide), heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. heels overlapping).

**Description of holotype.** Adult male. Body moderate-sized, SVL 38.0 mm; head width slightly larger than head length, HWD/HDL 1.09; snout pointed in dorsal view, projecting, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eye large, ED/HDL 0.40, pupil vertical; nostril oblique ovoid; canthus rostralis well developed, forming the beginning of a fleshy, protruding ridge, that continues over the upper eyelid, and transitions into a supratympanic fold that terminates in the scapular region; loreal region slightly oblique; internasal distance slightly larger than interorbital distance; tympanum distinct, moderate-sized, TD/ED 0.54; large ovoid choanae at the base of the maxilla; presence of vomerine ridge bearing vomerine teeth; margin of tongue not notched posteriorly; internal vocal slits present near the rear of the lower mandible.

Radioulna length and hand length 0.24 of SVL; fingers without webbing and lateral fringes, relative finger length II < I < IV < III; tips of fingers slightly dilated, round; presence of subarticular tubercles on finger III, and one subarticular tubercle at the bases of each finger; outer metacarpal tubercles indistinct, inner metacarpal tubercles distinct and observably enlarged. Hindlimbs short, tibio-tarsal articulation reaching the region between tympanum and eye when hindlimb is stretched along the side of the body; heels not meeting when the flexed hindlimbs are held at right angles to the
Figure 3. *Megophrys dongguanensis* sp. nov. in life: A–E SYS a001973, the male holotype F SYS a001492, a male paratype with more distinct skin ridges, granules and tubercles on dorsal surface of body.

body axis; tibia length 0.41 of SVL and foot length 0.61 of SVL; relative toe length I < II < V < III < IV; tips of toes round and slightly dilated; presence of rudimentary webbing on toes but absence of lateral fringes and tarsal folds; one subarticular tubercle at the bases of each toe; presence of a long ovoid inner metatarsal tubercle and absence of outer metatarsal tubercle.
Dorsal skin texture rough with dense granules; granules forming discontinuous X-shaped ridge with two discontinuous dorsolateral ridges on both sides at the central trunk; several large tubercles present on dorsal surface of flanks, thighs, shanks and forearms; four small tubercles present on the edge of upper eyelid, one of which is more prominent; distinct narrow supratympanic fold curving posteroventrally from posterior corner of eye to a level above insertion of arm; ventral skin texture smooth, several granules present on surface of abandon, ventral and posterior surface of thighs; pectoral gland small, closer to axilla; single femoral gland on rear of thigh.

**Measurements of holotype (in mm).** SVL 38.0, HDL 12.0, HDW 13.1, SNT 4.5, IND 3.9, IOD 3.6, ED 4.8, TD 2.6, TED 2.1, HND 9.1, RAD 9.2, FTL 23.2, TIB 15.6.

**Coloration of holotype in life.** (Fig. 3A–E) Yellowish brown dorsally, with a dark triangular marking between eyes. A wide oblique black band present on forearm. Dorsal surface of fingers and hindlimbs with dark grey transverse bands. Point of snout dark brown, presence of a vertical dark brown band below the eye. Tubercles on the edge of upper eyelid reddish. Supratympanic fold whitish tan. Ventral surface dark brown, with a black longitudinal band on surface of throat, several white spots present on ventral surface of limbs. Digits, inner and outer metacarpal tubercles greyish white, inner metatarsal tubercle greyish brown. Pectoral glands and femoral glands white. Iris yellowish brown.

**Coloration of holotype in preservative.** Yellowish brown fades to greyish brown dorsally. Triangular marking between eyes, oblique bands on dorsal forearms, transverse bands on dorsal fingers and hindlimbs become indistinct. Color of ventral surface fades, all bands and spots become indistinct.

**Variation.** Measurements of type series are listed in Table 4. All paratypes are very similar to holotype in morphology and color pattern. However, one male (SYS a001492) has more distinct skin ridges, granules and tubercles on dorsal surface of body (Fig. 3, F).

**Etymology.** The specific epithet “dongguanensis” is in reference to the type locality, Dongguan City of the new species. We propose the common English name “Dongguan Horned Toad” and Chinese name “Dong Guan Jiao Chan (东莞角蟾).”

**Distribution and natural history.** Currently, *Megophrys dongguanensis* sp. nov. is only known from Mt. Yinping, Guangdong Province, China. It inhabits flowing montane streams and the nearby forest floor and leaf litter at elevations between 100–300 m. Advertisement calls of males were noticed from mid-December until April of the next year just before the rainy season. Males were found calling on rocks in the flowing streams. Tadpoles could be found in this period.

*Megophrys (Panophrys) nankunensis* J. Wang, Zeng & Y.Y. Wang, sp. nov.
http://zoobank.org/1F85DDB8-298D-47BB-B5BD-CA6D5A3E66A8
Fig. 4, Table 4

**Holotype.** SYS a004498, adult male, collected by Jian Wang and Hai-Long He on 20 October 2015 from Mt. Nankun (23°38’19”N, 113°53’24”E; 400 m a.s.l.), Longmen County, Huizhou City, Guangdong Province, China.
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Figure 4. *Megophrys nankunensis* sp. nov. in life: A–D SYS a004498, the male holotype E–F SYS a004507, the female paratype.

Paratypes (10 males & two females). Adult females, SYS a004506–4507, collected by Jian Wang and Hai-Long He on 20 October 2015; adult males, SYS a002023, 2032–2033, collected by Run-Lin Li on 20 March 2013, SYS a004499–4504, SYS a004505/CIB110007, collected by Jian Wang and Hai-Long He on 20 October 2015, all from Mt. Nankun at elevations between 300–650 m.

Diagnosis. (1) Body size small, SVL 29.9–34.9 mm in 11 adult males, 39.4–41.9 mm in two adult females; (2) head width slightly larger than head length, HDW/HDL ratio 1.00–1.20; (3) snout rounded in dorsal view, tip of snout slightly sharpened; (4) tympanum distinct, moderate-sized, TD/ED ratio 0.43–0.61; (5) strong vomerine ridge bearing vomerine teeth; (6) margin of tongue not notched behind; (7) shanks short, heels not meeting when the flexed hindlimbs are held at right angles.
to the body axis; tibia-tarsal articulation reaching forward to the region between tympanum and eye when hindlimb is stretched along the side of the body; (8) TIB/SVL ratio 0.35–0.42, FTL/SVL ratio 0.53–0.62; (9) absence of lateral fringes on fingers, presence of an indistinct subarticular tubercle on the bases of each finger, relative finger lengths II < I < IV < III; (10) toes with rudimentary webbing at their bases and without lateral fringes, subarticular tubercles only present on the bases of each toes; (11) dorsal surface with dense granules, surface of flanks and dorsal surface of limbs with large tubercles; (12) edge of eye lid with a small reddish horn-like tubercle; (13) supratympanic fold distinct, forming a depressed supraaxillary gland above insertion of arm; (14) dorsum beige to dark brown, with indistinct light brown patches, with an incomplete dark triangular marking between eyes; (15) males with a single subgular vocal sac, and dense dark villiform nuptial spines present on dorsal surface of first and second fingers during breeding season, respectively; (16) gravid females bear creamy yellow oocytes.

Comparisons. Comparative data of Megophrys nankunensis sp. nov. with M. dongduanensis sp. nov., M. feii and the 33 recognized members of Megophrys s.l. allocated to the subgenus Panophrys are listed in Table 5.

In the ML and BI phylogenetic trees (Fig. 2), Megophrys nankunensis sp. nov. is a sister taxon to M. dongguanensis sp. nov. (p=4.6–5.0%) with high node-supporting value (0.1 in BI, 100% in ML%), and differs from the later by the snout rounded in dorsal view, tip of snout slightly sharpened (vs. snout pointed in dorsal view, tip of snout not sharpened), supratympanic fold forming a depressed supraaxillary gland above insertion of arm (vs. supraaxillary gland absent).

With significantly smaller body size, SVL 29.9–34.9 mm in males and 39.4–41.9 mm in females, Megophrys nankunensis sp. nov. differs from the 12 members with larger SVL values: M. baolongensis (42.0–45.0 mm in males), M. binlingensis (45.1–51.0 mm in males), M. caudoprocta (81.3 mm in single male), M. hoanglienensis (37.4–47.6 mm in males), M. jingdongensis (53.0–56.5 mm in males, 63.5 mm in single female), M. latidactyla (38.9 mm in single male), M. omeimontis (56.0–59.5 mm in males, 68.0–72.5 mm in females), M. palpebralespinosa (36.2–38.0 mm in males), M. sangzhiensis (54.7 mm in single male), M. shuichengensis (102.0–118.3 mm in males, 99.8–115.6 mm in females), M. spinata (47.2–54.4 mm in males, 54.0–55.0 mm in females) and M. tuberogranulatus (50.5 in single female).

Megophrys nankunensis sp. nov. differs from 12 species occurring in eastern and southern China (M. acuta, M. brachykolos, M. boettgeri, M. cheni, M. huangshanensis, M. insularis, M. jinggangensis, M. kuatunensis, M. lini, M. lishuiensis, M. obesa and M. ombrophila) by the following combination of characters: presence of vomerine teeth (vs. absent in M. acuta, M. boettgeri, M. brachykolos, M. cheni, M. huangshanensis, M. kuatunensis, M. lini, M. lishuiensis, M. obesa and M. ombrophila), absence of lateral fringes on toes (vs. presence of narrow lateral fringes on toes in M. acuta, M. jinggangensis and M. kuatunensis; presence of wide lateral fringes on toes in M. boettgeri, M. cheni and M. lini), toes with rudimentary webbing (vs. toes without webbing in M. lishuiensis, M. kuatunensis and M. ombrophila), hindlimbs short, with heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. hindlimbs
comparatively longer, with heels meeting or overlapping in *M. cheni*, *M. boettgeri*, *M. kuatunensis*, *M. jinggangensis* and *M. lini*), tibio-tarsal articulation reaching forward to the region between tympanum and eye when hindlimb is stretched along the side of the body (vs. reaching forward to the shoulder in *M. brachykolos* and to the posterior edge of tympanum in *M. insularis*), relative finger lengths II < I < IV < III (vs. IV < I < II < III in *M. brachykolos* and I < II < IV < III in *M. obesa* and *M. ombrophila*); supratympanic fold forming a depressed supraaxillary gland above insertion of arm (vs. supraaxillary gland swollen in *M. insularis*; absent in other 11 species).

*Megophrys nankunensis* sp. nov. differs from the remaining nine members of the *Megophrys* s.l. allocated to the subgenus *Panophrys* which share a moderate or small body size, by the by the small horn-like tubercle at edge of upper eyelid (vs. horn-like tubercle indistinct or absent in *M. binchuanensis*, *M. minor*, *M. wuliangshanensis* and *M. wushanensis*; long point in *M. liboensis*), presence of vomerine teeth (vs. absent in *M. binchuanensis*, *M. leishanensis*, *M. minor*, *M. wuliangshanensis* and *M. wushanensis*), absence of lateral fringes on toes (vs. wide in *M. binchuanensis*, *M. liboensis*, *M. wushanensis* (wide in males); narrow in *M. rubrimera*), toes with rudimentary webbing (vs. toes without webbing in *M. daweimontis*, *M. rubrimera*, *M. wuliangshanensis* and *M. wushanensis* (in females); webbing indistinct or absent in *M. fansipanensis*), tibio-tarsal articulation reaching forward to the region between tympanum and eye when hindlimb is stretched along the side of the body (vs. reaching forward to the tip of snout in *M. daweimontis*), finger II shortest (vs. finger I shortest in *M. liboensis*), presence of an indistinct subarticular tubercle on the bases of each finger (vs. subarticular tubercle absent in *M. fansipanensis*), heels not meeting when the flexed hindlimbs are held at right angles to the body axis (heels meeting in *M. binchuanensis*; heels meeting or overlapping in *M. minor* and *M. wushanensis*; heels overlapping in *M. leishanensis*, *M. liboensis* and *M. wuliangshanensis*).

*Megophrys nankunensis* sp. nov. further differs from *M. feii*, for which molecular data are lacking and cannot be allocated to any subgenus base on morphology only (Yang et al. 2018) by the larger body size, SVL 29.9–34.9 mm in males and 39.4–41.9 mm in females (VS. 24.3–25.1 mm in males, 28.2–28.9 mm in females), presence of nuptial pad with nuptial spines in males during breeding season (vs. absent), presence of vomerine teeth (vs. absent), absence of lateral fringes on toes (vs. moderate or wide), heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. heels overlapping).

**Description of holotype.** Adult male. Habitus small, SVL 31.3 mm; head width slightly larger than head length, HDW/HDL 1.12; snout rounded in dorsal view, tip of snout slightly sharpened, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eye large, ED/HDL 0.38; nostril oblique ovoid; pupil vertical; canthus rostralis well developed, forming the beginning of a fleshy, protruding ridge, that continues over the upper eyelid, and transitions into a supratympanic fold that terminates in the scapular region; loreal region vertical; internasal distance slightly larger than interorbital distance; tympanum distinct, moderate-sized, TD/ED 0.44; large ovoid choanae at the base of the maxilla; strong vomerine
ridge bearing vomerine teeth; margin of tongue weakly notched posteriorly; internal vocal slits present near the rear of the lower mandible.

RAD/SVL 0.22, HND/SVL 0.22; absence of lateral fringes and webbing on fingers, relative finger lengths II < I < IV < III; tip of finger rounded, slightly swollen; presence of a distinct subarticular tubercle on the base of each finger; outer metacarpal tubercles indistinct, inner metacarpal tubercles distinct and observably enlarged. Hindlimbs short, tibio-tarsal articulation reaching forward the anterior margin of tympanum when hindlimb is stretched along the side of the body; heels not meeting when the flexed hindlimbs are held at right angles to the body axis; TIB/SVL 0.37 and FTL/SVL 0.55; relative toe lengths I < II < V < III < IV; tips of toes round and slightly dilated; presence of rudimentary webbing on toes but absence of lateral fringes and tarsal folds; presence of a subarticular tubercle only at the bases of each toes; presence of a long ovoid inner metatarsal tubercle and absence of outer metatarsal tubercle.

Dorsal skin texture smooth with dense granules, some of which forming a weak X-shaped skin ridge on center of trunk; surface of flanks with large tubercles; presence of a small horn-like tubercle at the edge of eyelid; distinct supratympanic fold curving posteroventrally from posterior corner of eye to a level above insertion of arm, forming a swollen supraaxillary gland above insertion of arm; ventral skin texture smooth with granules on the surface of abdomen; pectoral gland large, equal size to tip of fingers, closer to axilla; single large femoral gland on rear of thigh.

**Measurements of holotype (in mm).** SVL 31.3, HDL 9.6, HDW 10.8, SNT 3.4, IND 3.4, IOD 2.4, ED 3.7, TD 1.6, TED 1.0, HND 6.9, RAD 7.0, FTL 17.3, TIB 11.6.

**Coloration of holotype in life.** (Fig. 4A–D) Dorsal surface beige with obscure darker patches, with a distinct and incomplete dark triangular marking between eyes, unconnected with an incomplete X-shaped marking on center of trunk. Forearm with dark bands dorsally; hindlimb with broad black transverse bands. Tip of snout dark brown. A dark brown vertical band below the eye. Supratympanic fold white. Horn-like tubercle at the edge of the upper eyelid orange. Surface of throat and chest dark brown, with scarlet spots. Posterior region of abdomen white, with dark brown and scarlet spots. Ventral surface of limbs white with brown patches. Ventral surface of hand and foot light brown, subarticular tubercle at the base of each fingers and toes, outer metacarpal tubercle, inner metatarsal tubercle and inner metacarpal tubercle pink. Pectoral and femoral glands white. Iris white.

**Coloration of holotype in preservative.** On dorsal surface the beige fades to dark grey. Dark interorbital triangular marking becomes more indistinct. Ventral surface pale in color, grey-brownish grounding, markings and mottling more distinct, all scarlet spots absent.

**Variation.** Measurements and body proportions of type series are given in Table 4. All paratype specimens were very similar in morphology and color pattern. However, the holotype has the dorsal surface beige (vs. reddish brown in paratypes SYS a002033, 4501, and dark brown in paratypes SYS a004502–4506, 4507 (Fig. 4E–F)), dorsal skin texture smooth, granules and tubercles weak (vs. dorsal skin texture relatively rough with more distinct granules and tubercles in paratypes SYS a004502,
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Figure 5. Ecology and behavior of Megophrys nankunensis sp. nov. A an adult male observed under the rock in the flowing stream B pair of M. nankunensis sp. nov. observed exposed on leave litters in a flowing stream, about 2.5 m wide, prior to amplexus.

4504–4507), and ventral surface of hand and foot light brown (vs. ventral surface of hand and foot grey white in paratypes SYS a004502–4504).

**Etymology.** The specific epithet “nankunensis” is in reference to the type locality of the new species: Mt. Nankun. We propose the common English name “Nankunshan Horned Toad” and Chinese name “Nan Kun Shan Jiao Chan (南昆山角蟾)”.

**Distribution and habits.** Currently, Megophrys nankunensis sp. nov. is known only from the type locality, Mt. Nankun in Longmen County, Guangdong Province, China. It inhabits forest floor, leaf litter and the nearby undergrowth rocky mountainous streams (2–3 m wide) surrounded by moist subtropical evergreen broadleaved forests
at elevations between 300–600 m. Breeding season of *M. nankunensis* sp. nov. is from October to the following March, males were found calling under the leaf litter or rocks (Fig. 5A) on the ground in the flowing streams, besides, a pair were observed exposed on the floor in a flowing stream, about 2.5 m wide, prior to amplexus (Fig. 5B) at 20:09 P.M. on 20 October 2015. Tadpoles were not observed in this period.

*Megophrys (Panophrys) jiulianensis* J. Wang, Zeng, Lyu & Y.Y. Wang, sp. nov.  
http://zoobank.org/2B18FD8D-520D-4531-AA9B-852E0E2AC92A

Fig. 6, Table 6

**Holotype.** SYS a002112, adult male, collected by Yu-Long Li on 2 May 2013 from Daqiutian Protection Station (24°34’34.99"N, 114°26’28.53"E; 560 m a.s.l.) of Mt. Jiulian, Longnan County, Ganzhou City, Jiangxi Province, China.

**Paratypes (nine males & two females).** SYS a002110, 2111, adult females, collected by Yu-Long Li on 3 May 2013 from Xiagongtang Protection Station (24°32’16.74"N, 114°27’56.82"E; 770 m a.s.l.) of Mt. Jiulian; SYS a001007, 1009, adult males, collected by Run-Lin Li on 23 July 2010 from Daqiutian Protection Station of Mt. Jiulian; SYS a002107–2109, 2113–2114, SYS a002115/CIB110008, adult males, collected by Yu-Long Li on 1–4 May 2013 from Xiagongtang Protection Station and Daqiutian Protection Station of Mt. Jiulian at elevations between 400–800 m a.s.l.; SYS a002031, adult male, collected by Run-Lin Li on 20 March 2013 from Mt. Nankun (23°38’21.94"N, 113°50’39.49"E; 610 m a.s.l.), Longmen County, Huizhou City, Guangdong Province, China.

**Diagnosis.** (1) Body slender and small-sized, SVL 30.4–33.9 mm in nine adult males, 34.1–37.5 mm in two adult females; (2) head width slightly larger than head length, HDW/HDL ratio 1.04–1.06; (3) snout rounded in dorsal view; (4) eye large, tympanum distinct, moderate-sized, TD/ED ratio 0.50–0.59; (5) weak vomerine ridge bearing vomerine teeth; (6) tongue weakly notched posteriorly; (7) hindlimbs slender, heels overlapping when the flexed hindlimbs are held at right angles to the body axis, tibia-tarsal articulation reaching forward to the middle of eye when hindlimb is stretched along the side of the body; (8) absence of lateral fringes on fingers, presence of an indistinct subarticular tubercle on the bases of each finger, relative finger lengths II < I < IV < III; (9) toes with rudimentary webbing at their bases and without lateral fringes, subarticular tubercles only present at the base of toe I and II; (10) dorsal skin rough, presence of black spines on granules of dorsal skin, and occasionally present on canthus rostralis and margin of tympanum, presence of large tubercles on flanks, dorsal body and limbs; (11) four prominent parallel dorsolateral ridges with granules bearing black spines on back of trunk, the middle two ridges forming a X-shaped ridge occasionally; (12) a reddish horn-like tubercle bearing a black spine at its tip at the edge of eye lid; (13) distinct supratympanic fold bearing black spines; (14) beige to brownish red above, with an hollow dark triangle between eyes and a rectangular dark marking on the center of the back of trunk; (15) males with a single subgular vocal sac, and presence of nuptial pads bear-
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ing darker nuptial spines on dorsal surface of the first and second fingers in adult males during breeding season, respectively; (16) gravid females bear creamy yellow oocytes.

Comparisons. Comparative data of *Megophrys jiulianensis* sp. nov. with *M. dongduanensis* sp. nov., *M. nankunensis* sp. nov., *M. feii* and the 33 recognized members of the *Megophrys* s.l. allocated to the subgenus *Panophrys* are listed in Table 5.

*Megophrys jiulianensis* sp. nov. is sympatric with *M. nankunensis* sp. nov. in Mt. Nan-kun, but it can be easily distinguished from the later by heels overlapping when the flexed hindlimbs are held at right angles to the body axis (vs. heels not meeting), TIB/SVL ratio 0.61–0.68 (vs. TIB/SVL ratio 0.35–0.42), supratympanic fold not forming a supraaxillary gland above insertion of arm (vs. supratympanic fold forming a depressed supraaxillary gland), presence of black spines on dorsal skin (vs. absent); besides, *M. jiulianensis* sp. nov. differs from *M. dongguanensis* sp. nov. by the notched tongue vs. (not notched), heels overlapping when the flexed hindlimbs are held at right angles to the body axis (vs. heels not meeting), TIB/SVL ratio 0.61–0.68 (vs. TIB/SVL ratio 0.41–0.46).

With significantly smaller body size, SVL 30.4–33.9 mm in males and 34.1–37.5 mm in females, *M. jiulianensis* sp. nov. differs from the 17 members with larger SVL values: *M. baolongensis* (42.0–45.0 mm in males), *M. binchuanensis* (40.2–42.5 mm in females), *M. binlingensis* (45.1–51.0 mm in males), *M. caudoprocta* (81.3 mm in single male), *M. daueimontis* (40.0–46.0 mm in females), *M. fansipanensis* (41.7–42.5 mm in females), *M. hoanglienensis* (37.4–47.6 mm in males, 59.6 mm in single female), *M. jingdongensis* (53.0–56.5 mm in males, 63.5 mm in single female), *M. liboensis* (34.7–67.7 mm in males, 60.8–70.6 mm in females), *M. minor* (34.5–41.2 mm in males), *M. omeimontis* (56.0–59.5 mm in males, 68.0–72.5 mm in females), *M. palpebralespinosa* (36.2–38.0 mm in males), *M. sangzhiensis* (54.7 mm in single male), *M. shuichengensis* (102.0–118.3 mm in males, 99.8–115.6 mm in females), *M. spinata* (47.2–54.4 mm in males, 54.0–55.0 mm in females), *M. tuberogranulatus* (50.5 mm in single female) and *M. wuliangshanensis* (41.3 mm in single female).

*Megophrys jiulianensis* sp. nov. differs from 12 species occurring in eastern and southern China (*M. acuta*, *M. brachykolos*, *M. boettgeri*, *M. cheni*, *M. huangshanensis*, *M. insularis*, *M. jinggangensis*, *M. kuatunensis*, *M. lini*, *M. lishuiensis*, *M. obesa*, *M. ombrophila*) by the following combination of characters: presence of vomerine teeth (vs. absent in *M. leishanensis* and *M. wushanensis*), tongue notched posteriorly (vs. not notched in *M. acuta*, *M. brachykolos*, *M. jinggangensis*, *M. lini*, *M. lishuiensis*, *M. obesa* and *M. ombrophila*), absence of lateral fringes on toes (vs. narrow in *M. acuta*, *M. jinggangensis* and *M. kuatunensis*; wide in *M. boettgeri*, *M. cheni* and *M. lini*), heels overlapping when the flexed hindlimbs are held at right angles to the body axis (vs. heels not meeting in *M. acuta*, *M. brachykolos*, *M. insularis*, *M. obesa* and *M. ombrophila*).

*Megophrys jiulianensis* sp. nov. differs from the remaining four members of the *Megophrys* s.l. allocated to the subgenus *Panophrys* which share a moderate or small body size, by the presence of vomerine teeth (vs. absent in *M. leishanensis* and *M. wushanensis*), tongue notched posteriorly (vs. not notched in *M. leishanensis*, *M. wushanen-
sis and *M. latidactyla*), absence of lateral fringes on toes (vs. narrow in *M. rubrimera*; wide in *M. latidactyla* and *M. wushanensis* (wide in females)), toe webbing rudimentary (vs. absence of webbing on toes in *M. rubrimera*).

*Megophrys jiulianensis* sp. nov. further differs from *M. feii*, for which molecular data are lacking and cannot be allocated to any subgenus base on morphology only (Yang et al. 2018) by the larger body size, SVL 30.4–33.9 mm in males and 34.1–37.5 mm in females (VS. 24.3–25.1 mm in males, 28.2–28.9 mm in females), presence of nuptial pad with nuptial spines in males during breeding season (vs. absent), presence of vomerine teeth (vs. absent), absence of lateral fringes on toes (vs. moderate or wide).

**Description of holotype.** Adult male. Habitus slender and small, SVL 32.0 mm; head width slightly larger than head length, HDW/HWL 1.04; snout rounded in dorsal view, projecting, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eye large, ED/HDL 0.39; nostril oblique ovoid; pupil vertical; canthus rostralis well developed, forming the beginning of a fleshy, protruding ridge, that continues over the upper eyelid, and transitions into a supratympanic fold that terminates in the scapular region; loreal region vertical; internasal distance slightly larger than interorbital distance; tympanum distinct, moderate-sized, TD/ED 0.52; large ovoid choanae at the base of the maxilla; weak vomerine ridge bearing vomerine teeth; margin of tongue weakly notched posteriorly; internal vocal slits present near the rear of the lower mandible.

Rad/SVL 0.25; absence of lateral fringes and webbing on fingers, relative finger lengths II < I < IV < III; tip of finger rounded, slightly swollen; presence of an indistinct subarticular tubercle on the base of each finger; outer metacarpal tubercles indistinct, inner metacarpal tubercles distinct and observably enlarged. Hindlimbs long, tibio-tarsal articulation reaching forward to the middle of eye when hindlimb is stretched along the side of the body; heels overlapping when the flexed hindlimbs are held at right angles to the body axis; TIB/SVL 0.46 and FTL/SVL 0.62; relative toe lengths I < II < V < III < IV; tips of toes round and slightly dilated; presence of rudimentary webbing on toes but absence of lateral fringes and tarsal folds; presence of a subarticular tubercle only at the bases of the first and second toes; presence of a long ovoid inner metatarsal tubercle and absence of outer metatarsal tubercle.

Dorsum rough with dense granules bearing spines; canthus rostralis, margin of tympanum, supratympanic fold and upper lip with dense spines; presence of large tubercles bearing spines on dorsal surface of body, surface of flanks and dorsal and posterolateral surface of limbs; prominent parallel dorsolateral ridges with granules bearing spines on back of trunk; presence of a horn-like tubercle bearing a spine at its tip at the edge of eye lid; distinct supratympanic fold curving posteroventrally from posterior corner of eye to a level above insertion of arm; ventral skin texture smooth, the lower lip bears spines; sides of belly with large tubercles; ventral skin texture of thighs smooth with a few small tubercles, posterior surface and surface around anus with large tubercles bearing spines; surface of tibia-tarsal with a few tubercles bearing spines; presence of spines on lateral sides of fingers and toes; pectoral
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Gland moderate-sized, closer to axilla; single femoral gland on rear of thigh, distinctly smaller than pectoral gland.

**Measurements of holotype (in mm).** SVL 32.2, HDL 11.5, HDW 11.4, SNT 3.6, IND 3.5, IOD 3.3, ED 4.2, TD 2.3, TED 1.7, HND 8.0, RAD 8.1, FTL 20.5, TIB 14.7.

*Figure 6.* General life aspect in life of *Megophrys jiulianensis* sp. nov.: A–D SYS a002112, the male holotype E–F SYS a002111, the female paratype.
Coloration of holotype in life. (Fig. 6A–D) Dorsal surface yellowish brown, with an incomplete dark triangular marking between eyes. Spines on dorsal surface, granules and tubercles black. Forearm with a distinct, black oblique band. Transverse bands on hindlimb indistinct. Tip of snout grayish brown. A grayish-brown vertical band below the eye. Tubercle at the edge of the upper eyelid red. Ventral surface yellow, scattered with dense dark gray spots and black scarlet blotches; ventral surface of limbs flesh colored with pink and black spots. Palms and soles dark brown, inner metatarsal tubercle, outer metacarpal tubercle and inner metacarpal tubercle orange red, tip of digits orange-red. Pectoral glands and femoral glands white. Iris white.

Coloration of holotype in preservative. Dorsum yellowish brown fades to grayish brown, scattered with black spots. Greyish black triangular marking between the eyes become more distinct. Ventral surface paled in color, brown grounding, markings and mottling become more distinct.

Variation. Measurements and body proportions of type series are given in Table 6.

Table 6. Measurements (in mm; minimum-maximum, mean ± SD) of the type series of *Megophrys jiulianensis* sp. nov.

| Species | *Megophrys jiulianensis* sp. nov. |
|---------|----------------------------------|
|         | Males (n = 9)                    | Females (n = 2) |
| SVL     | 30.4–33.9 (32.2 ± 1.2)           | 34.1–37.5       |
| HDL     | 10.7–11.6 (11.2 ± 0.4)           | 12.0–12.4       |
| HDW     | 10.9–11.8 (11.4 ± 0.4)           | 12.5–13.2       |
| SNT     | 3.4–3.8 (3.6 ± 0.2)              | 3.9–4.1         |
| IND     | 3.2–3.6 (3.5 ± 0.1)              | 3.5–3.8         |
| IOD     | 3.2–3.5 (3.3 ± 0.1)              | 3.6             |
| ED      | 3.9–4.4 (4.2 ± 0.2)              | 4.3–4.4         |
| TD      | 2.1–2.5 (2.3 ± 0.1)              | 2.2–2.4         |
| TED     | 1.6–2.0 (1.7 ± 0.1)              | 2.1–2.5         |
| HND     | 7.4–10.6 (8.0 ± 0.4)             | 8.3–9.5         |
| RAD     | 7.7–8.5 (8.1 ± 0.3)              | 8.3–9.8         |
| FTL     | 14.1–15.2 (14.7 ± 0.4)           | 16.0–17.8       |
| TIB     | 19.8–21.1 (20.5 ± 0.5)           | 21.6–25.5       |
| HDL/SVL | 0.34–0.37 (0.35 ± 0.01)          | 0.33–0.35       |
| HDW/SVL | 0.34–0.37 (0.35 ± 0.01)          | 0.35–0.37       |
| HDW/HDL | 1.00–1.04 (1.02 ± 0.02)          | 1.04–1.06       |
| SNT/HDL | 0.32–0.34 (0.32 ± 0.01)          | 0.33            |
| SNT/SVL | 0.11–0.12 (0.11 ± 0.00)          | 0.11            |
| IND/HDW | 0.29–0.33 (0.30 ± 0.01)          | 0.28–0.29       |
| IOD/HDW | 0.28–0.30 (0.29 ± 0.01)          | 0.27–0.29       |
| ED/HDL  | 0.36–0.39 (0.38 ± 0.01)          | 0.35–0.36       |
| ED/SVL  | 0.12–0.14 (0.13 ± 0.01)          | 0.12–0.13       |
| TD/ED   | 0.50–0.59 (0.55 ± 0.03)          | 0.51–0.55       |
| TED/TD  | 0.68–0.87 (0.75 ± 0.07)          | 0.95–1.04       |
| HND/SVL | 0.24–0.26 (0.25 ± 0.01)          | 0.24–0.25       |
| RAD/SVL | 0.24–0.27 (0.25 ± 0.01)          | 0.24–0.26       |
| TIB/SVL | 0.44–0.48 (0.46 ± 0.01)          | 0.47            |
| FTL/SVL | 0.61–0.67 (0.64 ± 0.02)          | 0.63–0.68       |
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Figure 7. Ecology and behavior of *Megophrys jiulianensis* sp. nov.: A The male paratype SYS a002031 observed calling on a leaf (showing subgular vocal sac) B a female individual observed feeding on an earthworm after rain, both from Mt. Nankun in Guangdong Province.
All paratype specimens were very similar in morphology and color pattern. However, dorsal skin texture is more rough with well-developed spines in the female specimen SYS a002111 (Fig. 6E–F), dorsal surface yellowish brown in the other female specimen SYS a002110, and the middle two ridges on dorsum forming an X-shaped skin ridge in the male specimen SYS a002108.

**Etymology.** The specific epithet “jiulianensis” is in reference to the known localities of the new species: Mt. Jiulian and Nankunshan Nature Reserve located in the Jiulian Mountains range. We propose the common English name “Jiulianshan Horned Toad” and Chinese name “Jiu Lian Shan Jiao Chan (九连山角蟾)”.

**Distribution and natural history.** Currently, *Megophrys jiulianensis* sp. nov. is known from Mt. Nankun in Guangdong Province and the type locality, Jiulian Nature Reserve in Jiangxi Province, China. It inhabits forest floor, leaf litter and the nearby undergrowth mountainous streams surrounded by moist subtropical evergreen broadleaved forests at elevations between 500–800 m. Breeding season of *M. jiulianensis* sp. nov. is from March to July, males were usually found staying while calling on leaves (Fig. 7A), about 0.1–0.3 m above the ground. After the rain, numerous individuals can be easily found on the road, and a female individual from Mt. Nankun was observed feeding on an earthworm (Fig. 7B) on 20:45 p.m., 21 March 2016. Tadpoles could be found all year round.

*Megophrys jiulianensis* sp. nov. is sympatric with *M. nankunensis* sp. nov. and *M. mangshanensis* at Mt. Nankun.

*Megophrys (Panophrys) nanlingensis* Lyu, J. Wang, Liu & Y.Y. Wang, sp. nov.

http://zoobank.org/F9567F3F-D374-4CE8-A3A6-01C5F6A17A2D

Fig. 8, Table 7

**Holotype.** SYS a001964, adult male, collected by Run-Lin Li on 21 December 2012 from Nanling Nature Reserve (24°54’48.80"N, 113°01’12.34"E; 1008m a.s.l.), Ruyuan County, Shaoguan City, Guangdong Province, China.

**Paratypes (nine males).** SYS a001959–1962, SYS a001963/CIB110010, adult males, collected on 21 December 2012 by Run-Lin Li from the same stream as the holotype (1000–1300 m a.s.l.); SYS a002233, 2356–2358, collected on 1–3 October 2013 by Ying-Yong Wang and Zu-Yao Liu from Mt. Qiyun (25°52’22.84"N, 114°01’52.09"E; 691–1355m a.s.l.), Chongyi County, Ganzhou City, Jiangxi Province, China.

**Diagnosis.** (1) Body small-sized, SVL 30.5–37.3 mm in 10 adult males; (2) snout rounded in dorsal view; (3) tympanum distinct, moderate-sized, TD/ED ratio 0.43–0.57; (4) vomerine ridge and vomerine teeth present; (5) tongue notched posteriorly; (6) absence of lateral fringes and webbing on fingers, presence of narrow lateral fringes and rudimentary webbing on toes; (7) presence of a subarticular tubercle at the base of each finger and toe; (8) hindlimbs slender, heels overlapping, tibio-tarsal articulation reaching between the posterior corner to the center of eye; (9) TIB/SVL ratio 0.45–0.51 and FTL/SVL ratio 0.61–0.73; (10) dense conical granules present on surface of temporal region, upper lip, and from loreal region to the tip of snout; (11) granules
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and tubercles on dorsal surface forming a discontinuous X-shaped ridge and a pair of discontinuous dorsolateral ridges on back of trunk; (12) supratympanic fold distinct, whitish tan; (13) brown dorsally, with a dark triangular marking with light yellow edge between eyes, and an X-shaped or V-shaped marking with light yellow edge on the center of the back of trunk; (14) presence of a single subgular vocal sac in males; (15) nuptial pads and nuptial spines invisible in males during breeding season.

Comparisons. Comparative data of Megophrys nanlingensis sp. nov. with M. dongguanensis sp. nov., M. nanlingensis sp. nov., M. jiulianensis sp. nov., M. feii and the 33 recognized members of Megophrys s.l. allocated to the subgenus Panophrys are listed in Table 5.

Megophrys nanlingensis sp. nov. differs from M. dongguanensis sp. nov., M. nankunensis sp. nov. and M. jiulianensis sp. nov. by the heels overlapping when hindlimb is stretched along the side of the body (vs. heels not meeting in M. dongguanensis sp. nov. and M. nankunensis sp. nov.), presence of lateral fringes on toes (vs. absent in M. dongguanensis sp. nov., M. nankunensis sp. nov. and M. jiulianensis sp. nov.), tongue notched posteriorly (vs. not notched in M. dongguanensis sp. nov. and M. nankunensis sp. nov.), skin relatively smooth and lacking black horny spines (vs. skin rough with black horny spines in M. jiulianensis sp. nov.).

With the smaller body size, SVL 30.5–37.3 mm in males, Megophrys nanlingensis sp. nov. differs from the nine members with larger SVL values: M. baolongensis (42.0–45.0 mm in males), M. binlingensis (45.1–51.0 mm in males), M. caudoprocta (81.3 mm in single male), M. jingdongensis (53.0–56.5 mm in males), M. latidactyla (38.9 mm in single male), M. omeimontis (56.0–59.5 mm in males), M. sangzhiensis (54.7 mm in single male), M. shuichengensis (102.0–118.3 mm in males) and M. spinata (47.2–54.4 mm in males).

Megophrys nanlingensis sp. nov. differs from 12 species occurring in eastern and southern China (M. acuta, M. brachykolos, M. boettgeri, M. cheni, M. huangshanensis, M. insularis, M. jinggangensis, M. kuatanensis, M. lini, M. lishuaiensis, M. obesa and M. ombrophila) by the following combination of characters: presence of vomerine teeth (vs. absent in M. acuta, M. boettgeri, M. brachykolos, M. cheni, M. huangshanensis, M. kuatanensis, M. lini, M. lishuaiensis, M. obesa and M. ombrophila), margin of tongue notched posteriorly (vs. not notched in M. acuta, M. brachykolos, M. jinggangensis, M. lini, M. lishuaiensis, M. obesa and M. ombrophila), hindlimbs comparatively longer, with heels overlapping when the flexed hindlimbs are held at right angles to the body axis (vs. hindlimbs short, with heels not meeting in M. acuta, M. brachykolos, M. huangshanensis, M. insularis, M. obesa and M. ombrophila).

Megophrys nanlingensis sp. nov. differs from the remaining 12 members of the Megophrys s.l. allocated to the subgenus Panophrys which share a moderate or small body size, by the small horn-like tubercle at edge of the upper eyelid (vs. horn-like tubercle indistinct or absent in M. binchuanensis, M. minor, M. wuliangshanensis and M. wushanensis; slightly large in M. palpebralespinosa; long point in M. liboensis), presence of vomerine teeth (vs. absent in M. binchuanensis, M. leishanensis, M. minor,
M. wuliangshanensis and M. wushanensis), tongue notched posteriorly (vs. tongue not notched in M. palpebralespinosa, M. tuberogranulatus and M. wushanensis), toes with narrow lateral fringes (vs. wide in M. binchuanensis, M. liboensis, M. palpebralespinosa and M. wushanensis (in males)); absent in M. daweimontis, M. leishanensis, M. minor, M. tuberogranulatus, M. wuliangshanensis, M. wushanensis (in females); indistinct or absent in M. hoanglienensis), toes webbing rudimentary (vs. toes without webbing in M. daweimontis, M. fansipanensis, M. rubrimera and M. wuliangshanensis; indistinct or absent in M. fansipanensis and M. hoanglienensis; at least one-fourth webbed in M. palpebralespinosa), subarticular tubercles present (vs. absent in M. palpebralespinosa and M. rubrimera).

Megophrys nanlingensis sp. nov. further differs from M. feii, for which molecular data are lacking and cannot be allocated to any subgenus based on morphology only (Yang et al. 2018) by the larger body size, SVL 30.5–37.3 mm in males (VS. 24.3–25.1 mm in males), presence of nuptial pad with nuptial spines in males during breeding season (vs. absent), presence of vomerine teeth (vs. absent), presence of narrow lateral fringes on toes (vs. moderate or wide).

Description of holotype. Adult male. Body size small, SVL 32.5 mm; head length and head width almost isometric, HDW/HDL 0.99; snout rounded in dorsal view, projecting, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eye large, ED/HDL 0.37, pupil vertical; nostril oblique ovoid; canthus rostralis well developed; loreal region slightly oblique; internasal distance slightly larger than interorbital distance; tympanum distinct, moderate-sized, TD/ED 0.48; large ovoid choanae at the base of the maxilla; presence of vomerine ridge bearing vomerine teeth; margin of tongue notched posteriorly; internal vocal slits present near the rear of the lower mandible.

RAD/SVL 0.25, HND/SVL 0.24; fingers without webbing and lateral fringes, relative finger length II < I < IV < III; tips of fingers slightly dilated, round; one subarticular tubercle at the bases of each finger; outer and inner metacarpal tubercles distinct, and the inner one observably enlarged. Hindlimbs slender, tibio-tarsal articulation reaching forward to the center of the eye when hindlimb is stretched along the side of the body; heels overlapping when the flexed hindlimbs are held at right angles to the body axis; TIB/SVL 0.49 and FTL/SVL 0.69; relative toe length I < II < V < III < IV; tips of toes round and slightly dilated; toes with narrow lateral fringes, rudimentary webbing; one subarticular tubercle at the bases of each toes; presence of a long ovoid inner metatarsal tubercle and absence of outer metatarsal tubercle.

Dorsal skin texture rough; head surface rough, with small tapered granules densely covering from temporal region, upper lip, loreal region to tip of snout; granules forming discontinuous X-shaped ridge with two discontinuous dorsolateral ridges on both sides at the central trunk; large tubercles on flanks; a horn-like prominent tubercle on the edge of the upper eyelid; distinct supratympanic fold curving posterovertrally from posterior corner of eye to a level above insertion of arm; ventral skin texture smooth, with several large granules and tubercles on two sides; ventral skin texture of thighs
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**Figure 8.** *Megophrys nanlingensis* sp. nov. in life: **A–D** SYS a001964, male holotype **E, F** SYS a001963, female paratype.

smooth, with a few small tubercles; pectoral gland larger, closer to axilla; single femoral gland on rear of thigh.

**Measurements of holotype (in mm).** SVL 32.5, HDL 11.5, HDW 11.4, SNT 3.7, IND 3.5, IOD 3.3, ED 4.2, TD 2.0, TED 1.7, HND 8.0, RAD 7.8, FTL 22.3, TIB 15.9.

**Coloration of holotype in life.** (Fig. 8A–D) Brown dorsally, with a dark triangular marking with light yellow edge between eyes, and an X-shaped marking with light yellow edge on the center of the back of trunk. Dark brown transverse bands dorsally on lower arms and hindlimbs. Surface of snout brown. Black brown vertical band below the eye on each side. Temporal region brown, supratympanic fold white. Ventral surface pale grey, an indistinct longitudinal stripe on surface of throat. Scarlet spots on surface of chest. Belly whitish grey with dark brown marbling. A pair of black longitudinal stripes scattered with several white tubercles on surface of lateroventral flanks. Ventral surface of limbs light red and scattered with white spots. Ventral surface of hands and feet dark brown, tips of digits pale-grey. Metacarpal tubercle and metatarsal tubercle light red. Pectoral glands and femoral glands white. Iris reddish brown.

**Coloration of holotype in preservative.** Coloration of dorsal and ventral surface turned pale; transverse bands on limbs, dark longitudinal stripe on surface of throat and black patches on surface of lateroventral flanks became more distinct; scarlet spots on surface of chest faded.

**Variation.** Measurement data of type series are listed in Table 7.

All paratypes are very similar to holotype in morphology and color pattern. However, the male specimen SYS a001963 (Fig. 8E, F) is obviously large in snout-vent
Table 7. Measurements (in mm; minimum-maximum, mean ± SD) of the type series of *Megophrys nanlingensis* sp. nov.

| Species | Megophrys nanlingensis sp. nov. |
|---------|--------------------------------|
| Males (n = 10) |                                |
| SVL     | 30.5–37.3 (33.2 ± 1.9)         |
| HDL     | 10.9–12.7 (11.6 ± 0.5)         |
| HDW     | 10.7–13.8 (11.8 ± 0.9)         |
| SNT     | 3.4–3.8 (3.6 ± 0.1)            |
| IND     | 3.5–4.0 (3.7 ± 0.2)            |
| IOD     | 3.2–4.0 (3.4 ± 0.3)            |
| ED      | 4.1–4.9 (4.5 ± 0.3)            |
| TD      | 1.9–2.5 (2.2 ± 0.2)            |
| TED     | 1.6–2.2 (1.8 ± 0.2)            |
| HND     | 7.1–9.6 (8.0 ± 0.6)            |
| RAD     | 7.1–9.0 (8.1 ± 0.5)            |
| FTL     | 18.6–27.1 (22.4 ± 2.3)         |
| TIB     | 13.9–18.8 (16.0 ± 1.3)         |
| HDL/SVL | 0.33–0.36 (0.35 ± 0.01)        |
| HDW/SVL | 0.33–0.37 (0.35 ± 0.01)        |
| HDW/HDL | 0.97–1.09 (1.02 ± 0.04)        |
| SNT/HDL | 0.30–0.33 (0.31 ± 0.01)        |
| SNT/SVL | 0.10–0.12 (0.11 ± 0.01)        |
| IND/HDW | 0.29–0.35 (0.31 ± 0.02)        |
| IOD/HDW | 0.28–0.32 (0.29 ± 0.01)        |
| ED/HDL  | 0.37–0.41 (0.39 ± 0.01)        |
| ED/SVL  | 0.13–0.14 (0.14 ± 0.01)        |
| TD/ED   | 0.43–0.57 (0.48 ± 0.04)        |
| TED/TD  | 0.67–0.95 (0.83 ± 0.10)        |
| HND/SVL | 0.23–0.26 (0.24 ± 0.01)        |
| RAD/SVL | 0.23–0.26 (0.24 ± 0.01)        |
| TIB/SVL | 0.45–0.51 (0.48 ± 0.02)        |
| FTL/SVL | 0.61–0.73 (0.68 ± 0.04)        |

length than other specimens, with lighter reddish-brown iris, yellowish brown background coloration and comparatively smooth skin. The heels are significantly overlapping in all specimens from Nanling Nature Reserve but slightly overlapping in specimens from Mt. Qiyun.

**Etymology.** The specific epithet “nanlingensis” is in reference to the type locality of the new species, Nanling Nature Reserve of the Nanling Mountains. We propose the common English name “Nanling Horned Toad” and Chinese name “Nan Ling Jiao Chan (南岭角蟾)”.

**Distribution and natural history.** Currently, *Megophrys nanlingensis* sp. nov. is known from Nanling Nature Reserve and the neighboring Mangshan Nature Reserve (between elevations of 1000–1300 m), together with Mt. Qiyun (between elevations of 690–1400 m). It inhabits streams in bamboo forests. Males are frequently heard calling during August and December. Tadpoles could be found in this period.

*Megophrys nanlingensis* sp. nov. is sympatric with *M. mangshanensis* and *M. popei* in Nanling Nature Reserve and the neighboring Mangshan Nature Reserve.
**Megophrys (Panophrys) wugongensis** J. Wang, Lyu & Y.Y. Wang, sp. nov.

http://zoobank.org/51EED805-C594-4FA0-A03E-9BE8C11EAA40

Fig. 9, Table 8

**Holotype.** SYS a002625, adult male, collected by Guo-Ling Chen and Jian Zhao on 9 May 2014 from Yangshimu Scenic Area (27°34'47.93"N, 114°15'7.34"E; 550 m a.s.l.), Pingxiang City, Jiangxi Province, China.

**Paratypes (three males & nine females).** Adult males, SYS a004777/CIB110011, SYS a004796, 4800, collected by Zhi-Tong Lyu and Ying-Yong Wang on 23 May 2016, and adult females, SYS a002610–2611, collected by Guo-Ling Chen and Jian Zhao on 8 May 2014, SYS a004797–4799, 4801–4804, collected by Zhi-Tong Lyu and Ying-Yong Wang on 23 May 2016, from Wugongshan Scenic Area (27°34'3.94"N, 114°10'28.38"E; 1050–1080 m a.s.l.), Anfu County, Ji’an City, Jiangxi Province, China.

**Diagnosis.** (1) Body size small, SVL 31.0–34.1 mm in four adult males and body size moderate, SVL 38.5–42.8 mm in nine adult females; (2) tympanum distinct, slightly convex, moderate-sized, TD/ED ratio 0.47–0.52; (3) vomerine teeth absent; (4) margin of tongue not notched posteriorly; (5) hindlimbs short, heels not meeting, tibia-tarsal articulation reaching forward to the region between posterior corner of eye and posterior margin of tympanum; (6) TIB/SVL ratio 0.39–0.44, FTL/SVL ratio 0.56–0.64; (7) fingers without lateral fringes, presence of a subarticular tubercle at the bases of each finger, relative finger lengths II < I = IV < III; (8) toes with rudimentary webbing at their bases and without lateral fringes, subarticular tubercles only present at the base of each toe; (9) numerous granules present on dorsal surface of body, several large tubercles present on surface of flanks and dorsal surface of limbs; (10) presence of a small horn-like tubercle at the edge of the upper eyelid; (11) supratympanic fold distinct, whitish; (12) yellowish brown or reddish brown dorsally, with an incomplete dark triangular marking between eyes and an X-shaped marking on back of trunk; (13) ventral surface greyish brown, ventral surface of abdomen with creamy white nebulose patches and black spots; (14) males with a single subgular vocal sac; (15) gravid females bear creamy yellow oocytes.

**Comparisons.** Comparative data of *Megophrys wugongensis* sp. nov. with *M. dongduanensis* sp. nov., *M. nankunensis* sp. nov., *M. jiulianensis* sp. nov., *Megophrys nanlingensis* sp. nov., *M. feii* and the 33 recognized members of *Megophrys* s.l. allocated to the subgenus *Panophrys* are listed in Table 5. *Megophrys wugongensis* sp. nov. differs from *M. dongduanensis* sp. nov., *M. nankunensis* sp. nov., *M. jiulianensis* sp. nov. and *M. nanlingensis* sp. nov. by a combination of following characters: vomerine teeth absent (vs. vomerine teeth present), tongue not notched posteriorly (vs. tongue notched in *M. jiulianensis* sp. nov. and *M. nanlingensis* sp. nov.), absence of lateral fringes on toes (vs. presence of narrow lateral fringes on toes in *M. nanlingensis* sp. nov.), heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. heels overlapping in *M. jiulianensis* sp. nov. and *M. nanlingensis* sp. nov.), absence of black spines on dorsal skin (vs. present in *M. jiulianensis* sp. nov.), relative finger lengths II < I = IV < III (vs. II < I < IV < III in *M. nan-
kunensis sp. nov., M. jiulianensis sp. nov. and M. nanlingensis sp. nov.), ventral surface with creamy white nebulous patches (vs. absence of such patched on ventral surface in M. dongguanensis sp. nov. and M. nankunensis sp. nov.).

With the smaller body size, SVL 31.0–34.1 mm in males and 38.5–42.8 mm in females, Megophrys wugongensis sp. nov. differs from the 13 members with larger SVL values: M. baolongensis (42.0–45.0 mm in males), M. binlingensis (45.1–51.0 mm in males), M. caudoprocta (81.3 mm in single male), M. hoanglienensis (37.4–47.6 mm in males, 59.6 mm in single female), M. jingdongensis (53.0–56.5 mm in males 63.5 in single female), M. latidactyla (38.9 mm in single male), M. liboensis (34.7–67.7 mm in males, 60.8–70.6 mm in females), M. omeimontis (56.0–59.5 mm in males, 68.0–72.5 mm in females), M. palpebralespinosa (36.2–38.0 mm in males), M. sangzhiensis (54.7 mm in single male), M. shuichengensis (102.0–118.3 mm in males, 99.8–115.6 mm in females), M. spinata (47.2–54.4 mm in males, 54.0–55.0 mm in females), and M. tuberogranulatus (33.2–39.6 mm in males, 50.5 mm in single female).

Megophrys wugongensis sp. nov. differs from 12 species occurring in eastern and southern China (M. acuta, M. brachykolos, M. boettgeri, M. cheni, M. huangshanensis, M. insularis, M. jinggangensis, M. kuatunensis, M. lini, M. lishuiensis, M. obesa and M. ombrophila) by the following combination of characters: vomerine teeth absent (vs. present in M. insularis and M. jinggangensis), tongue not notched posteriorly (vs. tongue notched in M. boettgeri, M. huangshanensis, M. kuatunensis and M. insularis), toes without lateral fringes (vs. laterals fringes on toes narrow in M. acuta, M. kuatunensis and M. jinggangensis; wide in M. boettgeri, M. cheni and M. lini), toes with rudimentary webbing (vs. toes without webbing in M. huangshanensis, M. lishuiensis and M. ombrophila), hindlimbs short, with heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. hindlimbs comparatively longer, with heels overlapping in M. boettgeri, M. cheni, M. kuatunensis, M. jinggangensis and M. lini), relative finger lengths II < I = IV < III (vs. I < II ≤ IV < III in M. acuta and M. ombrophila; IV < II < I < III in M. brachykolos; I < II = IV < III in M. lishuiensis; I < II ≤ IV < III in M. obesa), males bearing nuptial pads with nuptial spines during breeding season (vs. nuptials absence in adult males of M. acuta), ventral surface with creamy white nebulous patches (vs. absence of such patched in M. brachykolos and M. obesa).

Megophrys nanlingensis sp. nov. differs from the remaining eight members of the Megophrys s.l. allocated to the subgenus Panophrys which share a moderate or small body size, by a combination of following characters: horn-like tubercle small at edge of the upper eyelid (vs. horn-like tubercle indistinct or absent in M. binchuanensis, M. minor, M. wuiliangshanensis and M. wushanensis), absence of vomerine teeth (vs. present in M. daoweimontis, M. fansipanensis and M. rubrimera), tongue not notched posteriorly (vs. tongue notched in M. minor, M. fansipanensis and M. rubrimera), toes without lateral fringes (vs. lateral fringes wide in M. binchuanensis, M. wushanensis (in males); narrow in M. rubrimera), toes with rudimentary webbing (vs. toes without webbing in M. daoweimontis, M. fansipanensis, M. rubrimera and M. wuiliangshanensis), heels not meeting when the flexed hindlimbs are held at right angles to the body axis (vs. heels overlapping in M. minor and M. wuiliangshanensis), heels not meeting when the flexed hindlimbs are held at right angles.
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**Figure 9.** *Megophrys wugongensis* sp. nov. in life: A–C SYS a002625, male holotype D SYS a002610, female paratype E, F SYS a002611, female paratype.

to the body axis (heels meeting in *M. binchuanensis*; heels meeting or overlapping in *M. minor* and *M. wushanensis*; heels overlapping in *M. leishanensis* and *M. wuliangshanensis*).

*Megophrys wugongensis* sp. nov. further differs from *M. feii*, for which molecular data are lacking and cannot be allocated to any subgenus base on morphology only...
(Yang et al. 2018) by the larger body size, SVL 31.0–34.1 mm in males and 38.5–42.8 mm in females (VS. 24.3–25.1 mm in males, 28.2–28.9 mm in females), presence of nuptial pad with nuptial spines in males during breeding season (vs. absent), absence of lateral fringes on toes (vs. moderate or wide).

**Description of holotype.** Adult male. Habitus small, SVL 31.0 mm; head width slightly larger than head length, HDW/HWL 1.03; snout rounded in dorsal view, tip of snout slightly sharpened, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eye large, ED/HDL 0.41; nostril oblique ovoid; pupil vertical; canthus rostralis well developed; loreal region vertical; internasal distance slightly larger than interorbital distance; tympanum distinct, moderate-sized, TD/ED 0.47; large ovoid choanae at the base of the maxilla; weak vomerine ridge present, vomerine teeth absent; margin of tongue not notched posteriorly; internal vocal slits present near the rear of the lower mandible.

RAD/SVL 0.24, HND/SVL 0.22; absence of lateral fringes and webbing on fingers, relative finger lengths II < I = IV < III; tip of finger rounded, slightly swollen; presence of a distinct subarticular tubercle on the base of each finger; outer metacarpal tubercles indistinct, inner metacarpal tubercles distinct and observably enlarged. Hindlimbs short, tibio-tarsal articulation reaching forward the posterior corner of eye when hindlimb is stretched along the side of the body; heels not meeting when the flexed hindlimbs are held at right angles to the body axis; TIB/SVL 0.43 and FTL/SVL 0.61; relative toe lengths I < II < V < III < IV; tips of toes round and slightly dilated; presence of rudimentary webbing on toes but absence of lateral fringes and tarsal folds; presence of a subarticular tubercle only at the bases of each toes; presence of a long ovoid inner metatarsal tubercle and absence of outer metatarsal tubercle.

Dorsal skin texture rough with dense granules, some of which forming an X-shaped skin ridge on center of trunk; surface of flanks with large tubercles; presence of a small horn-like tubercle at the edge of eye lid; distinct supratympanic fold curving posteroventrally from posterior corner of eye to a level above insertion of arm; superior margin of tympanum in connect with supratympanic fold; ventral skin texture smooth with granules on the surface of abdomen; pectoral gland large, closer to axilla; single large femoral gland on rear of thigh.

**Measurements of holotype (in mm).** SVL 30.8, HDL 11.9, HDW 11.7, SNT 3.5, IND 3.0, IOD 2.8, ED 3.5, TD 1.8, TED 1.7, HND 8.5, RAD 7.2, FTL 21.8, TIB 15.1

**Coloration of holotype in life.** (Fig. 9A–C) Dorsal surface reddish brown, with a distinct and dark triangular marking with yellow edges between eyes. Hindlimb with broad black transverse bands. A dark brown vertical band below the eye. Canthus rostralis and supratympanic fold white. Horn-like tubercle at the edge of the upper eyelid yellow. Surface of throat and chest dark brown, with scarlet marbling, posterior region of abdomen white. Ventral surface of limbs brown with white spots and patches. Ventral surface of hand and foot brown, inner and outer metatarsal tubercles and inner metacarpal tubercle pink. Pectoral and femoral glands white. Iris reddish brown.

**Coloration of holotype in preservative.** Dorsum dark brown, markings on dorsal surface became indistinct, transverse bands on limbs became dark grey and became more
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**Table 8.** Measurements (in mm; minimum-maximum, mean ± SD) of the type series of *Megophrys wugongensis* sp. nov.

| Species | Megophrys wugongensis sp. nov. |
|---------|-------------------------------|
|         | Males (n = 4) | Females (n = 9) |
| SVL     | 31.0–34.1 (32.4 ± 1.3) | 38.5–42.8 (40.8 ± 1.3) |
| HDL     | 10.2–11.2 (10.7 ± 0.4)  | 11.8–13.2 (12.6 ± 0.4) |
| HDW     | 10.4–11.9 (11.0 ± 0.6)  | 12.6–13.9 (13.4 ± 0.4) |
| SNT     | 3.4–3.9 (3.8 ± 0.2)     | 4.2–4.8 (4.6 ± 0.2)    |
| IND     | 3.6–3.7 (3.7 ± 0.1)     | 3.6–4.2 (4.0 ± 0.2)    |
| IOD     | 3.1–3.4 (3.2 ± 0.1)     | 3.6–3.8 (3.7 ± 0.1)    |
| ED      | 4.1–4.4 (4.3 ± 0.1)     | 4.1–5.1 (4.4 ± 0.3)    |
| TD      | 2.0–2.2 (2.1 ± 0.1)     | 2.1–2.3 (2.2 ± 0.1)    |
| TED     | 1.7–2.2 (1.9 ± 0.2)     | 2.1–2.6 (2.4 ± 0.2)    |
| HND     | 6.5–7.3 (7.0 ± 0.3)     | 8.2–9.7 (8.7 ± 0.5)    |
| RAD     | 6.7–7.8 (7.4 ± 0.5)     | 8.1–9.8 (8.9 ± 0.6)    |
| FTL     | 17.8–20.9 (19.2 ± 1.3)  | 21.8–25.0 (23.3 ± 1.1) |
| TIB     | 12.4–14.3 (13.3 ± 0.8)  | 15.0–17.9 (16.0 ± 0.9) |
| HDL/SVL | 0.31–0.34 (0.33 ± 0.01) | 0.30–0.33 (0.31 ± 0.01) |
| HDW/SVL | 0.32–0.36 (0.34 ± 0.02) | 0.32–0.35 (0.33 ± 0.01) |
| HDW/HDL | 1.01–1.06 (1.03 ± 0.02) | 1.03–1.08 (1.06 ± 0.02) |
| SNT/HDL | 0.32–0.37 (0.35 ± 0.02) | 0.33–0.40 (0.36 ± 0.02) |
| SNT/SVL | 0.11–0.12 (0.12)        | 0.11–0.12 (0.11 ± 0.01) |
| IND/HDW | 0.31–0.35 (0.33 ± 0.02) | 0.27–0.32 (0.30 ± 0.02) |
| IOD/HDW | 0.27–0.31 (0.29 ± 0.02) | 0.27–0.30 (0.28 ± 0.01) |
| ED/HDL  | 0.37–0.41 (0.40 ± 0.02) | 0.31–0.40 (0.35 ± 0.03) |
| ED/SVL  | 0.13–0.14 (0.13 ± 0.01) | 0.10–0.13 (0.11 ± 0.01) |
| TD/ED   | 0.47–0.52 (0.49 ± 0.02) | 0.45–0.53 (0.51 ± 0.03) |
| TED/TD  | 0.85–1.10 (0.92 ± 0.12) | 0.91–1.14 (1.09 ± 0.07) |
| HND/SVL | 0.20–0.22 (0.21 ± 0.01) | 0.20–0.23 (0.21 ± 0.01) |
| RAD/SVL | 0.21–0.24 (0.23 ± 0.02) | 0.20–0.25 (0.22 ± 0.02) |
| TIB/SVL | 0.39–0.44 (0.41 ± 0.02) | 0.37–0.44 (0.39 ± 0.02) |
| FTL/SVL | 0.56–0.64 (0.59 ± 0.04) | 0.54–0.60 (0.57 ± 0.02) |

distinct. Surface of throat and chest light brown, posterior region of abdomen light yellow, ventral surface of limbs light brown, inner and outer metatarsal tubercles and inner metacarpal tubercle light yellow, all marbling, colored spots and patches absent.

**Variation.** Measurement data of type series are listed in Table 8.

All paratypes are very similar to holotype in morphology and color pattern. However, dorsal surface yellowish brown in female paratypes SYS a004798, 4801, 4804, markings on dorsal skin indistinct in male paratypes SYS a004777/CIB110011 and SYS a004796, and female paratypes SYS a002610 (Fig. 9D), 4797, 4799, presence of a rectangle marking on central back of trunk in the female paratype SYS a002611 (Fig. 9E–F).

**Etymology.** The specific epithet “wugongensis” is in reference to the type locality of the new species in the Wugong Mountains. We propose the common English name “Wugongshan Horned Toad” and Chinese name “Wu Gong Shan Jiao Chan (武功山角蟾)”.

**Distribution and habits.** Currently, *Megophrys wugongensis* sp. nov. is known from the type locality, Yangshimu Scenic Area, Pingxiang City, Jiangxi Province at approximate 550 m a.s.l., Wugongshan Scenic Area, Ji’an City, Jiangxi Province at approximate
1050–1080 m a.s.l., all located in the Luoxiao Mountains in eastern China. All specimens were collected on leaf litter near a stream in the bamboo forest, males were not heard calling. In consideration of the invisible nuptial pad and nuptial spines in all male specimens and the undeveloped fallopian tubes in all female specimens, the breeding season of \textit{M. wugongensis} sp. nov. still remains unknown. Tadpoles were not observed. \textit{Megophrys wugongensis} sp. nov. is sympatric with \textit{M. jinggangensis} in all localities.

\textit{Megophrys (Panophrys) mufumontana} J. Wang, Lyu & Y.Y. Wang, sp. nov.

http://zoobank.org/4FD2EE4D-A6D7-4F72-896C-A3866D74DFB7

Fig. 10, Table 9

\textbf{Holotype.} SYS a006391, adult male, collected by Zhi-Tong Lyu on 3 August 2017 from Mt. Mufu (28°58′18.45″N, 113°48′58.53″E; 1300 m a.s.l.), Pingjiang County, Yueyang City, Hunan Province, China.

\textbf{Paratypes (one male & two females).} Adult females, SYS a006390/CIB110012, SYS a006419, and the other adult male, SYS a006392, all collected by Zhi-Ting Lyu on 3 August 2017 from the same locality as the holotype.

\textbf{Diagnosis.} (1) Body size small, SVL 30.1–30.8 mm in two adult males and SVL 36.3 mm in two adult females; (2) head length slightly larger than head width, HDW/HDL ratio 0.98–0.99; (3) tympanum distinct, moderate-sized, TD/ED ratio 0.51–0.58, upper 1/4 part of the tympanum concealed by supratympanic fold; (4) vomerine teeth absent; (5) margin of tongue not notched posteriorly; (6) heels overlapping, tibia-tarsal articulation reach forward to the tympanum in males and to the eye in females; (7) TIB/SVL ratio 0.47–0.53, FTL/SVL ratio 0.68–0.74; (8) fingers without lateral fringes, presence of a subarticular tubercle at the bases of each finger, relative finger lengths II = IV < I < III; (9) toes with rudimentary webbing at their bases and narrow lateral fringes, subarticular tubercles only present at the base of each toe; (10) numerous granules scattered with tubercles present on dorsal surface of body, limbs and surface of flanks, some of which forming a V-shaped, \_/shaped or X-shaped skin ridge on central back of trunk; (11) presence of a small horn-like tubercle at the edge of the upper eyelid; (12) supratympanic fold distinct; (13) light brown to dark brown dorsally, with a dark triangular marking between eyes; (14) a pair of dark longitudinal and irregular marking with white edges on its upper side on ventrolateral surface of flanks; (15) surface of throat and chest greyish brown with dark brown patches and creamy white spots, surface of abdomen greyish white with creamy white and orange spots; (16) ventral surface of thighs with dense small whitish tubercles.

\textbf{Comparisons.} Comparative data of \textit{Megophrys mufumontana} sp. nov. with \textit{M. dongduanensis} sp. nov., \textit{M. nankunensis} sp. nov., \textit{M. jiulianensis} sp. nov., \textit{Megophrys nanlingensis} sp. nov., \textit{Megophrys wugongensis} sp. nov., \textit{M. feii} and the 33 recognized members of \textit{Megophrys} s.l. allocated to the subgenus \textit{Panophrys} are listed in Table 5.

\textit{Megophrys mufumontana} sp. nov. differs from \textit{M. dongguanensis} sp. nov., \textit{M. nankunensis} sp. nov., \textit{M. jiulianensis} sp. nov. and \textit{M. wugongensis} sp. nov. by upper 1/4 part
of the tympanum concealed by supratympanic fold (vs. tympanum entirely visible), the heels overlapping when hindlimb is stretched along the side of the body (vs. heels not meeting in *M. dongguanensis* sp. nov., *M. nankunensis* sp. nov., *M. jiulianensis* sp. nov. and *M. wugongensis* sp. nov.), presence of narrow lateral fringes on toes (vs. absent in *M. dongguanensis* sp. nov., *M. nankunensis* sp. nov. and *M. jiulianensis* sp. nov.), absence of vomerine teeth (vs. present in *M. dongguanensis* sp. nov., *M. nankunensis* sp. nov., *M. jiulianensis* sp. nov. and *M. nanlingensis* sp. nov.), tongue not notched posteriorly (vs. tongue notched in *M. jiulianensis* sp. nov. and *M. nanlingensis* sp. nov.), skin relatively smooth and lacking black horny spines (vs. skin rough with black horny spines in *M. jiulianensis* sp. nov.).

With the smaller body size, SVL 30.1–30.8 mm in males and 36.3 mm in females, *Megophrys mufumontana* sp. nov. differs from the 19 members with larger SVL values: *M. baolongensis* (42.0–45.0 mm in males), *M. binchuanensis* (32.0–36.0 mm in males, 40.2–42.5 mm in females), *M. binlingensis* (45.1–51.0 mm in males), *M. caudoprocta* (81.3 mm in single male), *M. daveimontis* (34.0–37.0 mm in males, 40.0–46.0 mm in females), *M. fansipanensis* (41.7–42.5 mm in females), *M. hoanglienensis* (37.4–47.6 mm in males, 59.6 mm in single female), *M. jingdongensis* (53.0–56.5 mm in males 63.5 in single female), *M. latidactyla* (38.9 mm in single male), *M. liboensis* (34.7–67.7 mm in males, 60.8–70.6 mm in females), *M. minor* (34.5–41.2 mm in males), *M. omeimontis* (56.0–59.5 mm in males, 68.0–72.5 mm in females), *M. palpebralespinosa* (36.2–38.0 mm in males), *M. sangzhiensis* (54.7 mm in single male), *M. shuichengensis* (102.0–118.3 mm in males, 99.8–115.6 mm in females), *M. tuberogranulatus* (33.2–39.6 mm in males, 50.5 mm in single female), *M. wushanensis* (38.4 mm in single female) and *M. wuliangshanensis* (41.3 mm in single female).

*Megophrys mufumontana* sp. nov. differs from 12 species occurring in eastern and southern China (*M. acuta*, *M. brachykolos*, *M. boettgeri*, *M. cheni*, *M. huangshanensis*, *M. insularis*, *M. jinggangensis*, *M. kuatunensis*, *M. lini*, *M. lishuiensis*, *M. ombrophila* and *M. ombrophila*; wide in *M. boettgeri* and *M. cheni*), toes with rudimentary webbing (vs. toes without webbing in *M. huangshanensis*, *M. kuatunensis*, *M. lishuiensis* and *M. ombrophila*), the heels overlapping when hindlimb is stretched along the side of the body (vs. heels not meeting in *M. acuta*, *M. brachykolos*, *M. insularis*, *M. ombrophila* and *M. ombrophila*).

*Megophrys mufumontana* sp. nov. differs from the remaining *M. leishanensis* and *M. rubrimera* allocated to the subgenus *Panophrys* by the absence of vomerine teeth (vs. present in *M. rubrimera*), tongue not notched posteriorly (vs. tongue notched in *M. rubrimera*), upper 1/4 part of the tympanum concealed by supratympanic fold (vs.}
Figure 10. *Megophrys mufumontana* sp. nov. in life: A–D SYS a006391, male paratype E–F SYS a006392, female paratype.

tympanum entirely visible in *M. leishanensis* and *M. rubrimera*), toes with narrow lateral fringes (vs. absent in *M. leishanensis*; indistinct or absent in *M. rubrimera*).

*Megophrys mufumontana* sp. nov. further differs from *M. feii*, for which molecular data are lacking and cannot be allocated to any subgenus base on morphology only (Yang et al. 2018) by the larger body size, SVL 30.1–30.8 mm in males and 36.3 mm in females (VS. 24.3–25.1 mm in males, 28.2–28.9 mm in females), tongue not notched posteriorly (vs. tongue notched), toes with narrow lateral fringes (vs. moderate or wide).

**Description of holotype.** Adult male. Habitus small, SVL 30.8 mm; head length slightly larger than head width, HDW/HWL 0.98; snout rounded in dorsal view, sloping backward to mouth in profile, protruding well beyond margin of lower jaw; top of head flat; eye large, ED/HDL 0.30; nostril oblique ovoid; pupil vertical; canthus
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Table 9. Measurements (in mm; minimum-maximum, mean ± SD) of the type series of Megophrys mufumontana sp. nov.

| Species         | Megophrys mufumontana sp. nov. |
|-----------------|---------------------------------|
|                 | Males (n = 2)                   | Females (n = 2)                      |
| SVL             | 30.1–30.8                       | 36.3                                 |
| HDL             | 11.6–11.9                       | 11.8–12.4                            |
| HDW             | 11.4–11.7                       | 11.7–12.3                            |
| SNT             | 3.5–3.7                         | 3.7–4.2                              |
| IND             | 3.0–3.1                         | 3.5–3.6                              |
| IOD             | 2.8–2.9                         | 3.2–3.3                              |
| ED              | 3.5–3.6                         | 3.7–3.8                              |
| TD              | 1.7–1.8                         | 2.1–2.2                              |
| TED             | 1.7–1.8                         | 1.8–1.9                              |
| HND             | 8.5–9.2                         | 9.4–9.9                              |
| RAD             | 7.2–7.7                         | 8.0–8.2                              |
| FTL             | 21.8–22.9                       | 24.8–25.1                            |
| TIB             | 15.1–16.3                       | 16.9–17.5                            |
| HDL/SVL         | 0.39                             | 0.33–0.34                            |
| HDW/SVL         | 0.38                             | 0.32–0.34                            |
| HDW/HDL         | 0.98                             | 0.99                                 |
| SNT/HDL         | 0.30–0.31                       | 0.31–0.34                            |
| SNT/SVL         | 0.12                             | 0.10–0.12                            |
| IND/HDW         | 0.26                             | 0.29–0.30                            |
| IOD/HDW         | 0.25                             | 0.27                                 |
| ED/HDL          | 0.30                             | 0.31                                 |
| ED/SVL          | 0.12                             | 0.10                                 |
| TD/ED           | 0.51–0.56                       | 0.57–0.58                            |
| TED/TD          | 0.90–0.94                       | 0.86                                 |
| HND/SVL         | 0.28–0.30                       | 0.26–0.27                            |
| RAD/SVL         | 0.24–0.25                       | 0.22–0.23                            |
| TIB/SVL         | 0.50–0.53                       | 0.47–0.48                            |
| FTL/SVL         | 0.72–0.74                       | 0.68–0.69                            |

rostralis well developed; loreal region vertical; internasal distance slightly larger than interorbital distance; tympanum distinct, moderate-sized, TD/ED 0.56; large ovoid choanae at the base of the maxilla; weak vomerine ridge present, vomerine teeth absent; margin of tongue not notched posteriorly.

RAD/SVL 0.25, HND/SVL 0.30; absence of lateral fringes and webbing on fingers, relative finger lengths II = IV < I < III; tip of finger rounded, slightly swollen; presence of a distinct subarticular tubercle on the base of each finger; outer metacarpal tubercles indistinct, inner metacarpal tubercles distinct and observably enlarged. Hindlimbs long, tibio-tarsal articulation reaching forward to the tympanum when hindlimb is stretched along the side of the body; heels overlapping when the flexed hindlimbs are held at right angles to the body axis; TIB/SVL 0.53 and FTL/SVL 0.74; relative toe lengths I < II < V < III < IV; tips of toes round and slightly dilated; presence of rudimentary webbing and narrow lateral fringes on toes but absence of tarsal folds; presence of a subarticular tubercle only at the bases of each toes; presence of a long ovoid inner metatarsal tubercle and absence of outer metatarsal tubercle.
Dorsal skin texture rough with dense granules and scattered with small tubercles, some of which forming a \_/ -shaped skin ridge on central back of trunk; presence of a small horn-like tubercle at the edge of upper eye lid; distinct supratympanic fold curving posteroventrally from posterior corner of eye to a level above insertion of arm; upper 1/4 part of the tympanum covered by supratympanic fold; ventral skin texture smooth with granules; pectoral gland large, closer to axilla; single large femoral gland on rear of thigh.

**Measurements of holotype (in mm).** SVL 30.1, HDL 11.6, HDW 11.4, SNT 3.5, IND 3.0, IOD 2.8, ED 3.5, TD 18, TED 1.7, HND 8.5, RAD 7.2, FTL 21.8, TIB 15.1.

**Coloration of holotype in life.** (Fig. 10A–D) Dorsal surface brown, with a distinct and incomplete dark triangular marking between eyes. Hindlimb with black transverse bands. A dark brown vertical band below the eye. Horn-like tubercle at the edge of the upper eyelid red. Surface of throat and chest greyish brown with brown patches. Surface of abdomen greyish white with creamy white and orange spots. Ventral surface of limbs pink with white spots and light-yellow patches. Ventral surface of hand and foot brown, inner and outer metatarsal tubercles and inner metacarpal tubercle pink. Pectoral and femoral glands white. Iris white.

**Coloration of holotype in preservative.** Coloration of dorsum dark brown, markings on dorsal surface and transverse bands on limbs became indistinct. Ventral surface of throat, chest and abdomen dark grey. All patches on ventral surface indistinct, all colored spots absent. Ventral surface of limbs light yellow.

**Variation.** Measurement data of type series are listed in Table 9. All paratypes are very similar to holotype SYS a006391 in morphology and color pattern. However, tibia-tarsal articulation reaching forward to the eye when hindlimb is stretched along the side of the body in all females, and granules and tubercles forming a \_/ -shaped skin ridge on central back of trunk in the holotype (vs. X-shaped in SYS a006390, 6419; V-shaped in SYS a006392 (Fig. 10E–F)).

**Etymology.** The specific epithet “mufumontana” is in reference to the type locality of the new species, Mt. Mufu. We propose the common English name “Mufushan Horned Toad” and Chinese name “Mu Fu Shan Jiao Chan (幕阜山角蟾)”.

**Distribution and habits.** Currently, *Megophrys mufumontana* sp. nov. is known only from Mt. Mufu, Pingjiang County, Yueyang City, Hunan Province, China at approximate 1300 m a.s.l. All specimens were collected on leaf litter near a stream (about 5 m wide) surrounded by moist subtropical evergreen broadleaved forests, males were not heard calling. Tadpoles were not observed. Because none of the males have nuptial pads developed and none of the females have fallopian tubes and eggs developed, the breeding season of *M. mufumontana* sp. nov. remains unknown.

**Discussion**

*Megophrys dongguanensis* sp. nov. is easily confused with *M. brachykolos* because of the relatively short shanks. In addition, the type locality of the new species is at a straight-line distance of approximately 72 km from the type locality (Hongkong Island), and at
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a straight-line distance of approximately 32 km from the closest locality (Sanzhoutian of Shenzhen City) of M. brachykolos. Currently, eight Megophrys species in the subgenus Panophrys were found to have comparatively short shanks with heels not meeting when thighs are adducted at right angles with respect to the body axis: M. dongguanensis sp. nov., M. nankunensis sp. nov., M. wugongensis sp. nov., M. acuta, M. brachykolos, M. insularis, M. megacephala and M. obesa.

In our previous study (Liu et al. 2018), 41 cryptic species within the subgenus Panophrys were revealed, and one of them was recently described as Megophrys leishanensis by Li et al. (2018). Moreover, except for M. mufumontana sp. nov. (not mentioned in Liu et al. (2018)), five of them are described in this study. Currently, the total number of recognized species of the subgenus Panophrys rises to 39, which makes it the most species-rich subgenus of Megophrys (≈46.4%). It’s worth noting that there remain still 33 undescribed species according to Liu et al. (2018), and 27 of them are found in southeastern China, which further reveals the unusually high level of species diversity in this region.

As the diversity of the subgenus Panophrys was confirmed to be extremely underestimated (Chen et al. 2017; Mahony et al. 2017; Liu et al. 2018), a number of new Panophrys species have been described since 2017 (i.e. Megophrys lishuiensis, M. insularis, M. rubrimerata, M. liboensis, and six new species in this study). However, all of these species have narrow distributions. For example, M. insularis is currently known only from an offshore island in Guangdong (Wang et al. 2017b), and M. liboensis is currently known only from a cave in Libo, Guizhou (Zhang et al. 2017). For the six new species in this study, M. dongguanensis sp. nov., M. nankunensis sp. nov., M. wugongensis sp. nov. and M. mufumontana sp. nov. are currently only found in their type localities. This situation of “micro-endemism” (Liu et al. 2018) has brought great challenges for the protection of these unique toads.

Among the six new species described in this paper, M. jiulianensis sp. nov. is sympatric with M. nankunensis sp. nov. in Mt. Nankun while also being sympatric with M. hongshanensis sp. nov. in Mt. Jiulian. Further, M. mufumontana sp. nov. is sympatric with a known congener M. jinggangensis in Mt. Mufu and M. wugongensis sp. nov. is sympatric with M. jinggangensis in Mt. Wugong. By combining the localities of these species in our phylogenetic trees (Fig. 2), our results also support the conclusion of “sympatric but distant phylogenetically” (Liu et al. 2018), that is, sympatric distribution is very common in horned toads within the subgenus Panophrys while they are distantly related in the phylogeny (Fei et al. 2012; Li et al. 2014; Wang et al. 2014; Liu et al. 2018). These geographical patterns of “sympatric but distant phylogenetically” and “micro-endemism” indicate that the Asian horned toads would be good candidates for studies on speciation and biogeography.

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**Appendix 1**

**Specimens of comparative species examined**

*Megophrys boettgeri* (n = 13): China: Jiangxi Province: Guixi City: Yangjifeng Nature Reserve (the middle area of Wuyi Mountains, 600–883 m a.s.l.): SYS a000312, 000315, 000328–000330, 000376, 000378; Guangfeng County: Tongboshan Nature Reserve (the eastern area of Wuyi Mountains, 450–821 m a.s.l.): SYS a001671–001673, 001683, 001700.

*Megophrys brachykolos* (n = 21): China: Hong Kong: SYS a001502–001503; Guangdong Province: Shenzhen City: Yangtaishan Forest Park (60–150 m a.s.l.): SYS a2051–002056, 002069–002074, 002413; Qiniangshan Geological Park (30–50 m a.s.l.): SYS a002405–002410.

*Megophrys caudoprocta* (n = 3): China: Hunan Province: Zhangjiajie City: Sangzhi County: Mt. Badagong (1100–1200 m a.s.l.): SYS a004281, 004308–4309.

*Megophrys cheni* (n = 19): China: Jiangxi Province: Jinggangshan City: Mt. Jinggang (1200–1260 m a.s.l.): SYS a001427–001429, SYS a001871–001873; Hunan Province: Yanling County: Taoyuandong Nature Reserve: Lishuzhou Village (1480–1530 m a.s.l.): SYS a002123–002127, Dayuan Farm (1480 m a.s.l.): SYS a002140–002145.

*Megophrys huangshanensis* (n = 10): China: Jiangxi Province: Wuyuan County: Mount Dazhang (600–900 m a.s.l.): SYS a001314–001323.

*Megophrys insularis* (n = 6): China: Guangdong Province: Shantou City: Nan’ao Island (50–500 m a.s.l.): SYS a002167–002171, SYS a003666/CIB 106881.

*Megophrys jingdongensis* (n = 2): Yunnan Province: Jingdong County: Mt. Wuliang (1800 m a.s.l.): SYS a003928–3929.
Megophrys jinggangensis (n = 10): China: Jiangxi Province: Jinggangshan City: Mt. Jinggang (700–900 m a.s.l.): SYS a001413–001416, 001430; Hunan Province: Yanling County: Taoyuandong Nature Reserve (800–1000 m a.s.l.): SYS a001859–001863.

Megophrys kuatunensis (n = 3): China: Fujian Province: Wuyishan City (=Ch’ungan Hsien): Guadun Village (= Kuatun Village, 1060–1220 m a.s.l.): SYS a001579 and 001590; Jiangxi Province: Guixi City: Yangjifeng Nature Reserve (the middle area of Wuyi Mountains, 950 m a.s.l.): SYS a000241.

Megophrys lini (n = 27): China: Jiangxi Province: Jinggangshan City: Mt. Jinggang (1100–1610 m a.s.l.): SYS a001417–001424, SYS a002375–002386; Suichuan County: Nanfengmian Nature Reserve (1150–1250 m a.s.l.): SYS a002369–002374; Hunan Province: Yanling County: Taoyuandong Nature Reserve: Niushiping Village (1360 m a.s.l.): SYS a002128.

Megophrys minor (n = 4): China: Sichuan Province: Dujiangyan City: Mt. Qingcheng: SYS a003209, 003211–3213.

Megophrys omeimontis (n = 6): China: Sichuan Province: Mt. Emei: SYS a001798–001801, 001940–001941.

Megophrys sangzhiensis (n = 6): China: Hunan Province: Zhangjiajie City: Sangzhi County: Mt. Badagong (1100–1200 m a.s.l.): SYS a004306–004307, 004313–004316.

Megophrys spinata (n = 2): China: Guizhou Province: Leishan County: Mt. Leigong: SYS a002226–002227.

Megophrys tuberogranulatus (n = 1): China: Hunan Province: Zhangjiajie City: Sangzhi County: Mt. Badagong (1100–1200 m a.s.l.): SYS a004310. Megophrys wuliangshanensis (n = 2): Yunnan Province: Jingdong County: Mt. Wuliang (1800 m a.s.l.): SYS a003924–3925.