



A new species of fossil *Calosoma* (Coleoptera: Carabidae) from the Geumgwangdong Formation (Early Miocene), South Korea

SOO BIN LEE^{1,2} & GI-SOO NAM^{1*}¹Department of Science Education, Gongju National University of Education 27 Ungjinro, Gongjusi, Chungcheongnamdo, South Korea.²[✉dinos20000@naver.com](mailto:dinos20000@naver.com); <https://orcid.org/0000-0003-2112-3897>*Corresponding author. [✉fossil@gjue.ac.kr](mailto:fossil@gjue.ac.kr); <https://orcid.org/0000-0003-0570-8270>

Abstract

In this paper, a new fossil species of *Calosoma* (Coleoptera: Carabidae) from the lower Miocene Geumgwangdong Formation, Pohang City, South Korea, is described. Compared with other Miocene *Calosoma* fossils, *Calosoma kimi* **sp. nov.** exhibits different characteristics in particular interval connection and scale patterns on the elytra. It is the first fossil *Calosoma* recorded from the Korean Peninsula. However, the taxonomic position of *C. kimi* **sp. nov.** within *Calosoma* is not clear at present though it is probably related to the complex of the subgenera *Australodrepa*, *Calodrepa*, and *Calosoma*.

Key words: early Miocene, Geumgwangdong Formation, ground beetle

Introduction

Species of the genus *Calosoma* Weber, 1801, which is also called “caterpillar hunter” (Gidaspow 1959), belongs to the family Carabidae Latreille 1802. Until now, 19 subgenera and 128 species of *Calosoma* have been reported (Bruschi 2013). According to Toussaint and Gillett (2018), the origin of *Calosoma* is estimated at 49.3–92.7 Ma. However, McKenna *et al.* (2019) revealed that the origin of the *Calosoma* is estimated at the Late Paleocene. Until now, fossil representatives of *Calosoma* have been reported in Europe, North America, and Asia (Table 1).

TABLE 1. List of fossil species of *Calosoma*

Species	Elytra length (mm)	Age	Locality	References
<i>C. kimi</i> sp. nov.	20.5	Miocene	Geumgwangdong (South Korea)	This study
<i>C. agassizi</i>	19~22.3	Oligocene	Aix-en-Provence (France)	Nel (1988)
<i>C. brunneum</i>	-	Miocene	Shanwang (China)	Zhang (1989)
<i>C. calvini</i>	14	Eocene	Florissant (USA)	Wickham (1909)
<i>C. caraboides</i>	-	Miocene	Locle (Switzerland)	Heer (1860)
<i>C. catenulatum</i>	-	Miocene	Oeningen (Germany)	Heer (1860)
<i>C. ceresti</i>	15~15.2	Oligocene	Aix-en-Provence (France)	Nel (1988)
<i>C. cockerelli</i>	9.3	Eocene	Florissant (USA)	Wickham (1910)
<i>C. aff. calidum</i>	12.4	Pliocene	Kobiwako Group (Japan)	Yahiro <i>et al.</i> (2018)
<i>C. deplanatum</i>	-	Miocene	Oeningen (Germany)	Heer (1860)
<i>C. emmonsii</i>	13	Eocene	Florissant (USA)	Scudder (1900)
<i>C. escheri</i>	-	Miocene	Oeningen (Germany)	Heer (1860)
<i>C. escrobiculatum</i>	-	Miocene	Oeningen (Germany)	Heer (1860)

.....continued on the next page

TABLE 1. (Continued)

Species	Elytra length (mm)	Age	Locality	References
<i>C. fernquisti</i>	20.5	Miocene	Deep Creep Canyon (USA)	Cockerell (1924)
<i>C. grasui</i>	-	Oligocene	Cozla (Romania)	Pauca & Ciobanu (1978)
<i>C. heeri</i>	-	Miocene	Oeningen (Germany)	Scudder (1895)
<i>C. inquisitor?</i>	-	Pliocene	Bushi Formation (Japan)	Hayashi (1996)
<i>C. inquisitor?</i>	-	Pliocene	Willershausen clay pit (Germany)	Gersdorf (1969)
<i>C. sycophanta</i>	-	Pliocene	Willershausen clay pit (Germany)	Gersdorf (1969)
<i>C. inquisitor</i>	-	Pleistocene	(Japan)	Fossil Insect Research Group for Nojiri-ko Excavation (1984)
<i>C. jaccardi</i>	-	Miocene	Locle (Switzerland)	Heer (1860)
<i>C. maximowiczi</i>	-	Pleistocene	(Japan)	Aiba (2015)
<i>C. cf. maderae</i>	-	Miocene	Shanwang (China)	Zhang (1989)
<i>C. maderae</i>	-	Pliocene	Willershausen clay pit (Germany)	Gersdorf (1976)
<i>C. nauckianum</i>	-	Miocene	Oeningen (Germany)	Heer (1860)
<i>C. semilaeve</i>	-	Pliocene	La Brea tar pit (USA)	

Numerous Miocene insect fossils were discovered from the Geumgwangdong Formation in the Korean Peninsula. However, only a few of them were studied, including Buprestidae (Kim 1976), Tettigoniidae (Kim & Lee 1975), Nepticulidae (Sohn *et al.* 2019), and the trace of insect damage on leaves (Paik *et al.* 2012). In this study, we report the first fossil *Calosoma* discovered from the Geumgwangdong Formation. It contains new characteristics such as new types of interval connections and two types of scale patterns on the elytra.

Material and methods

Two specimens of *Calosoma kimi* **sp. nov.** were used in this study. The specimens were excavated from the Geumgwangdong Formation, which is distributed across the Geumgwangdong area, Pohang City, Gyeongsangbukdo, South Korea (GPS: N35°57'30.5, E129°26'57.3).

We took photographs of specimens using a Digital Single Lens Reflex Canon EOS 700D equipped with a Canon EF 100 mm F2.8L Macro IS USM and a Canon EF MP-E 65 mm F2.8 1–5X Macro lens with Kenko extension tube. Sketches of fossils were drawn using Sai Tool (<https://www.systemax.jp/en/sai/>). Specimens are now deposited in the collection of the Gongju National University of Education, Gongju, South Korea (GNUE). The designated numbers are GNUE-311001 for the holotype and GNUE-311002 for the paratype.

Geological setting

In the Pohang Basin, which is one of the Neogene sedimental basins in South Korea, there are two Miocene sedimental groups: the Janggi Group and the Yeonil Group (Tateiwa 1924; Kim 1975; Yoon 1988; Paik *et al.* 2010). Specimens from this research were collected from the Geumgwangdong Formation, Janggi Group (Fig. 1) which is estimated as the Early Miocene (Paik *et al.* 2010). By utilizing the Ar–Ar dating, the Janggi Group is estimated to be 16.8 ± 2.2 Ma through extrusive basaltic rocks and 19.4 ± 2.1 Ma through lava flow from basaltic andesite (Paik *et al.* 2010). According to Paik *et al.* (2010), the lithology of the Geumgwangdong Formation is divided into five types on the basis of fissility and texture: paper shale, shale, shaly mudstone, laminated silty mudstone, and tuffaceous mudstone. Also, tuffaceous conglomerate, tuffaceous pebbly sandstone, and tuffaceous sandstone are subordinated, and therefore, Paik *et al.* (2010) suggested that the lithology of the Geumgwangdong Formation shows that it was deposited during a quiescent phase of volcanic activity.

On the basis of palynological evidence, Bong (1985) described that the flora of the Geumgwangdong Formation shows a modified type of the typical Aniai type, which is a flora of low-temperature climate conditions (Tanai 1961). Based on the study of sedimentary structure, the paleoenvironment of the Geumgwangdong Formation is considered to be a lake, and vertical aggradation of fine-grained sediments caused by the suspension of sedimentation was dominant (Paik *et al.* 2010).

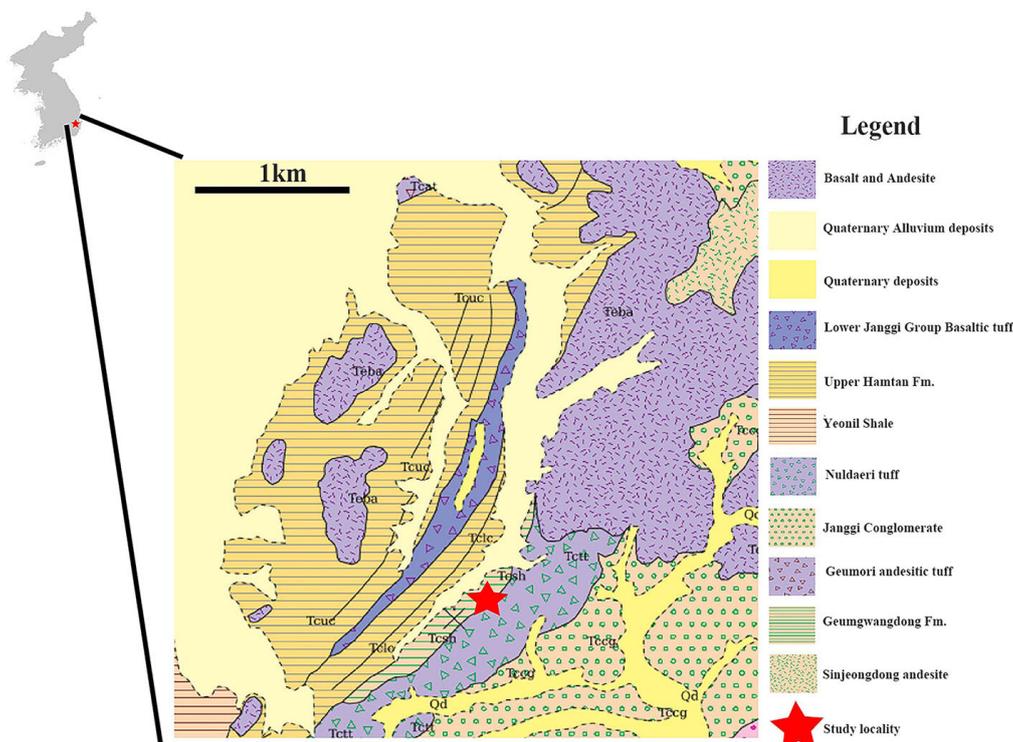


FIGURE 1. Map of the study area. (Map resource: https://data.kigam.re.kr/mgeo/map/main.do?process=geology_tree. Login is required.).

Systematic paleontology

Order Coleoptera Linnaeus, 1758

Family Carabidae Latreille, 1802

Genus *Calosoma* Weber, 1801

Species *Calosoma kimi* Lee & Nam, 2021 sp. nov.

Material. Holotype GNUE-311001, Paratype GNUE-311002.

Locality. Geumgwangri, Donghaemyeon, Namgu, Pohangsi, Gyeongsangbukdo, South Korea.

Geological Age. Early Miocene

Etymology. Honoring Professor Jong Heon Kim for his important work on fossils from Pohang, South Korea.

Diagnosis. The 5th interval connected to the 7th interval and the 6th interval surrounded at the apex of elytron; the 11th and 13th intervals connected and surround the 12th interval; the 10th and 14th intervals connected and surrounded the 11th and 13th; the 16th to 18th intervals smaller. Scales on the 13th to 16th interval small and deeply grooved, forming checkered patterns from the base to the middle part of the elytron and forming overlapping patterns from the middle part to the apex of the elytron.

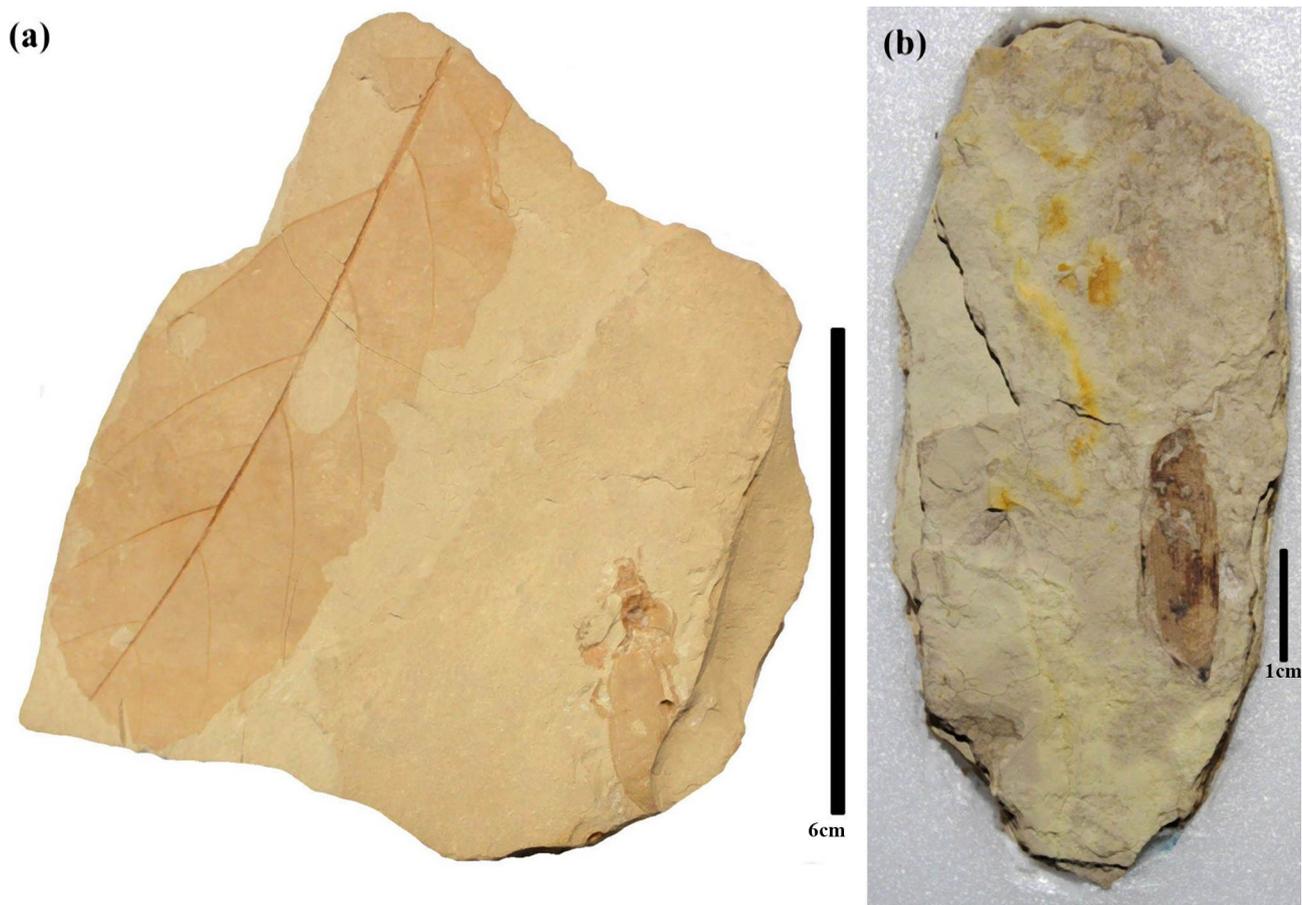


FIGURE 2. Photograph of specimens. **(a).** GNUE-311001. **(b).** GNUE-311002.

Description. GNUE-311001 is sedimented in shaly mudstone with a damaged leaf (*Fagus?*) (Fig. 2). The head, half of the thorax, both damaged elytra, and parts of profemur and protibia and right mesotarsus are preserved. The total length of the specimen from the tip of the head to the apex of the elytra is 30.7 mm, and the width from the margin of the elytron to the outer margin of the pronotum is 12.4 mm (Fig. 3a and b). The shape of the fossil is flat, probably because of sedimentation. GNUE-311002 is in mold form. It was sedimented in the shale, only preserved with the right elytron (Fig. 4a and b). The length of the GNUE-311002 is 23 mm, and the width is 6 mm.

Head: Head is well preserved with loss of left maxillary palp and several antennae segments on the GNUE-311001. The left 1st and 3rd antennomeres and the right 2nd and 3rd antennomeres are preserved. The right maxillary palp is well preserved. The length of the last and 2nd maxillary palpomeres is approximately 1 mm. Both dentaries are poorly preserved, but it seems that the dentaries are protruded. The right 1st and 2nd labial palpomeres are preserved. Compound eyes are not preserved, but a trace of the compound eyes is poorly preserved on the middle part of the head. The shape of the head is triangular. The length of the head is 3 mm, and the width is 4.7 mm.

Thorax: On the GNUE-311001, only a part of the right pronotum is preserved. The side of the pronotum is rounded and bordered in shape, which is a diagnostic feature of *Calosoma* (Hashmi *et al.* 2005). The shape of the pronotum is rounded but slightly angled at the middle part of the lateral margin. The length of the pronotum is 5 mm. The width of the right pronotum is 4 mm. Although the pronotum is not completely preserved, on the basis of the width of the right pronotum, we assume the full width of the pronotum is 8 mm.

Elytron: On the GNUE-311001, both elytra are partly preserved. One big hole is grooved on the left elytron and from the middle to the apex of the medial part of the left elytron, and the outline of the left elytron is also partly not preserved. On the right elytron, only a part of the wing base is preserved. GNUE-311002 consists of partly preserved elytron (Fig. 4). The shape of the elytron is quadrangle-like. The medial outlet line is thin. The total countable striae are 19 and intervals are 18. The 1st interval is small. The 4th to 8th intervals are large and become smaller from the 9th interval. The 16th to 18th intervals are smallest and fainter than other intervals. Transversal lines are clearly showing from the 5th to 16th intervals. Grooved dimples are shown on the 4th, 8th, and 12th intervals, creating a triploid pattern

(Jeannel 1940). The 5th and 7th intervals are connected at the apex of the elytron and surrounded by the 6th interval. The 11th and 13th intervals are connected at the near margin of the elytron and surround the 12th interval. The 10th and 14th intervals meet and surround the 11th to 13th intervals at the apex of the elytron. These interval connection patterns are clearly visible on GNUE-311002 (Fig. 5).

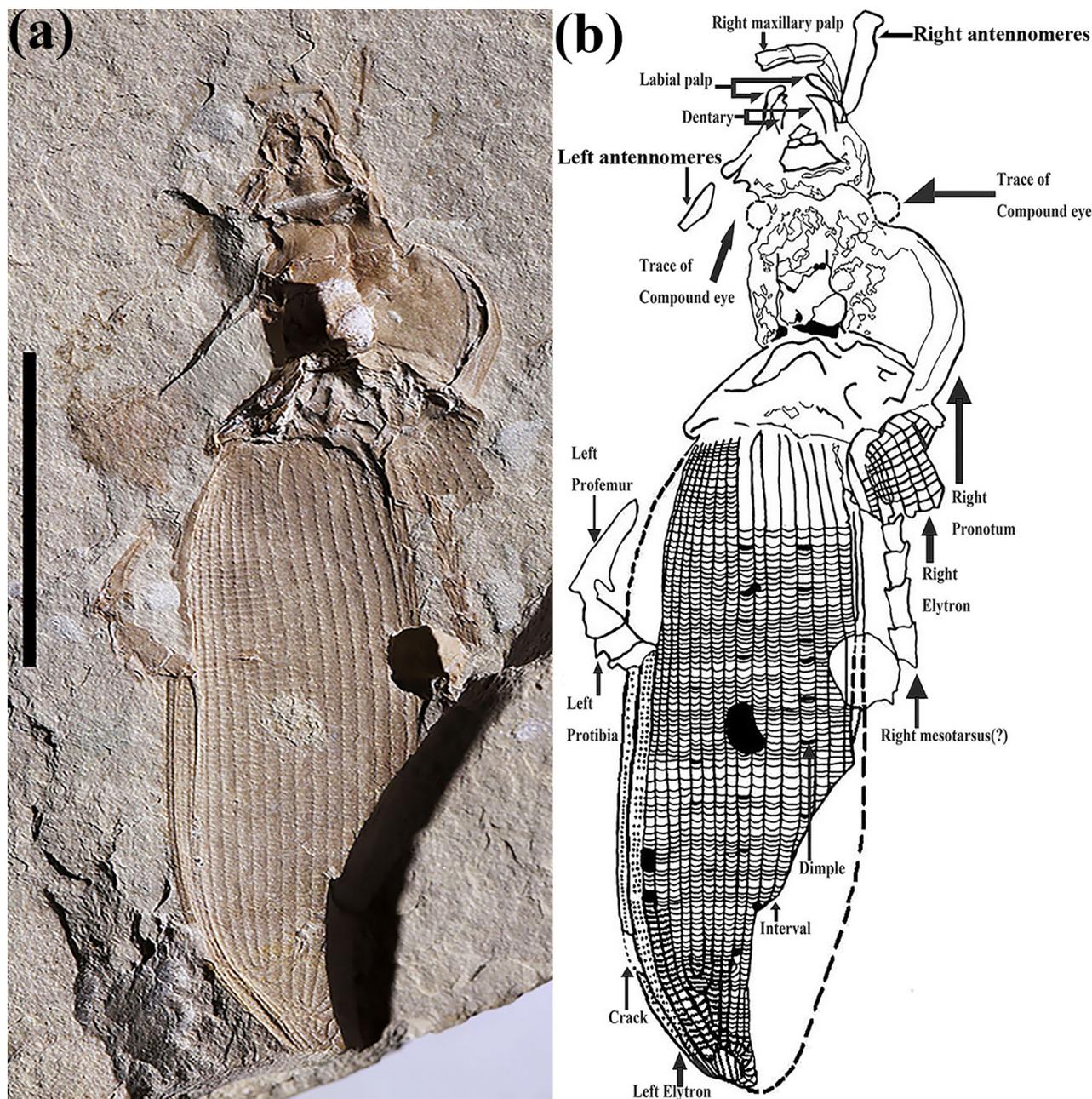


FIGURE 3. *Calosoma kimi* sp. nov. holotype (GNUE-311001). (a). Photograph of the specimen. (b). Sketch of the specimen.

The scales are deeply grooved from the 9th to 15th interval. The scales on the 17th and 18th intervals are extremely small. From the wing base to the middle of the elytron, the scales are arranged in a check pattern. However, from the middle to the margin of the elytron, the scales are arranged in an overlapping pattern (Fig. 6).

Leg: On GNUE-311001, part of the left profemur and protibia segments and the right leg tarsus (assumed mesotarsus) are preserved. The tarsus on the right leg is forward to the upside. We assume that it is broken and folded upward.

Discussions

GNUE-311001 is inferred to be a male since it contains a dilated triangular shape of protibia segments which is one of the characteristics of male *Calosoma* (Bruschi 2013). The diagnostic feature of *C. kimi* **sp. nov.** is its connection patterns of the intervals and the two types of scale patterns on the elytron.

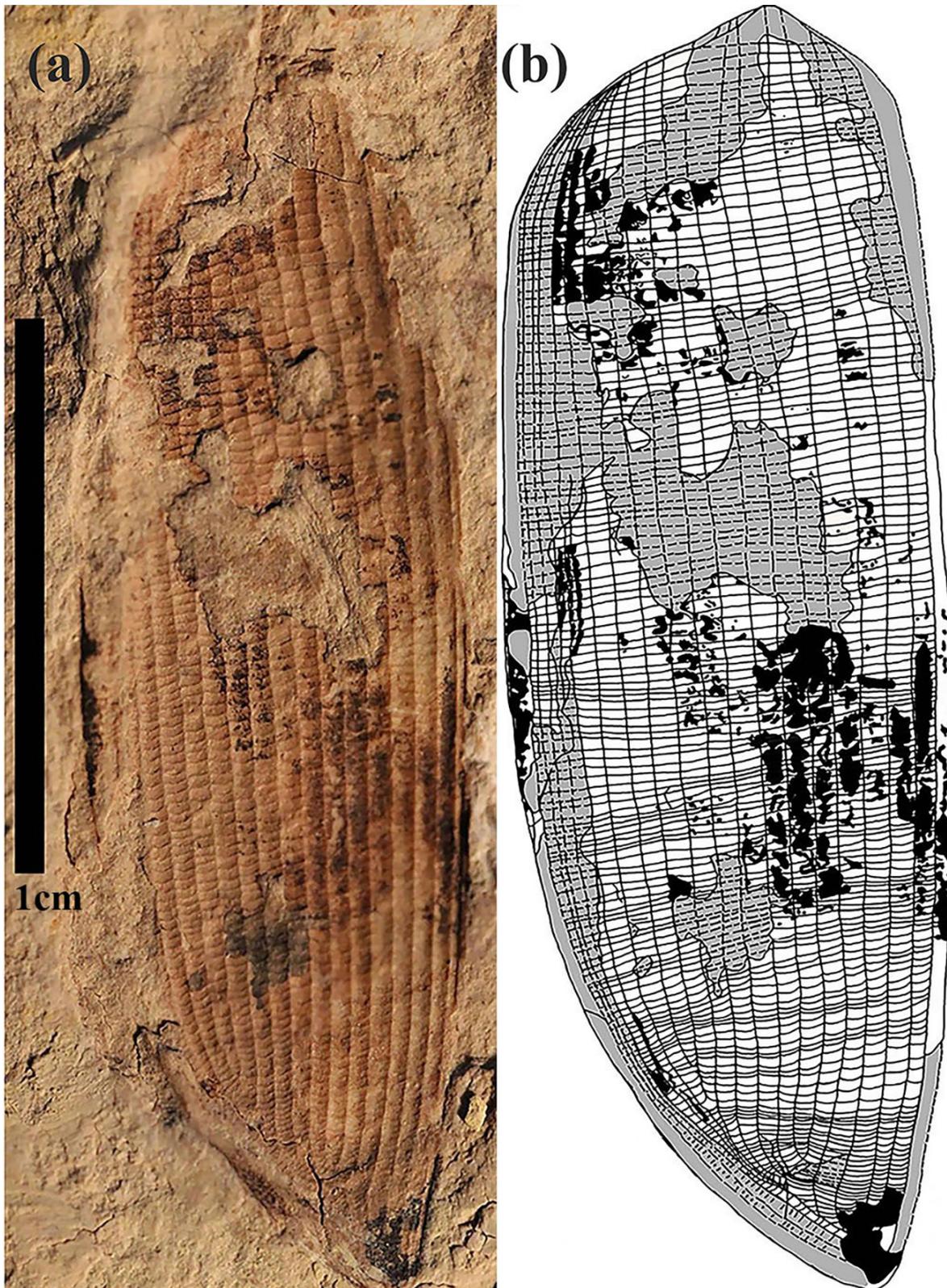


FIGURE 4. *Calosoma kimi* **sp. nov.** paratype (GNUE-311002). (a). Photograph of the specimen. (b). Sketch of the specimen.

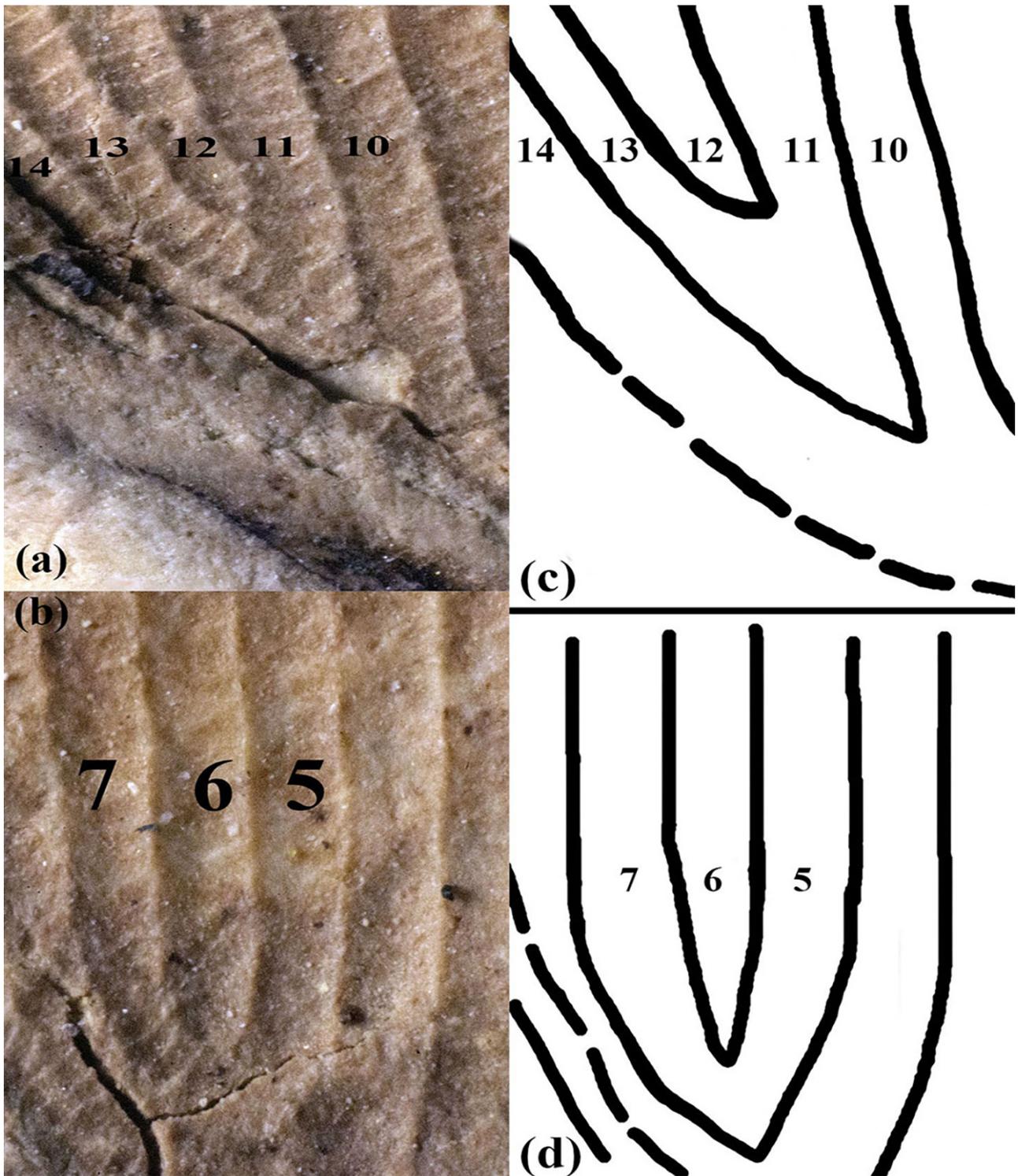


FIGURE 5. The apex of the wing of *C.kimi* sp. nov. paratype (GNUE-311002). (a). Photograph of the 10th to 14th interval connection patterns. (b). Sketch of the 10th to 14th interval connection patterns. (c). Photograph of the 5th to 7th interval connection patterns. (d). Sketch of the 5th to 7th interval connection patterns.

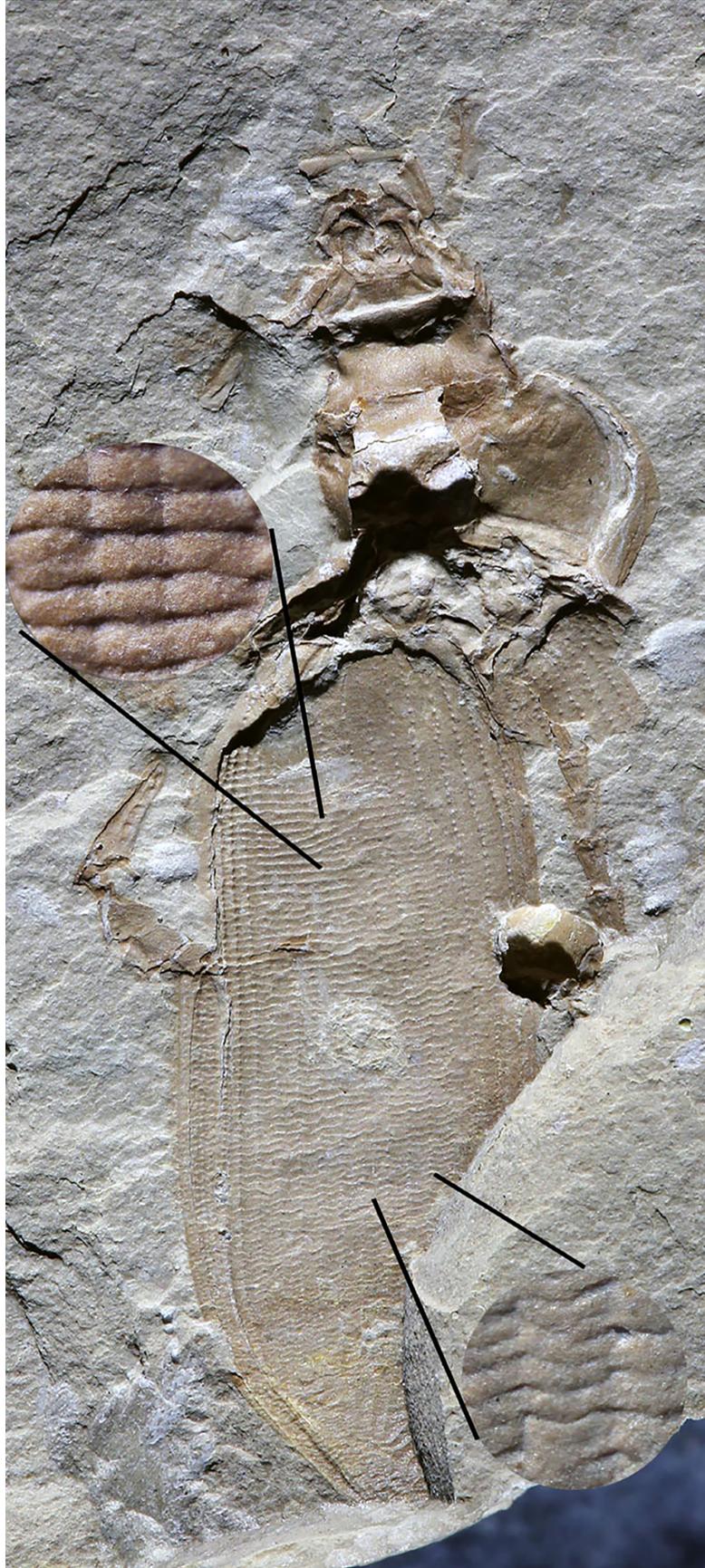


FIGURE 6. Scales on elytron of *C. kimi* **sp. nov.** Scales on the above represents a checkered patterns. Scales on the bottom represents an overlapping patterns.

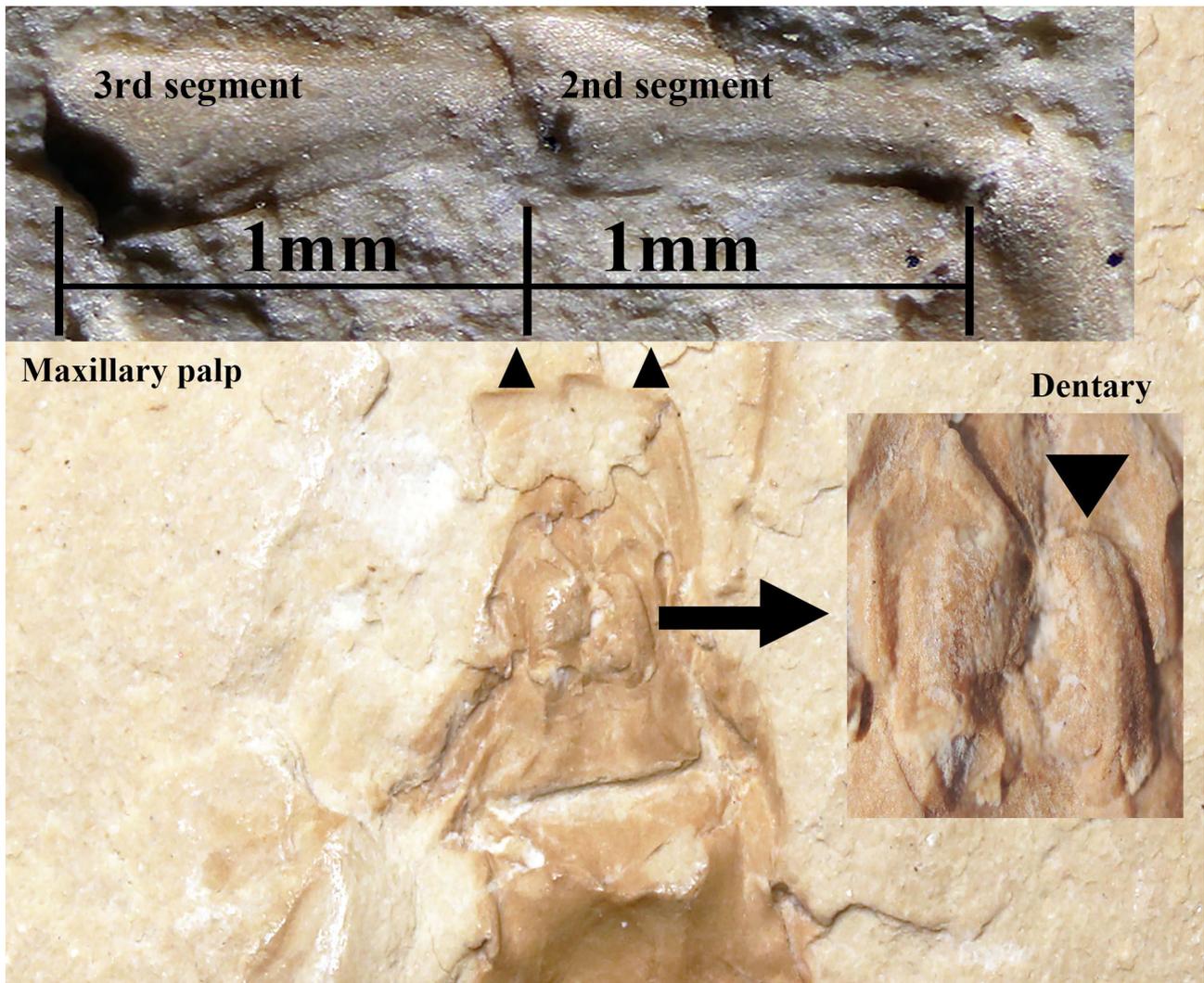


FIGURE 7. Head of the *Calosoma kimi* **sp. nov.** holotype (GNUE-311001).

C. kimi **sp. nov.** shows several characteristics of Carabidae (Ball *et al.* 2000), including: 1) The head is prognathous and narrower than the prothorax; 2) The antennae are inserted between the eyes; 3) The width of the prothorax shows a tendency that it is narrower than the elytra; 4) The pronotum is reflexed; and 5) The striae on the elytra are linear and continuous.

Based on morphological features such as the shape of the elytra and pronotum and body size, the genus *Calosoma* can be divided into 19 subgenera (Jeannel 1940; Bruschi 2013). Among them, the subgenera *Australodrepa*, *Calodrepa*, and *Calosoma* share the following characteristics: 1) The lateral margin of the pronotum discontinued before the hind angles that are small, pointed, and often bent inward; 2) the last segments of the maxillary palps are quite the same length, or hardly wider than the preceding ones; 3) the tooth of the mentum is small and only slightly protruding; 4) the lingula of the male aedeagus is not sclerified. In *Calosoma kimi* **sp. nov.**, although the maxillary palps and the mentum tooth (Fig. 7) are similar to the above three subgenera, but its position still cannot be determined because the lateral margin of the pronotum and hind angle, and metaepisterna are not visible in both type specimens. Further studies based on more specimens would solve this problem in future.

Many *Calosoma* fossils were discovered from the Miocene. In Europe, *Calosoma caraboides* Heer, 1860, *C. catenulatum* Heer, 1860, *C. deplanatum* Heer, 1860, *C. escheri* Heer, 1860, *C. escrobiculatum* Heer, 1860, *C. heeri* Scudder, 1895, *C. jaccardi* Heer, 1860, and *C. nauckianum* Heer, 1860 were reported from Germany and Switzerland. *C. fernquisti* Cockerell, 1924 was discovered from North America. In Asia, six species, *C. brunneum* Hong 1985, *C. cf. maderae* Fabricius, 1775, *C. maximowiczi* Morawitz, 1863, *C. inquisitor* Linnaeus, 1758, *C. aff. calidum* Fabricius, 1775 were recorded from China and Japan during Miocene to Pleistocene (Table 1).

The elytra on *C. kimi* **sp. nov.** do not show deeply grooved patterns on the 1st, 15th to 18th striae, versus deeply grooved in *C. brunneum*. *C. kimi* **sp. nov.** is similar to *C. cf. maderae* in: elytra contain same number of intervals (18) and the three marginal intervals are small and closely arranged though deeply instead of shallowly. Unfortunately, Zhang (1989) did not describe the interval connection patterns and scale patterns. According to Jeannel (1940), *C. maderae* contains a triploid pattern with split secondary intervals and tends to become a pentaploid pattern, which are not observed in *C. kimi* **sp. nov.**.

Calosoma kimi **sp. nov.** is easily separated from Japanese fossil species by its elytron has 19 striae, while 17 or 18 striae in *C. maximowiczi* from the photo of Aiba (2015). Shape of elytron on *C. aff. calidum* is differentiate from *C. kimi* **sp. nov.** with different interval connection pattern. Fig. 2A and C on Yahiro *et al.* (2018) shows 4th interval meets with 8th interval while *C. kimi* **sp. nov.** does not show same pattern. Since *C. inquisitor?* from Hayashi (1996) is poorly preserved and does not show any similar characteristics with *C. kimi* **sp. nov.** such as interval connection patterns or 2 types of scale, we concluded *C. kimi* **sp. nov.** can be differentiate from *C. inquisitor?* from Hayashi (1996).

Acknowledgments

We thank Eun Kyoung Jeong (Dalseong Country Office) for providing specimens (GNUE-311001), Prof. Jae Cheon Sohn (Gongju National University of Education), artist Do Yoon Kim (Seoul National University), Doo Young Kim (Gyeongbuk National University), Jongyun Jung (Korea Dinosaur Research Center) and Byung-Do Choi (Daegu National Science Museum) for their advice and suggestions. We also thank two anonymous reviewers for review and comments on our paper, and Enago (www.enago.co.kr) for the English language review.

References

- Aiba, H. (2015) *A guide Book of Fossils from the Shiobara Site*. Maruzen planet, Tokyo, 206 pp.
- Ball, G.E. & Bousquet, Y. (2000) Carabidae Latreille, 1810. In: Arnett, R.H. & Thomas, M.C. (Eds.), *American beetles: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, Boca Raton, Florida, pp. 32–132.
- Bong, P.Y. (1985) Palynology of the Neogene strata in the Pohang sedimentary basin. Ph.D. Thesis, Seoul National University, Seoul, 1–300.
- Boisduval, M. (1840) Sur une empreinte de Lepidoptère trouvée dans les marnes des environs d'Aix, en Provence, et communiquée par M. de Saporta. *Annales de la Société Entomologique de France*, 9, 371–374.
- Bruschi, S. (2013) *Calosoma of the world*. Natura Edizioni Scientifiche, Bologna, 393 pp.
- Cockerell, T.D.A. (1925) Fossil insects in the United States National Museum. *Proceedings of the United States National Museum*, 2503 (64), 1–15.
<https://doi.org/10.5479/si.00963801.64-2503.1>
- Fossil Insect Research Group for Nojiri-ko Excavation (1984) Fossil insects obtained from the Nojiri-ko Excavations in 1978 to 1982. *Monograph of the Association for the Geological Collaboration in Japan*, 27, 137–156. [in Japanese, with English abstract]
- Gersdorf, E. (1969) Käfer (Coleoptera) aus dem Jungtertiär Norddeutschlands. *Geologisches Jahrbuch*, 87, 295–332.
- Gersdorf, E. (1976) Dritter Beitrag über Käfer (Coleoptera) aus dem Jungtertiär von Willershausen, Bl. Northeim 4226. *Geologisches Jahrbuch A*, 36, 103–145.
- Gidaspow, T. (1959) North American caterpillar hunters of the genera *Calosoma* and *Callisthenes* (Coleoptera, Carabidae). *Bulletin of the American Museum of Natural History*, 116, 225–344.
- Grinnell, F. (1908) Quaternary myriapods and insects of California. *Bulletin of the Department of Geology, University of California*, 5, 207–215.
- Hashmi, S.N.A., Kamaluddin, S. & Hussain, S.Z. (2005) Revision of the genus *Calosoma* Weber (Coleoptera: Carabidae) with two new species from Pakistan with their cladistic relationships. *International Journal of Biology and Biotechnology*, 2 (2), 259–272.
- Hayashi, M. (1996) Insect fossil assemblage and paleoenvironments from the Early Pleistocene Bushi Formation in Saitama Prefecture, Japan. *Earth Science (Chikyū Kagaku)*, 50, 223–237.
- Heer, O. (1860) Ueber die fossilen Calosomen. In: *Programm der Eidgenössischen Polytechnischen Schule für das Schuljahr 1860/61*. Orell, Fuessli und Comp., Zürich, pp. I–X.
- Jeannel, R. (1940) *Les Calosomes. Mémoires du Musée National D'Histoire Naturelle*. Éditions du Musée, Paris, 255 pp.
- Kim, B.K. (1975) Stratigraphic studies on the lignite-bearing strata distributed in the Yeongil District, North Gyeongsang-Do, Korea. *Journal of Geological Society of Korea*, 11, 240–252.

- Kim, K.C. (1976) Fossil metallic wood-borer (Coleoptera, Buprestidae) from Miocene Geum-gwangdong Formation, Yeongil-gun Korea. *Bulletin of the Busan University, Natural Science*, 22, 121–126.
- Kim, K.C. & Lee, W.J. (1975) A fossil long horned katydid (Orthoptera: Tettigoniidae) from Miocene Geumgwangdong Formation, Yeongil-gun Korea. *Bulletin of the Busan University, Natural Science*, 20, 53–59.
- Latreille, P.A. (1802) *Histoire naturelle des fourmis: et recueil de mémoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes*. De l'imprimerie de Crapelet, Paris, 473 pp.
<https://doi.org/10.5962/bhl.title.11138>
- Linnaeus, C. (1758) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1. Salvius, Holmiae*, 823 pp.
<https://doi.org/10.5962/bhl.title.542>
- Lindroth, C. H. (1974) *Handbooks for the identification of British insects. Coleoptera, Carabidae. Vol. 4. No.2*. Royal Entomological Society of London, London, 148 pp.
- McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayer, C., Misof, B., Murin, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Slipinski, A. & Beutel, R.G. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences*, 116 (49), 24729–24737.
<https://doi.org/10.1073/pnas.1909655116>
- Nel, A. (1988) Les Calosomes fossiles de l'Oligocène du sud-est de la France [Col. Carabidae]. *Bulletin de la Société entomologique de France*, 93 (9), 257–268.
- Paik, I.S., Kang, H.C., Kim, H. J, Lee, H.I., Kim, K.S. & Jeong, E.K. (2010) The Geumgwangdong Formation of the Janggi Group, Pohang area: Stratigraphy, occurrences, and fossil leaf deposits. *Journal of the Geological Society of Korea*, 46 (6), 535–552. [in Koren, with English abstract]
- Paik, I.S., Kim, H.J., Kim, K.S., Jeong, E.K., Kang, C.H., Lee, H.I. & Uemura, K. (2012) Leaf beds in the Early Miocene lacustrine deposits of the Geumgwangdong Formation, Korea: occurrence, plant-insect interaction records, taphonomy and palaeoenvironmental implications. *Review of Palaeobotany and Palynology*, 170, 1–14.
<https://doi.org/10.1016/j.revpalbo.2011.10.011>
- Pauca, M. & Ciobanu, M. (1978) Asupra insectelor fosile din Romania si a prezentei unei noi specii di carabid din Oligocenul de la Piatra Neamt. *Anuarul Muzeului de Stiinta Naturale Piatra Neamt, Seria Geologie-Geografie*, 4, 151–158.
- Scudder, S.H. (1895) The Miocene insect-fauna of Oeningen, Baden. *Geological Magazine*, 2, 116–122
<https://doi.org/10.1017/S0016756800005963>
- Scudder, S.H. (1900) Adepagous and clavicorn Coleoptera from the Tertiary deposits at Florissant, Colorado with descriptions of a few other forms and a systematic list of the non-rhynchophorus Tertiary Coleoptera of North America. *Monographs of the United States Geological Survey Washington*, 40, 1–148.
<https://doi.org/10.5962/bhl.title.965>
- Sohn, J.C., Doorenweerd, C., Nam, K.S. & Choi, S.W. (2019) New leaf-mine fossil from the Geumgwangdong Formation, Pohang Basin, South Korea, associates pygmy moths (Lepidoptera, Nepticulidae) with beech trees (Fagaceae, Fagus) in the Miocene. *Journal of Paleontology*, 93 (2), 337–342.
<https://doi.org/10.1017/jpa.2018.83>
- Tanai, T. (1961) Neogene floral change in Japan. *Journal of the Faculty Science, Hokkaido University series 4 Geology and mineralogy*, 11, 119–398.
- Tateiwa, I. (1924) *Geological atlas of Chosen no. 2. Ennichi, Kyuryuho and Choyo sheets*. Geological Survey of Government, General of Chosen, Seoul, 16 pp. [in Japanese]
- Toussaint, E.F. & Gillett, C.P. (2018) Rekindling Jeannel's Gondwanan vision? Phylogenetics and evolution of Carabinae with a focus on *Calosoma* caterpillar hunter beetles. *Biological Journal of the Linnean Society*, 123 (1), 191–207.
<https://doi.org/10.1093/biolinnean/blx128>
- Weber, F. (1801) *Observationes entomologicae: continentes novorum quae condidit generum characteres, et nuper detectarum specierum descriptiones*. Bibliopoli Academici Novi, Kiliae, 116 pp.
<https://doi.org/10.5962/bhl.title.8639>
- Wickham, H.F. (1909) New fossil Coleoptera from Florissant. *American Journal of Science*, 28 (164), 126–130
<https://doi.org/10.2475/ajs.s4-28.164.126>
- Wickham, H.F. (1910) New fossil Coleoptera from Florissant, with notes on some already described. *American Journal Of Science*, 29 (169), 47–51.
<https://doi.org/10.2475/ajs.s4-29.169.47>
- Yahiro, K., Sugiyama, K. & Hayashi, M. (2018) Late Pliocene of Fossil *Calosoma* (Coleoptera, Carabidae) from the Koka Formation, Kobiwako Group in Shiga Prefecture, Japan. *Elytra*, New Series 8 (1), 227–233.
- Yoon, S. (1989) Tertiary Stratigraphy of the Southern Korean Peninsula. In: Liu, G., Ryuich, T. & Lin, Q. (Eds.), *Proceeding International Symposium of Pacific Neogene Continental and Marine Events*. Nanjing University Press, Nanjing, pp. 195–207.
- Zhang, J.F. (1989) *Fossil Insects From Shanwang, Shandong, China*. Shandong Science and Technology Publishing House, Jinan, 459 pp.