

A review of the Asian *Semigenetta*
Helbing, 1927 (Viverridae, Feliformia, Carnivora)
with a description of two new species,
Semigenetta qiae n. sp. from South China
and *Semigenetta thailandica* n. sp. from Thailand

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ABSTRACT

Semigenetta Helbing, 1927 is a small genet-like carnivoran in the family Viverridae Gray, 1821. The genus has a modest diversity in the Miocene of Eurasia. With its first documentation going back to 1850s, the European records are relatively continuous with five currently recognized species. Asian records have a much shorter history of studies with its first record, *S. huaiheensis* Qiu & Gu, being published in 1986. In the present paper, we review the Asian records of *Semigenetta* from China and Thailand, which so far are represented by three species based on fragmentary jaws and teeth. We recognize two new species, *S. qiae* n. sp. from the late Miocene (c. 6.2-6.9 Ma) of Lufeng Basin in central Yunnan Province, South China and *S. thailandica* n. sp. from the middle Miocene (13.4-13.2 Ma) of Mae Moh Basin in Lampang Province, northern Thailand. Zoogeographically, both *S. huaiheensis* and *S. thailandica* n. sp. seem traceable to their European ancestors, as independent immigration events. *Semigenetta thailandica* n. sp. may have given rise to *S. qiae* n. sp., i.e., *S. thailandica* n. sp. and *S. qiae* n. sp., both recovered from lignitic sediments, potentially form a southeast Asian clade. All Asian *Semigenetta* occur within the Oriental zoogeographic province, and like their European counterparts, presumably prefer warm, humid, and wooded environments. Their relatively conservative morphology and low diversity seem also indicative of a stable environment in subtropical refugia. *Semigenetta qiae* n. sp. from Lufeng is the last survivor of the genus in Asia.

KEY WORDS

Carnivora,
Viverridae,
Semigenetta,
Miocene,
China,
Thailand,
Asia,
zoogeography,
new species.

RÉSUMÉ

Une révision de *Semigenetta* Helbing, 1927 (Viverridae, Feliformia, Carnivora) en Asie avec une description de deux nouvelles espèces, *Semigenetta qiae* n. sp. en Chine du Sud et *Semigenetta thailandica* n. sp. en Thaïlande.

Semigenetta Helbing, 1927 est un petit carnivore de la famille des Viverridae Gray, 1821 ressemblant à une genette. Le genre a une diversité modeste dans le Miocène d'Eurasie. D'abord documenté dans les années 1850, le registre européen est relativement continu avec cinq espèces reconnues actuellement. Le registre asiatique a une histoire beaucoup plus courte avec une première occurrence, *S. huaiheensis* Qiu & Gu, publiée en 1986. Dans le présent article, nous révisons le registre asiatique de *Semigenetta* de Chine et de Thaïlande, qui, jusqu'à présent, compte trois espèces représentées par des fragments de mâchoires et des dents. Nous reconnaissons deux nouvelles espèces, *S. qiae* n. sp. du Miocène tardif (c. 6.2-6.9 Ma) du Bassin de Lufeng dans le centre de la province du Yunnan, Chine du Sud, et *S. thailandica* n. sp. du Miocène moyen (13.4-13.2 Ma) du Bassin de Mae Moh, dans la province de Lampang, au nord de la Thaïlande. D'un point de vue zoogéographique, *S. huaiheensis* et *S. thailandica* n. sp. semblent dériver d'ancêtres européens suite à des événements d'immigrations indépendants. *Semigenetta thailandica* n. sp. a pu donner naissance à *S. qiae* n. sp., i.e., *S. thailandica* n. sp. et *S. qiae* n. sp., tous deux découverts dans des lignites, forment potentiellement un clade en Asie du Sud-Est. Toutes les espèces asiatiques de *Semigenetta* proviennent de la province zoogéographique orientale, et comme leurs proche-parents européens, préféraient certainement des environnements boisés, chauds et humides. Leur morphologie relativement homogène et leur faible diversité semblent aussi indiquer un environnement relativement stable dans un refuge subtropical. *Semigenetta qiae* n. sp. de Lufeng est le dernier survivant du genre en Asie.

MOTS CLÉS

Carnivora,
Viverridae,
Semigenetta,
Miocène,
Chine,
Thaïlande,
Asie,
zoogéographie,
espèces nouvelles.

INTRODUCTION

The extinct genet-like carnivoran *Semigenetta* Helbing, 1927 belongs to the family Viverridae Gray, 1821 and has a modest diversity in the Miocene of Europe (Bonis 1994; Kargopoulos *et al.* 2021) and Asia (Qiu Z.-X. & Gu 1986; Bonis *et al.* 2021). From its initial establishment by Helbing (1927), *Semigenetta* was considered similar to the extant *Genetta*, with the exception of its reduced m2 and the absent M2. Based on the latest review by Kargopoulos *et al.* (2021), five species of *Semigenetta* have been recognized in Europe, whereas in Asia two or three are currently known in China and Thailand (Qiu Z.-X. & Gu 1986; Mein & Ginsburg 1997; Bonis *et al.* 2021).

Living genets, the genus *Genetta*, are nocturnal, solitary, small to medium predators found in Africa and Arabia, and introduced to southwestern Europe by humans. As members of the subfamily Genettinae Rochebrune, 1883 (Viverridae, Carnivora), *Genetta* is the most speciose carnivoran in Africa, with up to 15-17 living species (Gaubert & Begg 2007; Veron 2010), and has a fossil record that can be traced to the middle Miocene (about 14 Ma) of Africa (Werdelin & Peigné 2010). Despite this high modern diversity, *Genetta* spp. are conservative with relatively homogeneous dental morphology (see common genet in Larivière & Calzada 2001 as an example) and a full set of four upper and lower premolars plus two upper and lower molars (Gaubert *et al.* 2004).

Likened to the extant martens (*Martes* Pinel, 1792) in the family Mustelidae Fischer von Waldheim, 1817, genets occupy similar niches for small, agile omnivores (Kargopoulos *et al.* 2021), and also like *Martes*, both living and fossil genets remain conservative in their cranial and dental morphology through most of their evolution. These generalized morphologies and high diversity make it difficult to sort out their relationships based on morphology alone (Gaubert *et al.* 2004). As a result, the relationship, if any, between modern *Genetta* and extinct *Semigenetta* is not clear.

In a systematic review of carnivorans from the hominoid locality of Lufeng in Yunnan Province, South China by two of us (QJ + XW), we recognize a new species of *Semigenetta*, which is described herein. Since the taxonomic status of existing Asian species are somewhat controversial, we take this opportunity to review the Asian records.

MATERIAL AND METHODS

INSTITUTIONAL ABBREVIATIONS

GV	China University of Geosciences, Beijing;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
MM	Mae Moh fossils, housed at the Laboratoire Paléontologie Évolution Paléoeosystèmes Paléoprimatologie (PALEVOPRIM) of the University of Poitiers for study and will be returned to the Department of Mineral Resources, Bangkok;
MNNH	Muséum national d'Histoire naturelle, Paris;
NHMMUK	Natural History Museum (formerly British Museum), London;
PDYV	Yunnan Institute of Cultural Relics and Archaeology, Kunming.

HISTORY OF STUDIES ON SEMIGENETTA

During the mid-1800 through early 1900, several species of small viverrids from the early to middle Miocene of Europe were discovered. For example, “*Viverra*” *sansaniensis* Lartet, 1851 was based on specimens from the French locality of Sansan (Lartet 1851); “*Viverra*” *steinheimensis* Fraas, 1870 was discovered in the German locality of Steinheim (Fraas 1870); and “*Plesictis*” *mutatus* Filhol, 1883 was described from La Grive Saint-Alban of France (Filhol 1883). All of these early species were based on fragmentary jaws and teeth, and as their varied generic names suggest, early studies lacked a coherent view of their generic assignments.

Helbing (1927) established a new genus and species, *Semigenetta repelini* Helbing, 1927, based on two partial mandibles, plus substantial postcranial materials, from the village of Captieux, Gironde, in southwestern France. Helbing was aware of the similarity of his *S. repelini* to *S. sansaniensis* (Lartet, 1851), but nonetheless erected a new species, which was indeed later judged to be the same as *S. sansaniensis* (see Kargopoulos *et al.* 2021 for history). Helbing also emphasized that his *Semigenetta* was not related to *Progenetta* (Depéret, 1892), a taxon of larger size that is now considered to be a hyaenid (Werdelin 1988; Werdelin & Solounias 1991).

Thus defined, the genus *Semigenetta* has come to represent several European Miocene small genets. Since then, many of the early-named species have been synonymized under *S. sansaniensis* (Kargopoulos *et al.* 2021).

After *Semigenetta* was established, knowledge about this genus has gained steadily, especially in Europe. Roman & Viret (1934) described *S. cadeoti* Roman & Viret, 1934 from La Romieu. Dehm (1950) named *S. elegans* Dehm, 1950 from Wintershof-West. Petter (1976) erected *S. ripolli* Petter, 1976 from Can Llobateres (Vallesian) of Spain. Crusafont-Pairó & Golpe-Posse (1981) recognized *S. grandis* Crusafont-Pairó & Golpe-Posse, 1981 from late Miocene Castell de Barberà of Spain. Bonis (1973) described “*Plesictis*” *laugnacensis* Bonis, 1973 based on two jaws from the Aquitanian site of Laugnac (Lot-et-Garonne). Bonis (1994) later recognized it as belonging to *Semigenetta* and also added a partial maxillary with P3-M1. Peigné (2012) revised *S. sansaniensis* from Sansan, France. Kargopoulos *et al.* (2021) referred two species, *S. sansaniensis* and *S. grandis*, from the late Miocene Hammerschmiede of Germany.

From China, Qiu Z.-X. & Gu (1986) recognized the first Asian species, *Semigenetta huaiheensis* Qiu & Gu, 1986, from the early Miocene Xiacaowan of Jiangsu Province based on a right jaw with p2-m1. This was the first *Semigenetta* record outside Europe but recently Kargopoulos *et al.* (2021) synonymized *S. huaiheensis* with *S. elegans* from Wintershof-West.

Most recently, Jiangzuo *et al.* (2023) assigned to *Semigenetta* sp. a left jaw fragment with p3 (broken), p4, and m1 trigonid from the middle Miocene Shinanu area in Linxia Basin, Gansu Province. This specimen (GV 87038) was originally referred to *Pseudaelurus* sp. by Cao *et al.* (1990), but it is undoubtedly not a felid. However, the broken m1 in this jaw shows signs of it being a hyaenid by possessing a distinct ridge in the posterolingual aspect of the paraconid. It seems to be a basal hyaenid of *Protictitherium-Tungurictis* grade (Wang X. *et al.* 2020), but more primitive (less hypocarnivorous) than the proteline *Gansuyaena* Galiano, Tseng, Solounias, Wang, Qiu & White, 2022 (Galiano *et al.* 2022). We thus exclude the Linxia Basin “*Semigenetta* sp.” by Jiangzuo *et al.* (2023) from this treatment.

In Thailand, Mein & Ginsburg (1997) mentioned a “*Semigenetta* indet” from the middle Miocene of Li Mae Long. Most recently, Bonis *et al.* (2021) described a left jaw of *Semigenetta* cf. *S. steinheimensis* from the middle Miocene of Mae Moh, Thailand. However, this latter species was also synonymized under *S. sansaniensis* by Kargopoulos *et al.* (2021).

Bonis (1994) was the first to attempt a systematic summary of *Semigenetta* from Europe and recognized five species as part of an evolutionary progression. These were, from smallest to largest, *S. laugnacensis* (Bonis, 1973), *S. elegans*, *S. sansaniensis*, *S. steinheimensis*, and *S. grandis*. More recently, however, Kargopoulos *et al.* (2021) reviewed all Eurasian records of *Semigenetta* and recognized the following five species as valid: *S. laugnacensis*, *S. cadeoti*, *S. elegans*, *S. sansaniensis*, and *S. grandis*, treating the Chinese *S. huaiheensis* as a junior synonym of *S. elegans*.

SYSTEMATIC PALAEOONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder FELIFORMIA Kretzoi, 1945
Family VIVERRIDAE Gray, 1821
Subfamily GENETTINAE Rochebrune, 1883

Genus *Semigenetta* Helbing, 1927

TYPE SPECIES. — *Viverra sansaniensis* Lartet, 1851.

INCLUDED SPECIES. — *Semigenetta sansaniensis* (Lartet, 1851), *S. cadeoti* Roman & Viret, 1934, *S. laugnacensis* (Bonis, 1973), *S. elegans* Dehm, 1950, *S. grandis* Crusafont Pairó & Golpe Posse, 1981, *S. huaiheensis* Qiu & Gu, 1986, *S. qiae* n. sp., and *S. thailandica* n. sp.

GEOGRAPHIC AND CHRONOLOGICAL DISTRIBUTION. — Late Agenian (MN2b) to late Vallesian (MN10) of Europe; Shanwangian (early Miocene) and Baodean (late Miocene) in China; late middle Miocene of Thailand (Q-K coal zone of the Mae Moh Basin, 13.4–13.2 Ma).

EMENDED DIAGNOSIS. — Mandible bearing a deep masseter fossa, long and narrow angular process, canine with a well-marked buccal groove; a p4 with marked anterior and posterior accessory cuspids; reduction of m1 talonid, hypoconid present, m1 entoconid and hypoconulid absent or present as a low ridge, m2 reduced; loss of M2 (Bonis *et al.* 2021; Kargopoulos *et al.* 2021).

REMARKS

Early feliform carnivorans can be divided into long-snouted (dolichocephaly) and short-snouted (brachycephaly) forms (Hunt 1998). The dolichocephalic feliforms are unusual because feliforms often trended toward short snout and hypercarnivory. Examples of long-snouted feliforms include the extinct *Haplogale* Schlosser, 1887 from the Quercy fissures and the modern genet *Genetta*. The long snouts and jaws with diastemata between premolars probably represent a derived feature for some genet-like feliforms, including the extinct *Haplogale* (Hunt 2001). Such a lengthened rostrum may be analogous to early North American canine canids, such as *Leptocyon* Matthew, 1918 and its living canine descendants (Wang X. *et al.* 2008; Tedford *et al.* 2009).

Our knowledge of *Semigenetta* is still quite poor and comparisons with other small feliforms are limited to fragmentary jaws and teeth. Although no intact skull is known, *Semigenetta* generally has a slender jaw but its premolars are not separated by long diastemata. Exactly how *Semigenetta* is (or is not) related to the living genet has not been closely examined, although Helbing (1927) regarded his newly erected *Semigenetta* as representing a small group of fossil genets in Europe. The loss of the M2 and a short m2 in all known species of *Semigenetta* suggest that this genus is not trending toward dolichocephaly as does *Genetta*, and lacking a shared derived character, *Semigenetta* and *Genetta* may or may not be closely related to each other.

The genera *Genetta* and *Semigenetta* represent some of the most generalized forms in the family Viverridae. They lack some of the advanced dental characters shown in hypocarnivorous, bunodont paradoxurines and related forms in Africa, such as *Kichechia* Savage, 1965 (Savage 1965), *Orangictis*

Morales, Pickford, Soria & Fraile, 2001 (Morales *et al.* 2001; Morales & Pickford 2011), *Tugenictis* Morales & Pickford, 2005 (Morales & Pickford 2005, 2011), *Pseudocivetta* Petter, 1967 (Petter 1967, 1973), *Kanuites* Dehghani & Werdelin, 2008 (Dehghani & Werdelin 2008; Werdelin 2019), *Ketketictis* Morlo, Miller & El-Barkooky, 2007 (Morlo *et al.* 2007) and in Asia, *Mioparadoxurus* Morales & Pickford, 2011 (Petter 1967, 1973; Morales & Pickford 2011) and *Siamictis* Grohé, Bonis, Chaimanee, Chavasseau, Rughumrung, Yamee, Suraprasit, Gilbert, Surault, Blondel & Jaeger, 2020 (Grohé *et al.* 2020). Similarly, the southeast Asian otter civet (*Cynogale* Gray, 1837) also has hypocarnivorous molars (Gervais 1854: 29), and evidently not related to the Lufeng form, although, according to Grohé *et al.* (2020), it is related to another Lufeng viverrid described by Qi (2004), *Lufengictis peii* Qi, 2004. Among Asian records, Lydekker (1884) described *Viverra bakerii* Lydekker, 1884 and *V. durandi* Lydekker, 1884 from the Siwaliks of Pakistan, the latter being placed in *Vishnuictis durandi* (Lydekker, 1884) by Pilgrim (1932) and Colbert (1935). Both of these species have an unreduced M2 and thus easily distinguished from *Semigenetta*. Most recently, Grohé *et al.* (2020) erected a new genus *Siamictis* within the subfamily Paradoxurinae from the middle Miocene of Thailand.

Véron (2010) published the latest molecular relationship of viverrids, in which subfamilies Genettinae and Viverrinae are sister groups. Morphological characters are seen as highly convergent given the constraint of molecular relationships, although the above sister relationship is recovered without molecular constraint (Gaubert *et al.* 2005). How fossil taxa are related to this phylogenetic framework of living viverrids has not been explored (Véron 1995). With the exception of the loss of M2 (a character that independently occurs numerous times among carnivorans), dental morphology of *Semigenetta* is largely primitive, as in most stem feliform carnivorans.

From the deep-history paleontologic perspective, Hunt (2001) had envisioned a lineage of the extinct Palaeoprionodon with living linsangs (*Prionodon* Horsfield, 1822 and *Poiana* Gray, 1864). However, modern molecular phylogeny suggests that *Prionodon* and *Poiana* do not belong to the same clade, but *Poiana* was at the base of a *Poiana-Genetta* clade (Veron 2010), implying greater complexities than can be discerned from the fossil records only.

Heizmann (1973: fig. 22) remarked about the increasing body size among European forms, a trend also echoed by Golpe-Posse (1981) and Bonis (1994). In his synthesis of the contents of *Semigenetta* from the Miocene of Europe, Bonis (1994) recognized five species of roughly increasing size: *S. laugnacensis* (Bonis 1973) from Laugnac, France (MN2b), *S. elegans* from Wintershof-West, Germany (MN3), *S. sansaniensis* (Lartet, 1851) from Sansan, France (MN6), *S. steinheimensis* Fraas, 1870 from Steinheim am Albuch, Germany (late MN7–8), and *S. grandis* Crusafont & Golpe-Posse, 1981 from Castell de Barará, Spain (MN9). This systematic scheme was later adopted by Bonis *et al.* (2021), except *Semigenetta elegans* in Bonis (1994) becomes *S. gracilis* Dehm, 1950 in Bonis *et al.* (2021). The above species generally increase in body size, following a similar theme by Bonis (1994). For those species

TABLE 1. Dental measurements (in mm) of *Semigenetta* Helbing, 1927 from East and Southeast Asia and their close European species, adopted from Dehm (1950) for *S. elegans* Dehm, 1950 (numbers in parentheses are sample sizes), Qiu & Gu (1986) for *S. huaiheensis* Qiu & Gu, 1986, Bonis *et al.* (2021) for *S. thailandica* n. sp., and Kargopoulos *et al.* (2021) for *S. sansaniensis* (Lartet, 1851). See Kargopoulos *et al.* (2021) for measurements of additional European species.

	Asia					Europe
	China			Thailand		
	S. qiae n. sp. Lufeng		S. huaiheensis Qiu & Gu, 1986 Xiacaowan		S. thailandica n. sp. Mae Moh	
	IVPP V27106	IVPP V27120	IVPP V8068	MM 106	S. elegans Dehm, 1950 Wintershof-West	S. sansaniensis (Lartet, 1851) various
M1 buccal length	–	4.5	–	–	–	–
M1 width	–	4.6	–	–	–	–
p1 length	–	–	5.0	–	–	2.2-2.8 (5)
p1 width	–	–	1.9	–	–	1.3-1.7 (5)
p2 length	4.7	–	–	5.5	4.5-4.8 (2)	4.7-6.4 (13)
p2 width	1.6	–	–	3.0	–	2.0-2.6 (13)
p3 length	5.0	–	6.1	7.3	5.7-6.4 (9)	6.4-8.4 (18)
p3 width	2.0	–	2.4	3.9	–	1.8-3.5 (17)
p4 length	5.9	–	7.0	9.4	6.1-7.3 (10)	7.0-9.0 (18)
p4 width	2.4	2.1	2.9	4.6	–	2.9-4.1 (17)
m1 length	6.9	6.4	8.7	10.5	7.7-8.8 (10)	9.0-11.4 (22)
m1 trigonid length	5.0	4.6	–	7.6	–	–
m1 trigonid width	3.1	3.1	4.0	5.2	–	4.1-5.4 (22)
m1 talonid width	2.8	3.0	–	4.3	–	–
m2 length	–	–	–	–	2.7 (2)	–
jaw depth at m1-2	6.9	–	11.8	–	–	–

that do not fall in this trend, such as *S. cadeoti* Roman & Viret, 1934 and *S. ripolli* Petter, 1976, Bonis *et al.* (2021) suspected that they might belong to other genera. Shortly after the above, Kargopoulos *et al.* (2021) did a review of Eurasian *Semigenetta*, in which they recognized five species.

Helbing's (1927) original type species of *Semigenetta* is *S. repelini* from Captieux in southwestern France. Heizmann (1973), however, remarked that the Captieux sample is indistinguishable from *S. sansaniensis*, which had priority. Bonis (1994: 87) agreed with Heizmann's assessment and further pointed out that accepting such a synonym would leave the genus *Semigenetta* without a type species and logically should be discarded. To avoid such an awkward situation and appealing to prevailing (greater than half a century) usage, Bonis (1994) proposed to conserve *Semigenetta* by designating *Viverra sansaniensis* Lartet, 1851 as its type species, whose holotype is MNNH Sa 813. Bonis' proposal of fixing of the type species appears to be a valid taxonomic action because *V. sansaniensis* is eligible for type fixation as the species was originally included in Helbing's discussion (article 67.2 of International Commission on Zoological Nomenclature 1999).

Semigenetta qiae n. sp.
(Figs 1–5; Table 1)

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MATERIAL EXAMINED. — **Holotype.** China, Lufeng, Lufeng Basin, Shihuiba; IVPP V27106, partial left dentary with p2-m1 and m2 alveolus.

DIAGNOSIS. — Possessing known diagnostic characters of the genus, *Semigenetta qiae* n. sp. differs from all other species of the genus in its small size, enlarged anterior and posterior accessory cusps in lower premolars, slightly more hypocarnivorous lower carnassial with relatively enlarged and more basined m1 talonid and taller metaconid. *S. qiae* n. sp. has more laterally shifted main cusps and accessory cusps in the lower premolars than in *S. thailandica* n. sp.

REFERRED SPECIMEN. — IVPP V27120, right maxillary fragment with P4 (broken)-M1 and left maxillary fragment with M1, fragmentary right dentary with posterior root of p3, p4-m1, Lufeng Basin, Yunnan Province.

ETYMOLOGY. — In honor of Professor Qi Guoqin for her contributions to fossil mammals of South China in general and Lufeng fossil site in particular.

TYPE LOCALITY. — China, Lufeng, Lufeng Basin, Shihuiba. IVPP 75033 loc. at 25°13'15"N, 102°03'09"E, about 1 km northwest of the village of Shihuiba and 9 km north of the county of Lufeng at the northern margin of Lufeng Basin (Dong & Qi 2013) (Fig. 1). Initial excavations of the fossil site in 1975 were conducted by personnel of the IVPP, Yunnan Provincial Museum, and Lufeng Cultural Heritage Bureau.

GEOLOGY, FAUNA AND AGE. — Discoveries in 1975–1976 of hominoids in a fossil site (IVPP loc 75033) near the village of Shihuiba a few km from the county of Lufeng (Xu *et al.* 1978; Xu & Lu 1979) has attracted much international attention. Multiple excavations ensued in subsequent years in Neogene deposits in the Lufeng Basin, consisting of fluvio-lacustrine and lignite beds with a thickness of 20–30 m, but fossils being concentrated in a 3–8 m lignite (Qi 1979; Badgley *et al.* 1988). Early descriptions of litho- and biostratigraphy of the Shihuiba Formation were attempted (Qi 1979, 1985b; Chen 1986; Badgley *et al.* 1988), as well as in more recent years (Dong & Qi 2013). The paleoecological settings and fossil pollens were also studied (Sun X.-J. & Wu 1980; Badgley *et al.* 1988).

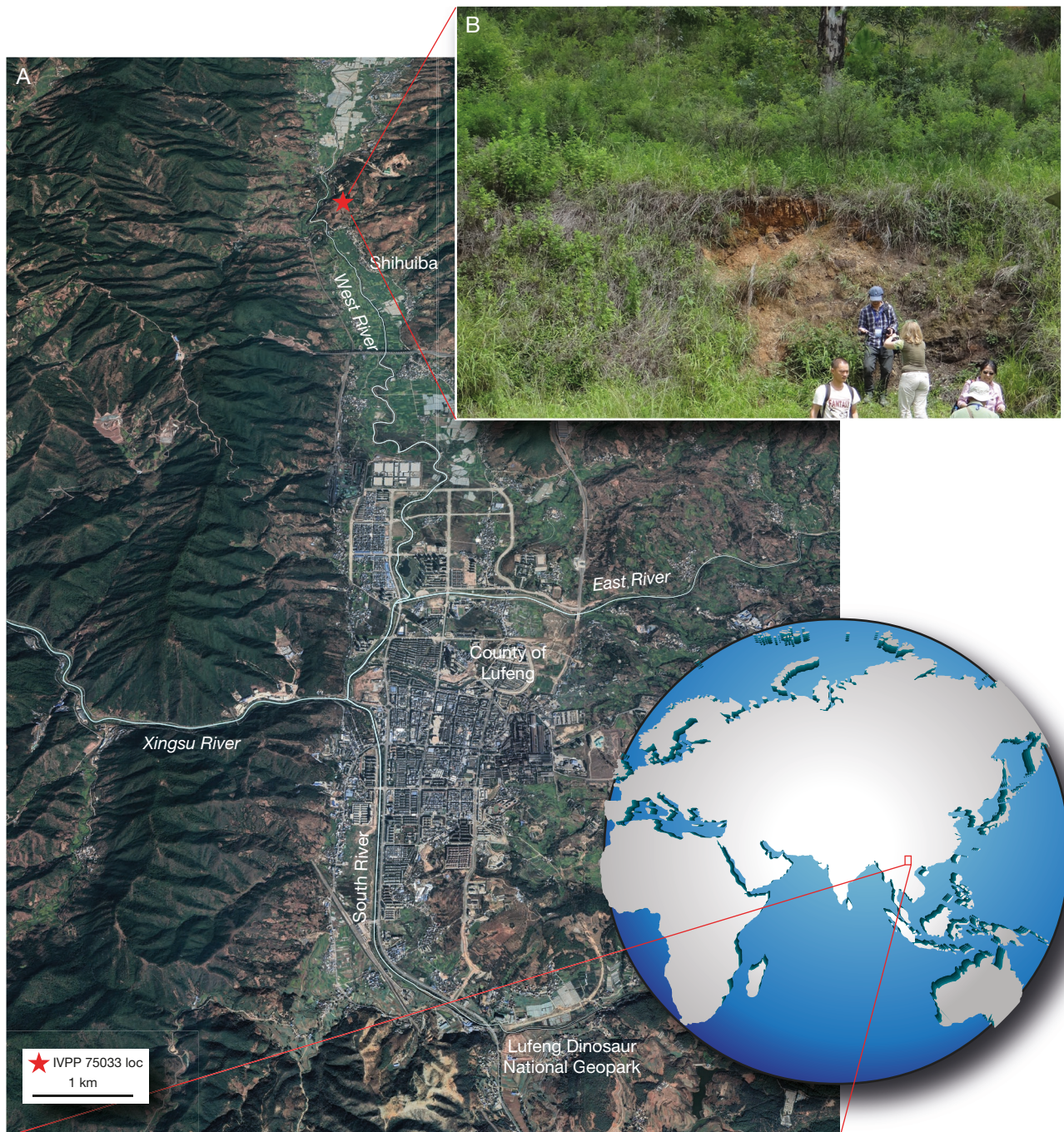


FIG. 1. — **A**, Satellite image of Lufeng Basin, downloaded from Google Earth (Google Earth Pro (Version 7.3.6.9345) 2023) on February 24, 2023; **B**, *Lufengpithecus* Wu, 1987 fossil site (IVPP 75033 locality) at the Lufeng hominoid monument (not visible), now extensively covered by modern vegetation (as compared to fresh exposures in Badgley *et al.* 1988: fig. 1). Credits: B, Xiaoming Wang, taken on August 5, 2013.

The Lufeng Basin is controlled by the Xianshuihe-Xiaojiang and Sagaing left-lateral strike-slip fault system, as well as associated dip-slip extensions (Wang E.-C. *et al.* 1998; Li *et al.* 2015). This fault system mostly runs along the eastern edge of the Tibetan Plateau and a splay of these faults, the Lufeng Fault (F2 in Li *et al.* 2015: fig. 1), passes through the Lufeng Basin. Further south at Kaiyuan, activation of the Xiaojiang Faults (F4) was initiated at around 11–12 Ma, although Paleogene sediments are also present along the fault system (Li *et al.* 2015). Several Neogene basins in eastern Yunnan are apparently all controlled by the above fault system, including Yuanmou, Lufeng, Zhaotong, and Kaiyuan basins.

A diverse vertebrate fauna is known in the Shihuiba section, including more than 100 taxa of fishes, reptiles, birds and mammals (Qi 1979; Dong & Qi 2013). Various carnivorans from Lufeng have been described by Qi and her colleagues (Qi 1983, 1984, 1985a; 2004, 2006, 2014; Qiu Z.-X. & Qi 1989, 1990, as well as syntheses on *Hipparion* horse (Sun B.-Y. 2013), suoids (Han 1983; van der Made & Han 1994), hominoids (Xu *et al.* 1978; Xu & Lu 1979; Wu *et al.* 1983), plus small mammals (Flynn & Qi 1982). Based on biochronological assessment of the rhizomyid rodents from Siwalik of Pakistan and Lufeng, Flynn & Qi (1982) estimated an age of *c.* 8 Ma for the Lufeng Fauna, although this



FIG. 2. — *Semigenetta qiae* n. sp., IVPP V27106, holotype: **A**, lingual view; **B**, buccal view of left dentary. Scale bar: 10 mm.

estimate was later revised to be at least 1 million years younger (Badgley *et al.* 1988: 179). Recent assessment on the fossil records of the striped rabbits, *Nesolagus* Forsyth-Major, 1899, is also consistent with a divergence time of about 7 Ma based on mitochondrial evidence (Flynn *et al.* 2019). Two sections at the Lufeng hominoid sites were sampled for magnetostratigraphic studies (Yue & Zhang 2006). The resulting six normal and six reversed magnetochrons were correlated to part of C3r through C4Bn.1n, spanning *c.* 5.8–7.6 Ma in GTS2020 calibration (Raffi *et al.* 2020). The hominoid-producing lignite beds (including the *Semigenetta* specimen), however, were restricted to C3An.2n and C3Ar, which is *c.* 6.2–6.9 Ma in the late Miocene (Dong & Qi 2013).

DESCRIPTION AND COMPARISON

An associated right P4-M1 and an isolated left M1 are preserved in similar condition as the right lower jaw with p4-m1, with extensive crush on the bones embedded within a dark, lignitic matrix. These are catalogued as a single specimen, IVPP V27120, with similar stage of wear on the teeth, and we treat them as belonging to the same individual.

The right P4 is broken and partially embedded within a crushed bone matrix. Both parastyle and protocone are missing, and the only observable structure is the presence of a narrow lingual cingulum and a carnassial notch that are

consistent with a general basal feliform morphology. This narrow cingulum seems to be absent in known records of European species of *Semigenetta* (Dehm 1950; Viret 1951; Bonis 1994), although the Hammerschmiede sample apparently has this lingual cingulum at the base of the metastyle as well as on its buccal side (Kargopoulos *et al.* 2021).

Both the left and right M1s are broken in the lingual half but the general outlines of the teeth are still intact. A prominent parastyle is the most outstanding feature, as is consistent with upper M1s of *Semigenetta*, such as *S. laugnacensis* (Bonis 1994: fig. 2), *S. elegans* (Dehm 1950: fig. 224), *S. sansaniensis* (Viret 1951: pl. I, fig. 18b), and a referred specimen (NHMUK M5306) of *S. sansaniensis* from la Grive-Saint-Alban (Isère), France. Associated with the large parastyle, the paracone is also larger than the metacone. Although not well preserved, the lingual part of the M1s appears to be consisted of a protocone without a surrounding cingulum. Also consistent with European *Semigenetta*, there is no paraconule and metaconule on M1s.

There is no evidence for the presence of an M2, although the poor preservation of IVPP V27120 makes this less certain. Assuming this is the case, the lack of an M2 is consistent with the diagnosis of *Semigenetta*.

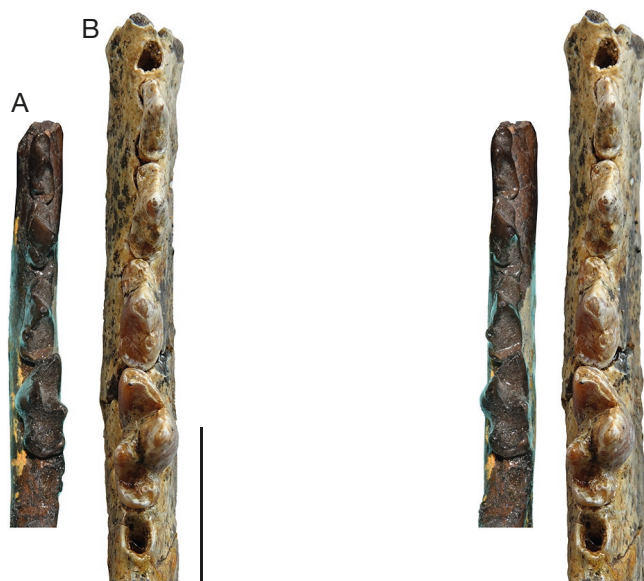


FIG. 3. — **A**, *Semigenetta qiae* n. sp., IVPP V27106, holotype, left dentary; **B**, *Semigenetta huaiheensis* Qiu & Gu, 1986, IVPP V8086, holotype, right dentary. Both stereo photos of occlusal views. Scale bar: 10 mm.

The left dentary in the holotype (IVPP V27106) is long and slender with relatively uniform depth and minimum tapering toward the anterior end, in contrast to a more distinct subangular lobe in *S. huaiheensis* (compare Figure 2 and Figure 6). Below the p2, the posterior end of the symphysis is slightly deepened.

The most prominent feature of the lower premolars is their large, discrete, anterior and posterior accessory cusps, plus a small posterior cingular cuspid. These conspicuously cuspidate premolars are highly distinct and differ from those of other species of *Semigenetta*. This distinction is particularly striking for the anterior accessory cusps. This is especially pronounced in the anterior premolars, such as the p2 and p3, which typically have a more diminished accessory cuspid in older and more primitive species of *Semigenetta*.

The p2 is a slender tooth (see measurements in Table 1) without a cingulid on both lingual or labial sides. It is dominated by the main cuspid, which is positioned toward the buccal side of the tooth and flanked by the anterior and posterior accessory cusps in lateral view. Of these two cusps, the posterior accessory cuspid is larger and taller-crowned.

The p3 is transitional between p2 and p4, as in most carnivorans. The posterior accessory cuspid is more integrated to the main cuspid as does in the p4. The anterior accessory cuspid, however, is more blade-like.

The p4 features prominently enlarged anterior and posterior accessory cusps. The anterior accessory cuspid is blade-like, following the anterior ridge of the main cuspid. This structure is apparently dislocated and rotated in the referred specimen, IVPP V27120. The posterior accessory cuspid is also highly integrated into the posterior ridge of the main cuspid, forming a serrated blade. The p4 is also slightly widened at its posterior end, forming a short talonid basin with the posterior cingular cuspid as its posterior rim, best

seen in IVPP V27120. The p4 posterior accessory cuspid is also buccally positioned, which is a character shared with *S. thailandica* n. sp. from Thailand.

As in *Semigenetta sansaniensis* from La Grive (Viret 1951: pl. I, fig. 17c) and from Captieux (Helbing 1927: fig. 1c), the m1 trigonid of *S. qiae* n. sp. has a straight shearing blade with the paraconid blade lacking a lingual bend as compared to *S. huaiheensis* (Fig. 3). The metaconid is slightly taller than paraconid, whereas most European species have a metaconid equal to or slightly lower than paraconid, as does the Chinese *S. huaiheensis*.

The main distinction of the lower carnassials (m1s) is its relatively large (both length and width) and basined talonid. Although still narrower than the trigonid, the talonid is relatively wider than those of all other species of *Semigenetta*. Related to this enlargement of the talonid is the more basin-like structure with about equal size of the hypoconid and entoconid, both of which are ridge-like and enclosing a shallow basin. This slight hypocarnivorous tendency in *S. qiae* n. sp. is distinguishable from all European species.

A single-rooted m2 alveolus is present in the holotype, but no m2 is preserved in either holotype or referred specimen.

DISCUSSION

In her summary account of Lufeng carnivorans, Qi (1985a) listed up to six species under Viverridae, most of them as unidentified or indeterminate taxa based on fragmentary dental materials. Of these, several isolated teeth of what she tentatively called “Paradoxurinae gen. et sp. indet.” were later described as a new genus and species, *Lufengictis peii* (Qi 2004). Morphologically *L. peii* is a highly hypocarnivorous form with short, low-crowned, bunodont lower molars and quadrate upper molars, and is far removed from the genets. The remaining viverrid taxa in Qi’s list (1985a) cannot be positively matched with materials of *S. qiae* n. sp. because she did not list individual catalogue number.

The presence of a partial P4 and nearly complete left and right M1s in IVPP V27120 allow a brief discussion on the morphology of the upper cheek teeth. In overall dental morphology, IVPP V27120 is quite similar to that of *Viverra modica* Gaillard, 1899 (Viret 1951: fig. 16), *Semigenetta sansaniensis* (Viret 1951: pl. I, figs 17, 18), *S. laugnacensis* (Bonis 1994: fig. 2), and *S. elegans* (Dehm 1950) in its primitive form of triangular outline in M1 with a prominent parastyle.

Of the viverrids Pilgrim (1932: pl. IV) figured, his *Viverra* (?) *chinjiensis* Pilgrim, 1932 has large posterior accessory cusps on p2-4 and seems to share similarities to the Lufeng form. However, this form has a distinctly hypocarnivorous appearance with its relatively large and basined m1 talonid and an elongated m2 with a shortened trigonid and reduced paraconid, as is also the case in *Vishnuictis africana* Morales & Pickford, 2008 (Morales & Pickford 2008). This species has also been recorded elsewhere in South and Southeast Asia (see Grohé *et al.* 2020: 36). Morales & Pickford (2008) noted that this species should be referred to *Vishnuictis*.

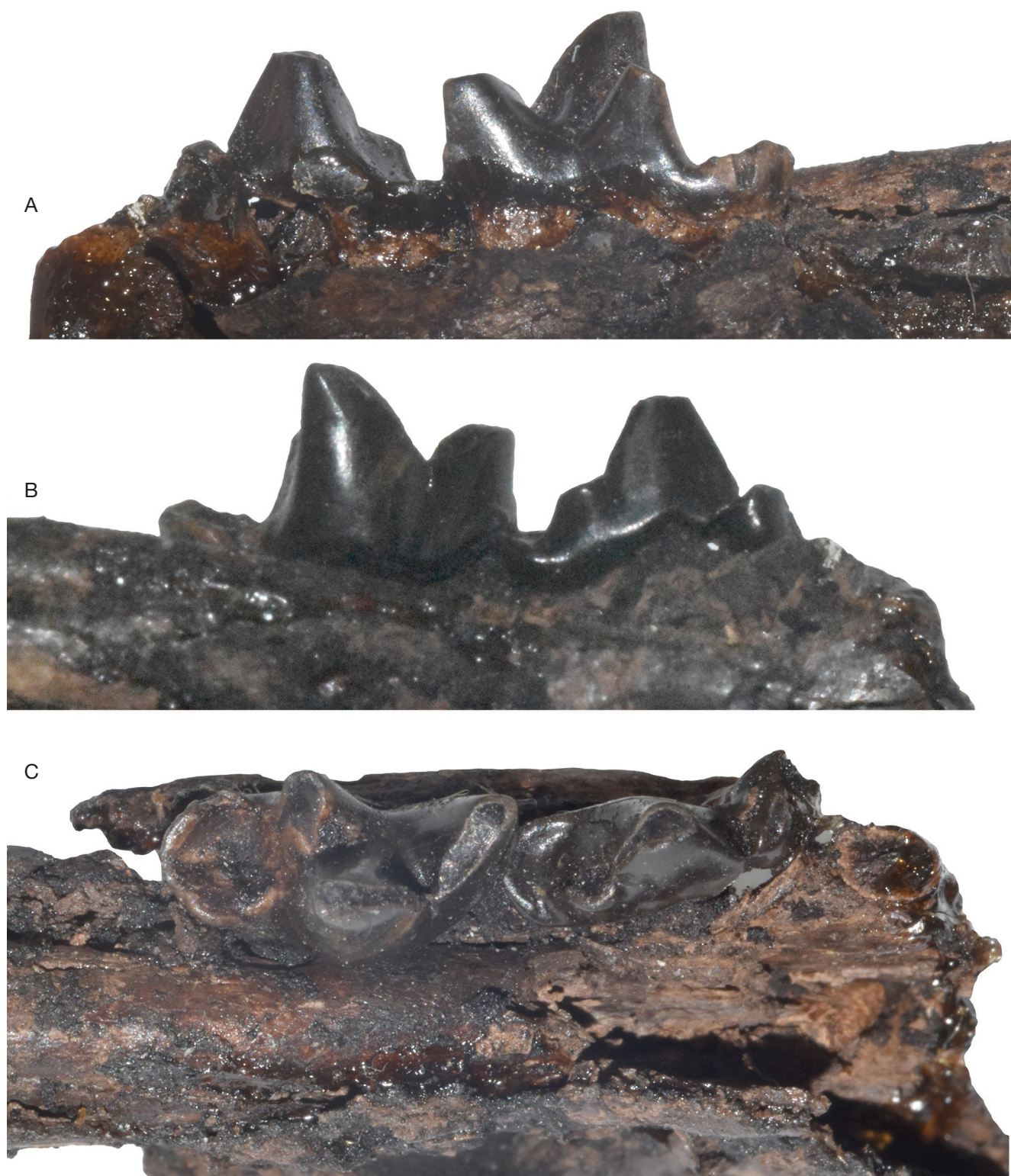


FIG. 4. — *Semigenetta qiae* n. sp., IVPP V27120, fragmentary right dentary with p4-m1: **A**, lingual; **B**, buccal; **C**, occlusal views. Scale bar: 5 mm.

Pilgrim's (1932) *Vishnuictis salmontanus* Pilgrim, 1932, is represented by an articulated skull and jaw and the nature of their teeth is not clear, except a separate jaw fragment. Qi (2006: fig. 3.36-1a) figured a right M1 of *Vishnuictis* cf. *V. salmontanus* from the Yuanmou region. This tooth,

however, is substantially more hypocarnivorous in its much-reduced parastyle and quadrate outline. Whatever this Yuanmou tooth belongs, it shows little resemblance to our referred specimen (IVPP V27120) of *Semigenetta qiae* n. sp. Prasad (1968) named *Vishnuictis hariensis* and *Viverra nagrii* Prasad,

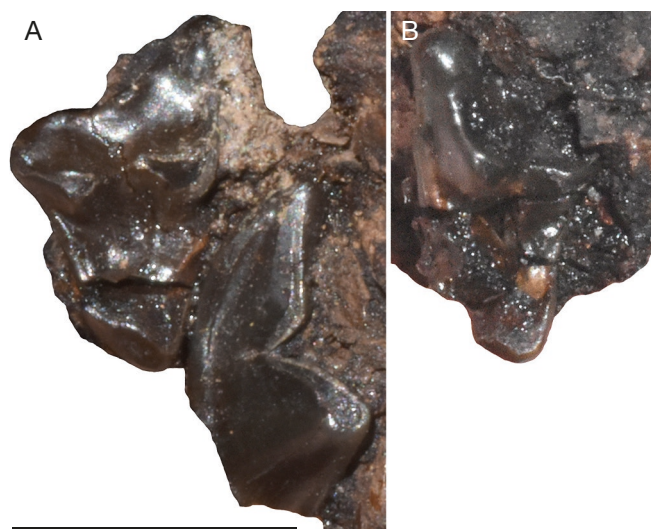


FIG. 5. — *Semigenetta qiae* n. sp., IVPP V27120: **A**, right maxillary fragment with P4 (broken)–M1, occlusal view; **B**, left maxillary fragment with M1, occlusal view. Scale bar: 5 mm.

1968 from Siwalik beds of India. Of these, the latter seems to have a similar p4 posterior accessory cuspid as the Lufeng form, but the material basis of these species are too poor to be certain of their true identity.

Finally, Zong (1997: fig. 5-3) named a new species, *Vishnuictis yuanmouensis*, based on a right mandible (PDYV2519.1) from the Yuanmou area (Loc. 8801, Xiaohe Fangliangzi). Qi (2006: 168) commented that this jaw likely belonged to *Semigenetta*. We did not have an opportunity to examine PDYV2519.1, but it does seem to possess some similarities to *Semigenetta*. However, its distinctly low-crowned premolars and reduced m1 talonid, and relatively large size, may be more consistent with *Aeluropsis* Lydekker, 1884 (Lydekker 1884).

Semigenetta huaiheensis Qiu & Gu, 1986 (Figs 3; 6; Table 1)

Semigenetta huaiheensis Qiu & Qiu, 2013: 147.

Semigenetta elegans – Kargopoulos *et al.* 2021: 25.

MATERIAL EXAMINED. — **Holotype.** China. Songlinzhuang, Sihong area, Jiangsu Province. Sihong Fauna, Xiacaowan Formation; IVPP V8068, partial right dentary with p1 alveolus, p2–m1, and m2 alveolus.

REFERRED SPECIMEN. — IVPP V8069, partially preserved left p4 (Qiu Z.-X. & Gu 1986: 21).

DIAGNOSIS. — Size comparable to the larger individuals of the smallest species of the genus, *S. elegans*, but differs from it by a more trenchant m1 talonid due to a more dominant, cuspid-like hypoconid at the expense of a low and narrow entoconid ridge and the more anterior position of the mandibular foramen. The convexity of the lower border of the lower jaw shows markedly at the level of m2 (modified from Qiu Z.-X. & Gu 1986).

LOCALITY. — China, Songlinzhuang, Sihong area, Jiangsu Province. Sihong Fauna, Xiacaowan Formation (Qiu Z.-D. & Qiu 2013), late Early Miocene Shanwangian (Qiu Z.-X. *et al.* 2013).

COMPARISON AND DISCUSSION

In their original description, Qiu Z.-X. & Gu (1986) considered their *S. huaiheensis* to be closest to *S. elegans* in lower carnassial size, but smaller than *S. sansaniensis*. They noted that the Chinese form has an entoconid ridge on m1 talonid, in contrast to more cuspidate condition in *S. elegans*, and in this feature, it is more comparable to *S. sansaniensis*. In particular, they emphasized the more convex outline, in the initial form of a subangular lobe, in the lower border of the mandible in *S. huaiheensis*, which seemed to differ from all other European taxa and thus constitute one of the main bases of a new species.

Kargopoulos *et al.* (2021), however, suggested that all characters listed in Qiu Z.-X. & Gu (1986) fall within intraspecific variations of European species. Kargopoulos *et al.* further argued that large geographic distance between China and Europe alone should not be a criterion for morphospecies recognition. As a result, *Semigenetta huaiheensis* was synonymized with *S. elegans*.

In evaluating the above controversy, we point out that *Semigenetta huaiheensis* seems to have a more trenchant m1 talonid due to a more dominant, cuspid-like hypoconid at the expense of a low and narrow entoconid ridge (Fig. 3). Apparently based on Dehm's (1950: figs 221–227) published figures, Qiu Z.-X. & Gu (1986) suggested that the type materials for *S. elegans* from Wintershof-West have cuspidate m1 entoconid and hypoconulid, instead of crest-like ones in *S. huaiheensis*, an observation also confirmed by Kargopoulos *et al.* (2021: 31) in their revised diagnosis of *S. elegans*. Kargopoulos *et al.* also noted that materials from other localities seem to show variations of this feature, citing Heizmann (1973) and Viret (1951). Viret's (1951: 69, 70) observation, however, was based on materials of *S. sansaniensis* from La Grive Saint-Alban. Therefore, Qiu Z.-X. and Gu's contrast between *S. huaiheensis* and *S. elegans* may still stand, given that talonid shapes are often a key indicator of evolutionary trends in carnivorans. Such a tendency toward a slightly more hypercarnivorous lower carnassial in *S. huaiheensis* is in contrast to its incipient subangular lobe, which is often associated with more hypocarnivorous dental morphology, such as in basal canine canids *Nyctereutes* Temminck, 1838 and *Urocyon* Baird, 1858 (Tedford *et al.* 2009). If the above observation is correct, there may be grounds to tentatively leave *S. huaiheensis* as a distinct species, pending verification of additional materials in the future.

We are unable to personally examine all the European materials, nor apparently were Kargopoulos *et al.* able to examine the Chinese forms. Overall, it is difficult to evaluate the merits of either side of above arguments, especially since not all published species has high quality photographs and illustrations. While some of Qiu Z.-X. & Gu's (1986) diagnostic characters may fall within the variations of European species, it may be prudent to wait for larger sample to become available, as the only way to fully address this issue is if new and more complete materials become available.



FIG. 6. — *Semigenetta huaiheensis* Qiu & Gu, 1986, IVPP V8086, holotype, right dentary: **A**, lingual; **B**, buccal view. Scale bar: 10 mm.

Regardless of the species status of *Semigenetta huaiheensis*, given its overall morphological similarity to *S. elegans*, it seems likely that the Chinese form represented an early dispersal from Europe to East Asia during the early middle Miocene, as also implied by Kargopoulos *et al.* (2021). Furthermore, because of the distinct morphological differences between *S. huaiheensis* and the new species from middle and late Miocene of China and Thailand described below, we may safely conclude that *S. huaiheensis* was an isolated dispersal event unrelated to the other Asian forms.

***Semigenetta thailandica* n. sp.**
(Fig. 7; Table 1)

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Semigenetta cf. *steinheimensis* – Bonis *et al.* 2021: 324, fig. 3.

MATERIAL EXAMINED. — **Holotype.** Northern Thailand. Lampang Province, Mae Moh Basin; MM-106, partial left dentary with c-p1 alveoli, p2-m1, and m2 alveolus.

DIAGNOSIS. — Middle-sized *Semigenetta*, low ascending ramus of dentary, large masseteric fossa, relatively low premolars, p4 clearly larger than p3, enlarged accessory cusps on p3-p4, weak acces-

sory cusps on p2, small diastema between p2-p3, talonid of m1 slightly narrower than trigonid and with cristid obliqua directed mesiodistally. Differs from other middle-sized *Semigenetta* species: *S. sansaniensis* by p4 clearly larger than p3, p2 less symmetric, larger accessory cusps, smaller p2 mesial cuspid; *S. qiaie* n. sp. by shorter and lower premolars relative to m1, p3 clearly smaller than p4, diastema between p2-p3, p2 with smaller distal accessory cuspid and with much smaller mesial one, wider extent of the masseteric fossa.

ETYMOLOGY. — The species name refers to the country from which the holotype was found.

TYPE LOCALITY. — Northern Thailand, Lampang Province, Mae Moh Basin, Na Khaem Formation in the K coal zone of the Mae Moh coal mine (Bonis *et al.* 2021). The Q and K coal zones of the Na Khaem Formation were magnetically correlated to C5AaR (Coster *et al.* 2010), with a GTS2020 (Raffi *et al.* 2020) calibrated age of 13.363–13.183 Ma in the late middle Miocene.

DESCRIPTIONS

See Bonis *et al.* (2021) for original descriptions and Figure 7 for a new illustration of the holotype.

COMPARISON AND DISCUSSION

Although the top of the ascending ramus is broken, the remaining portion seems to suggest a short ascending ramus, i.e., the posteriorly curved anterior rim of the masseteric



FIG. 7. — *Semigenetta thailandica* n. sp., MM-106, left dentary from Mae Moh, Thailand: **A**, occlusal; **B**, lingual; **C**, buccal views. Scale bar: 10 mm.

fossa is largely intact. If this is correctly interpreted (and confirmed by better materials in the future), it is perhaps the most remarkable feature, which is somewhat felid-like, in contrast to other European species that preserve this part of the morphology. Otherwise, the morphology of this species is generally consistent with *Semigenetta*.

In their description of MM-106, Bonis *et al.* (2021) referred it to *Semigenetta* cf. *S. steinheimensis* (Fraas 1870) because of its similarity in size and age relationship. They used this occurrence in Thailand as an example of long-distance migration from Europe, and they speculated that this species could have dispersed along a corridor around the Tibetan Plateau through either a Central Asian or a southern Asian route into Thailand during the middle Miocene.

Shortly after Bonis *et al.* (2021), Kargopoulos *et al.* (2021) commented that the newly published mandible from Thailand fits the generic diagnosis of *Semigenetta*, particularly regarding

its m1. However, they pointed out differences in its premolars with lower-crowned and shorter main cuspids as well as lower but larger anterior and posterior accessory cuspids. In their opinion, these premolar differences indicate a new species distinct from *S. sansaniensis* (including *S. steinheimensis*, which was synonymized under *S. sansaniensis* within their systematic scheme). Except the crown height in the main cuspid, the enlarged accessory cuspids in premolars in the Thai form is consistent with those in *S. qiaae* n. sp. If the enlarged premolar accessory cusps are considered shared derived character, then a distinct South China-Southeast Asia clade may exist.

Mein & Ginsburg (1997) illustrated a “?*Semigenetta* sp.” from the middle Miocene Li Mae Long of Thailand. However, of the three isolated teeth (identified as right p3, right dP4, and right dp3), none preserve enough diagnostic characters to be certain of their identification. Bonis *et al.* (2021) included the Li Mae Long record in *Semigenetta*.

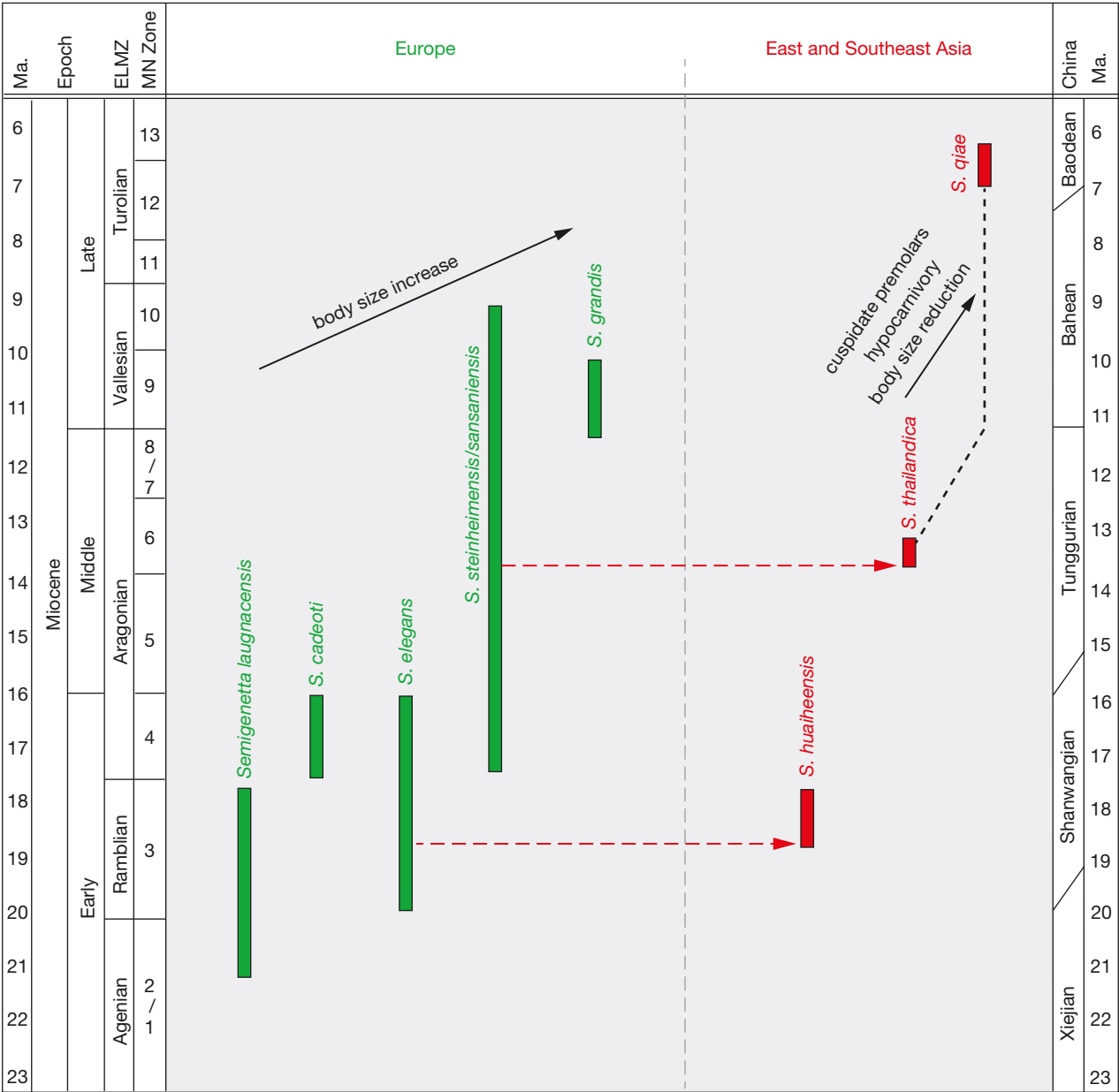


FIG. 8. — Chronologic ranges of Eurasian *Semigenetta* Helbing, 1927 and zoogeographic relationships. **Black arrows** indicate body size trends, which may not be true for all species or from all localities; **red arrows** indicate dispersal events. Species ranges of European taxa and European chronologic framework (European Land Mammal Zone [ELMZ]) follow that by Kargopoulos *et al.* (2021: fig. 1) and Chinese mammal chronology follows that by Qiu *et al.* (2013).

ZOOGEOGRAPHIC
AND ENVIRONMENTAL COMMENTS

Existing knowledge of East and Southeast Asian *Semigenetta*, consisting of largely fragmentary jaws, is still too poor to allow a proper phylogenetic analysis. The following remarks are thus necessarily speculative, pending additional and better materials. Europe is likely a diversification center for *Semigenetta* because of its diversity, continuity and number of *Semigenetta*-producing localities. Asian records still lack far behind with only three records (species) so far, but its chronologic range is roughly comparable to those from Europe, suggesting potential sample biases due to a relatively late start of vertebrate paleontology.

Following Bonis *et al.*'s (2021) and Kargopoulos *et al.*'s (2021) taxonomic frameworks, we envision at least two independent dispersal events, likely from Europe to Asia (Fig. 8). Considering the large chronologic gaps in Asian records, it seems more likely that the Asian appearances represent dispersals from Europe, with the exception of the last record, *S. qiae* n. sp. There are weak evidences that *S. thailandica* n. sp. and *S. qiae* n. sp. belong to an Asian clade, although such a relationship is still highly speculative pending availability of additional and better materials.

Recent phylogenetic studies seem to converge toward a monophyletic clade of *Poiana-Genetta*, which is in turn sister to a clade of *Viverricula-Civettictis-Viverra* (Gaubert *et al.*

2004; Gaubert & Cordeiro-Estrela 2006; Patou *et al.* 2008; Veron 2010; Hassanin *et al.* 2021). Such a relationship led to a hypothesis of Asia as the ancestral area of origins for family Viverridae and also for the Viverrinae clade (Gaubert & Cordeiro-Estrela 2006). No attempt, however, was made to reconcile the molecular relationships and the fossil records.

Within the genet lineage, molecular phylogenetic evidence suggests that African genets diverged about 7.5–8 Ma (Gaubert & Cordeiro-Estrela 2006; Gaubert & Begg 2007). Werdelin & Peigné (2010) listed Beni Mellal (middle Miocene, *c.* 14 Ma), Lothagam (late Miocene to early Pliocene), and Lemudong'o (late Miocene, *c.* 6 Ma) as potentially producing earliest African records of *Genetta*, although these records are represented by too fragmentary materials to be positively identified. The first definitive *Genetta* is found in Kanapoi (early Pliocene) (Werdelin & Peigné 2010). Eurasian *Semigenetta* is unlikely directly ancestral to living *Genetta* because of its early loss of the M2.

So far, records of *Semigenetta* are all from relatively humid environments of either western Europe or southern China and Thailand. *Semigenetta* is conspicuously absent from Central Asian countries and northern China. It thus seems safe to assume that *Semigenetta* likely prefers more wooded environments. Their relatively conservative morphology and low diversity are also consistent with a stable environment with little or no changes. Such a lack of morphological specialization may also be indicative of a generalized, omnivorous diets, perhaps similar to those of modern genets and foxes. *Semigenetta qiae* n. sp. from Lufeng appears to be the last survivor of the genus.

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