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Quaternary *Hystrix* (Rodentia, Mammalia) from North China: Taxonomy, stratigraphy and zoogeography, with discussions on the distribution of *Hystrix* in Palearctic Eurasia

Haowen Tong*

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xi-wai-da-jie, Beijing 100044, China

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Abstract

Today, *Hystrix* is a genus that only occurs in warm areas. However, during the Pleistocene and even the early Holocene, this species frequently appeared in the northern part of China, which belongs to the Palearctic Region. A total of 22 fossil *Hystrix*-bearing localities have been reported in North China, the time span of which covers almost all the stages of Quaternary Period. Among those localities, Tianyuan Cave, a recently discovered locality near Zhoukoudian, contains abundant *Hystrix* materials. This is the latest *Hystrix* record in North China. Currently, two *Hystrix* species have been recognized in North China, *Hystrix subcristata* and *Hystrix lagrelii*. The small porcupine from the Zhoukoudian area should be referred to *H. lagrelii* instead of *Atherurus* as previously proposed by other authors, and therefore the occurrence of *Atherurus* in the Palearctic Region is denied. Based on both fossil and extant records, it seems that *Hystrix* can be generally used as indicator of warm climate.

1. Introduction

It is well known that modern *Hystrix* can survive only in warm areas, but in the past, this animal frequently occurred in North China and other parts of the Palearctic Region. These occurrences of *Hystrix* fossils in North China are obviously evidence of environmental changes. The *Hystrix* fossils discovered in North China are therefore supposed to be important for paleoenvironment reconstructions. This paper deals with a brief introduction to the occurrence of *Hystrix* in North China, including its taxonomy, analysis of fossil materials, and geological ages of the localities. Additionally, the occurrences of *Hystrix* in other parts of Paleoarctic Region are discussed.

2. An overview of the taxonomy of fossil *Hystrix* from North China

Mammalia Linnaeus, 1758
Rodentia Bowdich, 1821
Hystricomorpha Brandt, 1855
Hystricidae Fischer von Waldheim, 1817
Hystrix Linnaeus, 1758

Comments on taxonomy: In North China, the *Hystrix* fossils are usually badly preserved. Because of the lack of representative materials, the taxonomy of *Hystrix* from China is still under debate. Most determinations are based on the tooth size, because the enamel pattern (Fig. 1) is unchanged since the Neogene. "The problem with specific distinction of porcupine teeth is that the occlusal morphology of *Hystrix* has changed little from the Miocene and Pliocene to the Recent. Moreover, occlusal morphology varies individually and shows extreme changes in the successive stages of wear. As a consequence, only size and tooth height can be used for specific distinction" (Van Weers, 2003a). "The number of these folds and their disposition do not change much from one species to

Abbreviations: C.K.T., choukoutien (= Zhoukoudian); Loc., locality

*Fax: +86 10 68337001.
E-mail address: tonghaowen@ivpp.ac.cn

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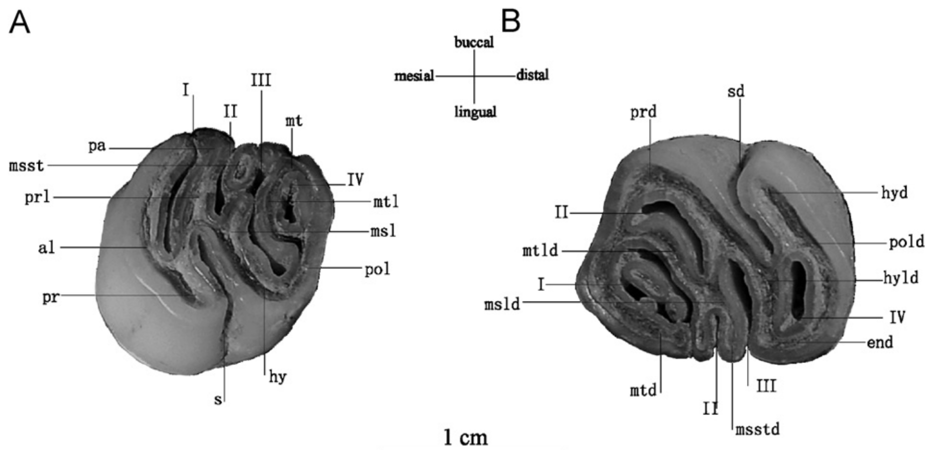

Fig. 1. Nomenclature of the cheek tooth structure of *Hystrix subcristata* (terminology after Van Weers, 1990; Wang and Qiu, 2002; Lopatin et al., 2003). (A) Left M2: al, anteroloph; hy, hypocone; msl, mesoloph; msst, mesostyle; mt, metacone; mtl, metaloph; pa, paracone; past, parastyle; pol, posteroloph, pr, protocone; prl, protoloph; s, sinus; I–IV, fold. (B) Right m1: ald, anterolophid; end, entoconid; hyd, hypoconid; hyld, hypolophid; msld, mesolophid; msstd, mesostylid; mtd, metaconid; mtld, metalophid; pold, posterolophid; prd, protoconid; sd, sinusid; I–IV, fold.

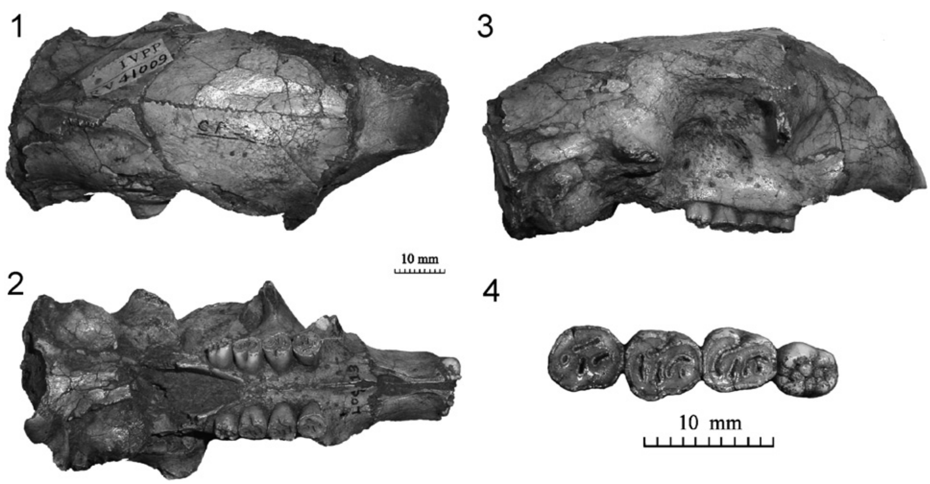

Fig. 2. Skull and upper dentition of *Hystrix lagrelii* from C.K.T. Loc.13. 1, dorsal view; 2, ventral view; 3, lateral view; 4, right upper tooth row (DP4-M3).

another. The conservative occlusal pattern of *Hystrix* cheek teeth does not allow the distinction of species. Nevertheless, the depth of folds, inversely correlative to the degree of hypsodonty, is informative of the evolutionary state of a *Hystrix* population'' (Sen, 1999). Only some very faint differences can be detected between the two *Hystrix* species in North China. *Hystrix subcristata* might have a more complicated enamel structures than *Hystrix lagrelii* (Figs. 1 and 2). However, the identification at the generic level is usually reliable.

H. lagrelii Lönnberg, 1924

1924 *H. lagrelii* Lönnberg, 1–15, pl. I
1936 *H. lagrelii*; Teilhard de Chardin, 20–22, Fig. 10
1941 *H. lagrelii*; Teilhard de Chardin and Pei, 58–61, Figs. 48a, 48b
1959 *H. lagrelii*; Chia, Chao and Li, 48
1976 *H. lagrelii*; Jinniushan Excavation Team, 123–125
1983 *H. lagrelii*; Huang and Guan, 71–72; pl. I, 2

Revised specific diagnosis: The smallest species of the genus *Hystrix*; nasal length, 33.3–40% of the occipito-nasal length, is relatively shorter than in other species; frontals developed; cheek teeth are hypsodont and more rounded in cross section; posterior edge of the palatal bone reaches the line between the middle parts of the two M2s.

Known materials: Two skulls and nine broken mandibles have been found up to now. Only the type specimen was described and published with photos; the fossils from C.K.T. Loc.9 and Loc.13 were published without photographs, only with line drawings (Teilhard de Chardin, 1936; Teilhard de Chardin and Pei, 1941); for the materials

Table 1
Hystrix lagrelii fossil bearing localities in North China

Age	Locality	Materials	Sources
Late Pleistocene	Gezidong	No note	Zhang (1981)
Middle Pleistocene	Jinniushan	No description	Jinniushan Excavation Team (1976)
	C.K.T. Loc.20	Mandibles with dp4-m3	Chia et al. (1959)
	C.K.T. Loc.9	Two mandibles and three teeth	Teilhard de Chardin (1936)
	C.K.T. Loc.13	One skull and three mandibles	Teilhard de Chardin and Pei (1941)
Early Pleistocene	Longya Cave	Partial left mandible with m1-3; partial right mandible with p4-m2	Huang and Guan (1983)
	Mianchi	One complete skull	Lönnberg (1924)

Table 2
Measurements of dentition of *Hystrix lagrelii* (in mm)

Dimensions	Type specimen Mianchi (Lönnberg, 1924)	*Hystrix lagrelii* from Zhoukoudian		
		C.K.T. Loc.13 (Teilhard de Chardin and Pei, 1941)	C.K.T. Loc.9 (Teilhard de Chardin, 1936)	C.K.T. Loc.20 (Chia et al., 1959)
Length of P4-M3	22	20.5	–	–
Length of p4-m3	–	22	21.1	22
Diastema length	–	12.2–12.6	9.2	14.4–15.2
Depth under m3	–	14.5–14.6	15.2	14.3–15
Depth under p4	–	16.6–18.1	17.2	17.3–18.6

from C.K.T. Loc.20, neither descriptions nor measurements are available in the literature.

Known localities: See Table 1.

Geologic age: Early to Late Pleistocene.

Discussion: The length of the tooth row is possibly a reliable feature to identify *H. lagrelii* (Table 2), which is much smaller than that of the other species of this genus. The materials of *H. lagrelii* from C.K.T.Loc.13 were previously referred to *Atherurus* by Zheng (1993). However, recent study supports a referral to *H. lagrelii*, because the hypsodonty of molars confirmed by X-ray scanning (Tong, 2005) is sound evidence to keep this species in the genus *Hystrix* and distinguish it from *Atherurus.* Although the tooth-row length is very close to that of *Atherurus*, which differs from *Hystrix* by the distinctly rooted and brachyodont teeth (Allen, 1940). Moreover, the rostrum and diastema are much longer and the mandibular body is shallower. Thus, there is no record of *Atherurus* in the Palearctic Region.

Post-cranials of *H. lagrelii* are currently not known. At C.K.T. Loc.9 and Loc.13, *H. lagrelii* co-existed with *H. subcristata*, and it seems that no ancestor-descendant relationships exist between these two species. Recently, Van Weers and Zheng (1998) have provided other examples of co-occurrence of different species of *Hystrix* in one locality. The premolars on the skull from C.K.T. Loc.13 and on the two mandibles from C.K.T. Loc.20 are deciduous ones instead of permanent teeth. This was recently confirmed by X-ray scanning.

Until now, *H. lagrelii* had not been found in South China.

H. subcristata Swinhoe, 1870

1979 *Hystrix brachyura subcristata*; Van Weers, 244
1993 *H. subcristata*; Zheng, 115–125
1995 *Hystrix hodgsoni*; Huang et al., 289
1998 *Hystrix kiangsenensis*; Van Weers and Zheng, pp. 47–65 [partim]

Revised specific diagnosis: Nasals long, extending considerably posterior to the level of the lacrymal bone. The outline of the combined nasals is posteriorly broadly convex and the extreme posterior extension in the midline reaches a level with the middle of the orbitotemporal fossa. The upper tooth rows are parallel. The first cheek tooth (P4) is the largest, with its mesiodistal diameter longer than buccolingual diametrer. However, the three molars possess a nearly circular outline (Allen, 1940). Lower incisors prominently curved. Coronoid process of the mandible is strongly reduced.

Known materials: Except two broken skulls from Tianyuan Cave, no other rather complete skull material has ever been found in North China. Most of the materials at hand are either jaw fragments or isolated teeth. Post-cranial bones are only known from the Tianyuan Cave.

Known localities: Table 3.

Early Pleistocene localities: Laochihe; Gongwangling; Nihewan; West Cave near Zhoukoudian.

Table 3
Measurements of dentition of *Hystrix subcristata*, compared with the living species (in mm)

Dimensions	*Hystrix subcristata* from Zhoukoudian area			Living species (Tong, 2005)
	West Cave (Cheng et al., 1996)	Loc.13 (Teilhard de Chardin and Pei, 1941)	Tianyuan Cave (Tong, 2005)	
Length of P4-M3	–	–	–	29–32
Length of p4-m3	36.5	34.5	31–35	31–33

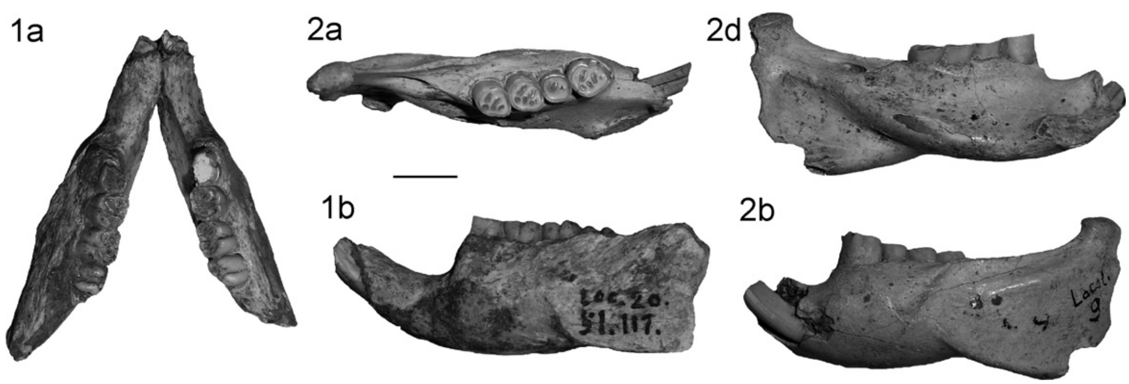

Fig. 3. Mandibles of *Hystrix lagrelii* from C.K.T. Loc.20 and Loc.9. 1, left and right mandibles with dp4-m3; 2, left mandible with p4-m3; 1a, 2a, occlusal view; 1b, 2b, buccal view; 2c, lingual view.

Middle Pleistocene localities: C.K.T. Loc.9; Yunyang in Henan; Chenjiawo; Lantian Xishuidong; Zhoukoudian localities 1, 6, 10, 13 and 20.

Late Pleistocene localities: Zhoukoudian localities 3, 15 and Upper Cave; Shanchengzi in Liaoning.

Late Pleistocene to Holocene locality: The geologic age of the *Hystrix* material from Tianyuan Cave is between 30.5 and 0.467 kyr B.P. (AMS dating), which is the latest record of porcupines in North China (Tong, 2005).

Geologic age: From Early Pleistocene to Holocene, most of the localities are of Middle Pleistocene and Late Pleistocene ages (Fig. 3; Table 4).

Discussion: This species is characterized by long nasals, and can be easily distinguished from *Hystrix javanica*, *H. brachyura* and *Hystrix indica* (Tong, 2005). In North China, most of the *Hystrix* localities are located in the Zhoukoudian area and are of Middle Pleistocene age. For a long time, the *Hystrix* materials from North China were referred to as the living species *H. subcristata*. Several years ago, Van Weers and Zheng (1998) referred the larger *Hystrix* from Zhoukoudian area to an extinct species, *H. kiangsenensis*. Recently, some more materials have been found in Tianyuan Cave, a human fossil-bearing locality near Zhoukoudian. Based on the study of the broken skulls and teeth as well as post-cranials, Tong (2005) suggested that the larger *Hystrix* from North China should rather be identified as *H. subcristata*. Table 3 and Fig. 4 show that the dimensions of the *Hystrix* materials from Zhoukoudian area closely correspond with that of the recent *H. subcristata* and therefore should be considered to belong to the same species. However, the fossil forms are a little larger than the extant ones: the latter's upper cheek tooth-row length is 27–30.3 mm and the lower is 29–32.5 mm (Allen, 1940). A mandible found in the West Cave in Zhoukoudian has a tooth-row length of 36.5 mm (Cheng et al., 1996), and another mandible from C.K.T. Loc.1 has a tooth-row length of 39.5 mm (alveolar). The latter specimen was referred to *Hystrix magna* by Van Weers and Zheng (1998). The present author does not agree with this consideration, since it is based only on dimensions of an isolated specimen and *H. magna* is really a distant species, both in distance and chronology. Concerning the intraspecific size variation, the present author emphasizes the broad size range of *Hystrix cristata* according to the data from Corbet and Jones (1965). They mentioned a range of the occipito-nasal length between 120 and 176 mm, meaning that the maximum is 47% larger than the minimum (Tong, 2004).

The fossil *Hystrix* material from Nihewan, consisting of only one tooth (P4), has not been identified to species level yet (Teilhard de Chardin, 1942).

In some morphological characters, such as the shapes of the nasal process of premaxillaries, nasals and frontals, *H. subcristata* resembles the Mediterranean species *Hystrix cristata*; both of them have slender skulls and the longest nasals inside the Genus *Hystrix* (Tong, 2005). However, *H. cristata* has a higher skull. On the other hand, *H. subcristata* has also some similarities with the Asian species *H. hodgsoni*, but the latter has relatively lower skull and smaller body size. Both these species were referred to

Table 4
Details of the *Hystrix subcristata* bearing localities at Zhoukoudian and other areas in North China

Age	Locality	Taxon determination	Materials	Sources
Late Pleistocene	Tianyuan Cave	*Hystrix subcristata*	Two broken skulls; mandible and fragments; isolated teeth (incisors, DP4, dp4, P4, M1/M2, M3, m1/m2, m3); atlas bones; limb bones (femur, tibia, ulnae, astragalus, Mc V, Mc III, Mt IV and phalanges)	Tong (2005)
	C.K.T. Upper Cave	*Hystrix* sp.	Mandibles and isolated teeth	Pei (1940)
	C.K.T. Loc.3	*Hystrix* sp.	Isolated teeth	Pei (1936)
	C.K.T. Loc.15	*Hystrix* sp.	One tooth only	Pei (1939)
	Shanchengzi	*Hystrix* sp.	No note	Zhang et al. (1986)
Middle Pleistocene	C.K.T. Loc.6	*Hystrix subcristata*	One m1 only	Young (1930)
	C.K.T. Loc.10	*Hystrix subcristata*	No note	Du (1950)
	C.K.T. Loc.1	*Hystrix subcristata*	Three broken mandibles and some isolated teeth	Young (1934)
	Xishuidong	*Hystrix* cf. *subcristata*	No note	Li and Xue (1996)
	Yunyang	*Hystrix subcristata*	No note	Qiu et al. (1982)
	C.K.T. Loc.13	*Hystrix subcristata*	One mandible with p4-m3	Teilhard de Chardin and Pei (1941)
	Chenjiawo	*Hystrix subcristata*	Gnawing marks on other bones	Chow and Li (1965)
	C.K.T. Loc.9	*Hystrix subcristata*	One mandible	Teilhard de Chardin (1936)
Early Pleistocene	Gongwangling	*Hystrix* cf. *subcristata*	One broken skull with P4-M2; one broken mandible with p4-m2; several isolated teeth	Hu and Qi (1978)
	Laochihe in Lantian	*Hystrix subcristata*	Broken maxilla M1-2	Ji (1975)
	C.K.T. West Cave	*Hystrix subcristata*	One mandible with p4-m3, one lower incisor, and one P4	Cheng et al. (1996)
	Nihewan	*Hystricidae*	One tooth only (P4)	Teilhard de Chardin (1942)

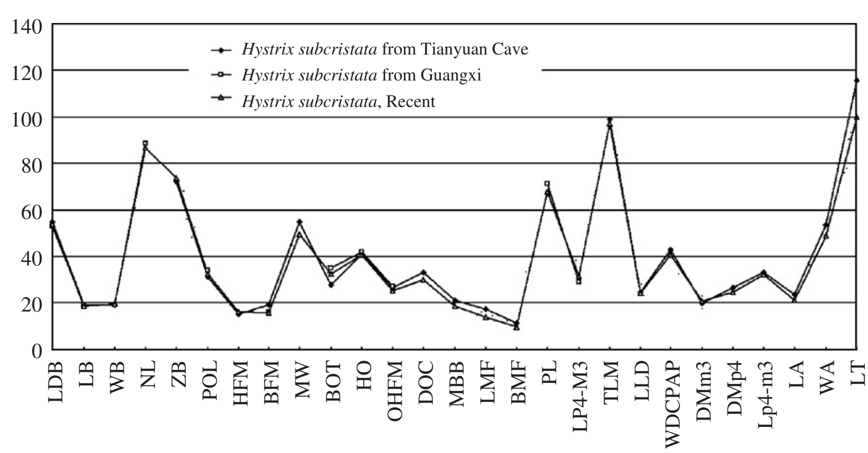

Fig. 4. Metric comparison between the materials from Tianyuan Cave, Guangxi and the recent *Hystrix subcristata*. The three curves are almost completely overlapping. Therefore, the *Hystrix* material from Tianyuan Cave can be referred to *Hystrix subcristata*. Abbreviations: BFM, breadth of foramen magnum; BMF, breadth of mandibular fossa; BOT, breadth of occipital at top; DMm3, depth of mandible below m3; DMp4, depth of mandible below p4; DOC, distance between occipital condyle; HFM, height of foramen magnum; HO, height of occipital; LDB, least distance between bullae; LA, length of atlas; LB, length of bullae; LLD, length of lower diastema; LMF, length of mandibular fossa; LP4-M3, length of P4-M3; Lp4-m3, length of p4-m3; LT, length of tibia; MBB, maximum breadth of basioccipital; MW, mastoid width; NL, nasal length; OHFM, occipital height above foramen magnum; PL, palatal length; POL, parieto-occipital length; TLM, total length of mandible; VDCPAP, vertical distance between condyloid process and angular process; WA, width of atlas; WB, width of bullae; ZB, zygomatic breadth.

the subgenus *Acanthion*, because the extant members of this group have only one black ring or colored part on the quills in contrast to more than one as in the subgenus *Hystrix* (Van Weers, 2003b). However, in skull morphology, *H. subcristata* and *H. hodgsoni* more resemble some species of the subgenus *Hystrix* than the subgenus *Acantion*. Thus, the current taxonomy of these taxa is still questionable.

The tooth-row length of the only complete skull (V10999) referred to *Hystrix magna* is not longer than that of *H. subcristata*. The tooth-row length of the specimen V10999 is 32 mm rather than 38 mm as given previously.

3. Discussion

3.1. Hystrix localities and their chronological sequences

A total of 22 localities with fossil *Hystrix* material have been reported in North China, more than half of which are located in the Zhoukoudian area (Fig. 5). All are situated in today's sub-humid area within the south temperate zone (or warm temperate zone) and the East Asian monsoon region. Therefore, to some extent, *Hystrix* fossils can be employed as evidence for warm and humid, or at least for sub-humid, climate. The reasons why *Hystrix* is absent from the living fauna of North China is still unclear. One possibility is that during the particular phases of the Quaternary, the climate was warmer than today's; another possibility is that human activity caused the disappearance of *Hystrix* from North China.

Most of the *Hystrix* fossils originate from cave deposits. Perhaps this has to do with the ecological habit of porcupines, which prefer to live in caves. However, few *Hystrix* fossil bearing localities are open air ones, such as Mianchi, Nihewan, Gongwangling, Chenjiawo and Yunyang.

There is no record of *Hystrix* fossils from the typical loess deposits. Only several localities are situated at the periphery of the loess plateau, such as the localities in Lantian area. This may indicate that *Hystrix* cannot survive in a loess environment.

The northernmost occurrence of *Hystrix* fossils in China is the locality of Gezidong in Liaoning Province (41°15′N, 124°50′E). However, this is not the northernmost locality of *Hystrix*.

In North China, most *Hystrix* remains are of Middle and Late Pleistocene ages, but the latest *Hystrix* even survived into the Holocene. Only two Neogene localities are known: the Late Miocene locality in Gansu Province (Wang and Qiu, 2002), and the Pliocene locality in Yushe Basin in Shanxi Province (Teilhard de Chardin, 1942). In Early Pleistocene localities, *Hystrix* was more frequent. However, its prime time was in Middle and Late Pleistocene (Fig. 6).

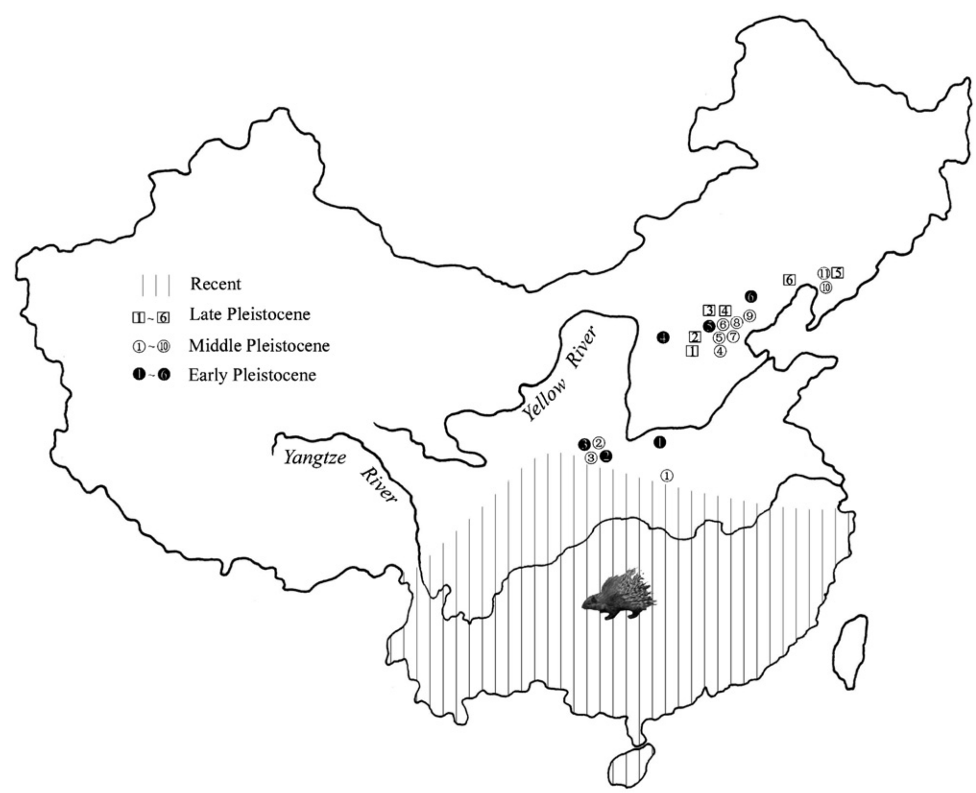

Fig. 5. Distribution map of Quaternary *Hystrix* fossil localities in North China, compared with the distribution pattern of the living form (the hatched area). ❶ Mianchi; ❷ Gongwangling; ❸ Laochihe, Lantian; ❹ Nihewan; ❺ West Cave; ❻ Longya Cave. ① Yunyang; ② Xishuidong; ③ Chenjiawo; ④ C.K.T. Loc.9; ⑤ C.K.T. Loc.13; ⑥ C.K.T. Loc.6; ⑦ C.K.T. Loc.10; ⑧ C.K.T. Loc.20; ⑨ C.K.T. Loc.1; ⑩ Jinniushan; ⑪ Miaohoushan; [1] C.K.T. Tianyuan Cave; [2] C.K.T. Loc.15; [3] C.K.T. Loc.3; [4] C.K.T. Upper Cave; [5] Shanchengzi; [6] Gezidong.

3.2. Distributions of Hystrix in Palearctic Region

In China, the extant *Hystrix* mainly occurs in the eastern region, reaching its northernmost distribution limit at around 33°N. In Central Asia, living populations of *Hystrix* can reach as far north as Tajikistan and Uzbekistan, at around 40°N (Fet and Fet, 2001). In Europe, living *Hystrix* can be found in Italy at around 44°N (Fig. 7).

In the Palearctic Region, most of the *Hystrix* fossil localities are outside of the range of the living forms, which are in the Apennine Peninsula, Caucasus, Near East and Asia Minor (Fig. 7). The northernmost locality is Mokhnevskaya Cave, Alexandrovskii District, Perm Province, Russia, at 59°26′N, 57°41′E (Baryshnikov, 2003). This is very far from the recent *Hystrix* distribution area, and is also isolated from other localities of fossil *Hystrix*. All these localities of extinct *Hystrix* mean that in the past the range of *Hystrix* distribution was much wider, and the climate was much warmer than at present.

Geographically, most *Hystrix* localities in Europe are concentrated in the southeastern part, which is close to the range of living forms. The knowledge of the Quaternary records in Central Asia is still very limited. It seems that *Hystrix* never reached Siberia and the Mongolian Plateau. The only locality far inland is Razboinichiya Cave (Baryshnikov, 2003), a Late Pleistocene locality in Altai, which is not far from Mongolia and Siberia.

Chronologically, most occurrences of *Hystrix* in North China are of Middle Pleistocene age; but in Europe the Late Pleistocene localities are dominant, and only a few Middle Pleistocene localities are known. In the Late Pleistocene, *Hystrix* was widespread in southeastern Europe, but its range contracted very quickly. In Europe all *Hystrix*-bearing localities are older than 40 ka, and the living form of *Hystrix* occupies almost all of Italy. In contrast, northern China has extinct *Hystrix*, which lived around 25 ka B.P. No fossil records of late Late Pleistocene and Holocene *Hystrix* in Europe are known. Thus, there existed a *Hystrix* vacuum between 40 ka B.P. and the present. Some scientists stated that the extant *Hystrix cristata* in Italy was introduced by the Romans as a game animal (Amori and Angelici, 1992).

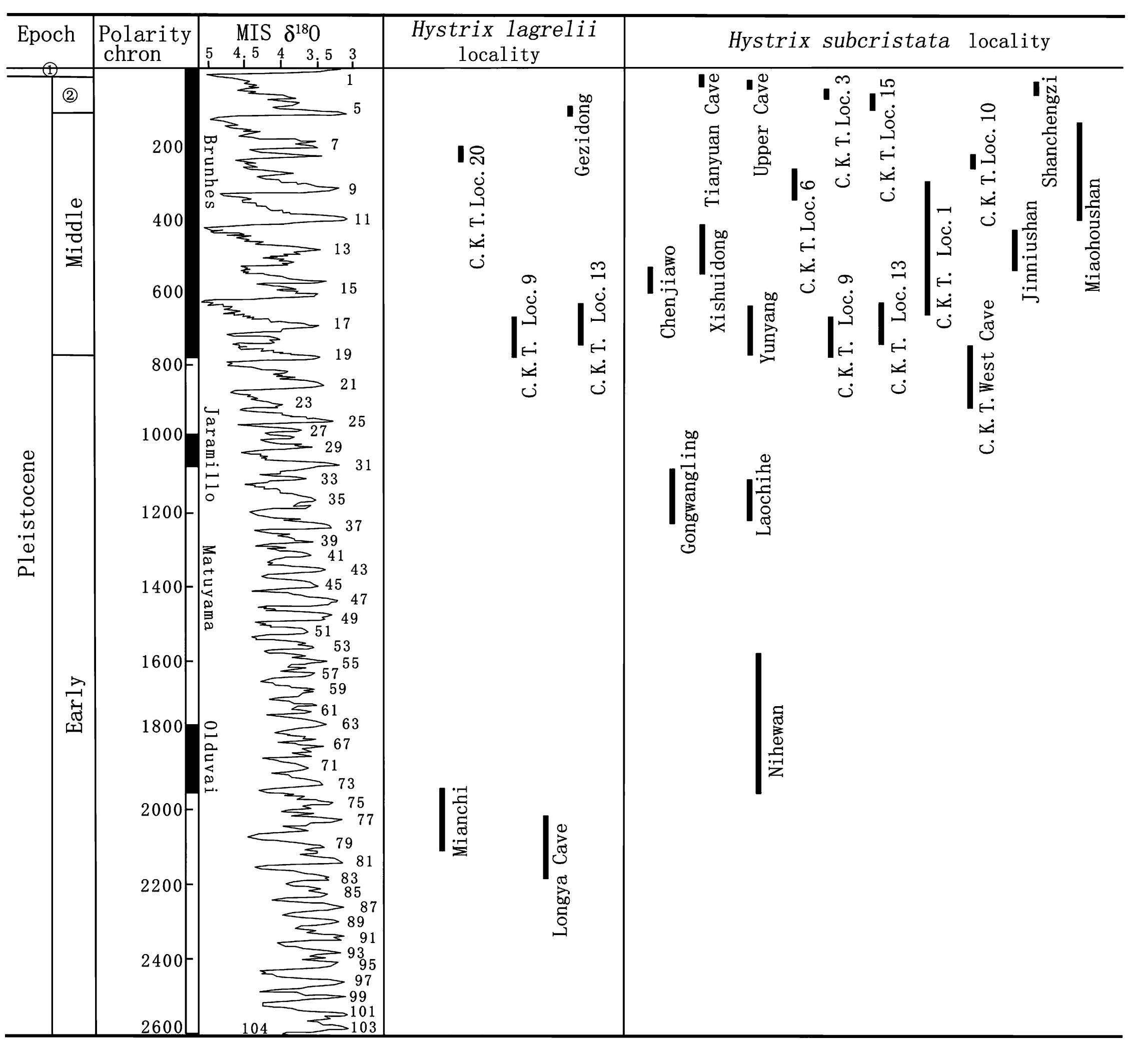

Fig. 6. Stratigraphic range of the Quaternary *Hystrix* bearing localities in North China according to the "Stratigraphical lexicon of China"; ① Holocene and ② Late Pleistocene.

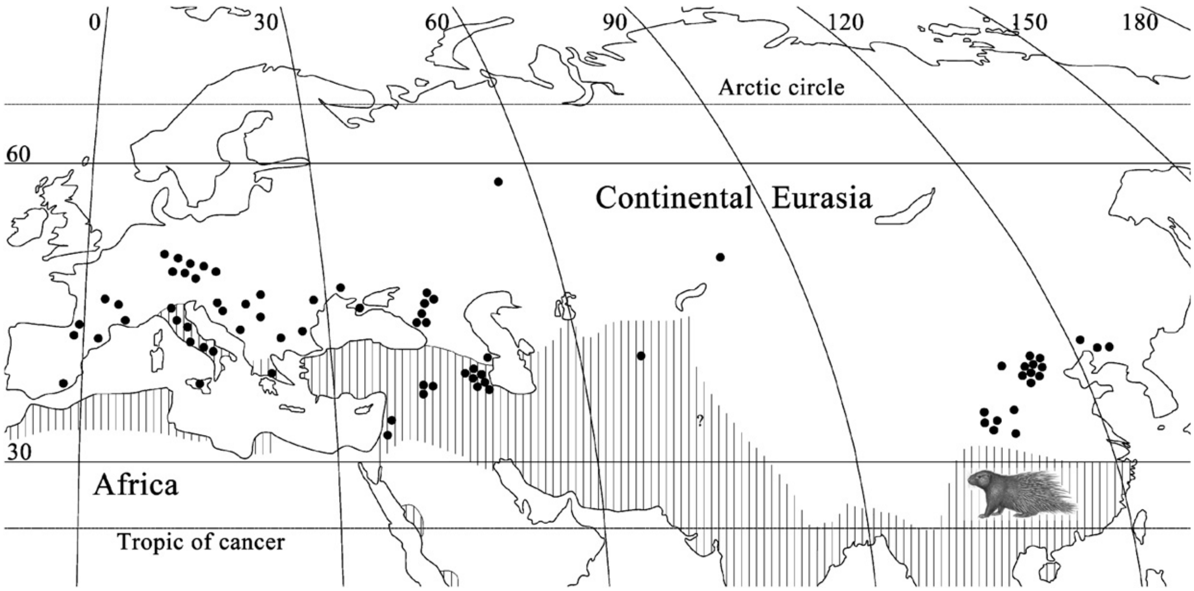

Fig. 7. Distribution map of both fossil and living porcupines in the continental Eurasia. Dots represent the fossil localities in the Palearctic Region; hatched areas represent the living forms (after Van Weers, 1994; Baryshnikov, 2003).

3.3. Paleoenvironmental implications

Based on the current geographical distribution of *Hystrix cristata*, representatives of the family Hystricidae are used as indicators of warm climate. This can be suggested also for the fossil members of this family from North China, because the majority of extinct *Hystrix* coexisted with warm-adapted animals, such as *Macaca* and *Dicerorhinus*. Porcupines are nocturnal animals and they need not less than 7 h for feeding at night. *H. indica* never occurred at latitudes where the minimal night duration is less than 7 h, which limits their distribution. The northern-most populations of this species occur in the Aralo-Caspian region of the USSR at about 44°N, where minimal night duration during summer time is 7.3 h (Alkon and Saltz, 1988). Moreover, the distribution of *Hystrix* is also controlled by temperature because the northern boundary of recent *Hystrix* falls within the zone of annual mean temperature is 10 °C.

These data confirm that *Hystrix* can be regarded as an indicator of warm climate.

4. Conclusions

1. In North China, two *Hystrix* species have been recognized from the Quaternary deposits: *H. lagrelii* and *H. subcristata*.
2. Twenty-two Quaternary localities of *Hystrix* fossils have been found in North China, half in the Zhoukoudian area.
3. Most of the *Hystrix* fossils were from cave deposits in the mountains; few were from open-air sites. There are no *Hystrix* fossils from typical loess deposits. Therefore, *Hystrix* could not survive in cold environments.
4. In North China, most *Hystrix* materials are of Middle and Late Pleistocene ages, and the latest *Hystrix* of the region survived into the Holocene. In contrast, in Europe they are known from deposits not younger than 40 ka.
5. The majority of fossil *Hystrix* coexisted with warm-adapted animals, and the modern distribution area is limited to latitudes lower than 44°N. Extinct *Hystrix* are probably an important indicator of warm climate.

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