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New eggysodontid (Mammalia, Perissodactyla) material from the Paleogene of the Guangnan Basin, Yunnan Province, China

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Key words　Guangnan, Yunnan; Eocene; Yanshan Formation; Eggysodontidae; biostratigraphy

Summary

Rhinocerotoid fossils are relatively abundant in Paleogene deposits in South China. Many previous studies have investigated Paleogene rhinocerotoids from Yunnan Province (Russell and Zhai, 1987; Zong et al., 1996). Zhang (1981) briefly reported some fossils from Xiaoguangnan Village, Guangnan, Yunnan Province, within the Guangnan Basin. Recently, a new specimen comprising a fragmentary left mandible was recovered from the Paleogene of Xiaoguangnan. The new fossil is referable to the rhinocerotoid clade Eggysodontidae. Mainly based on its less molarized p3-p4, the new specimen is regarded as intermediate between the primitive late Eocene taxon *Proeggysodon* and the derived Oligocene genera *Eggysodon* and *Allacerops*. Here we describe the new specimen and discuss the age of the Yanshan Formation. Terminology used to describe dental features follows Qiu and Wang (2007).

Order Perissodactyla Owen, 1758

Superfamily Rhinocerotoidea Gray, 1825

Family Eggysodontidae Breuning, 1923

Guangnanodon gen. nov.

Type species　*Guangnanodon youngi* gen. et sp. nov.

Included species　Only the type species.

Diagnosis　Same as for the type species.

Etymology　From “Guangnan”, where the fossil site is located.

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Guangnanodon youngi **gen. et sp. nov.**

(Fig. 1)

Holotype GNV-001, fragmentary left mandible with p3-m3, housed in Nationalities Museum of Guangnan County.

Type locality and horizon Xiaoguangnan Village, Liancheng Town, Guangnan County, Yunnan Province, China; Yanshan Formation.

Etymology The specific name honors Prof. Yang Zhongjian (C. C. Young), the founder of vertebrate paleontology in China, who initiated the studies of Paleogene stratigraphy of Yunnan Province.

Diagnosis Small eggysodontid. Moderately molarized lower premolars with weak entoconids and relatively complete entolophids on p3-p4; hypolophids slightly anterolingually oblique on p4 and m2; trigonid of m3 nearly as V-shaped as that of m2. Cingulids distinct at anterior and posterior bases of m1-m3. Buccal cingulids weak and continuous on p3, but interrupted at bases of protoconids and hypoconids of p4-m3; lingual cingulids interrupted at bases of metaconids of p3-p4, and only present in valley between metaconid and entoconid on m1-m3.

Description The fragmentary left mandible belonged to an old individual, and retains p3-m3. The left mental foramen is situated below the anterior end of p3. The length of the lower molar series is 85.5 mm. Measurements of the cheek teeth are given in Table 1.

The p3 is trapezoidal in occlusal outline, widening posteriorly. The trigonid is elongated, having a conical paraconid and a short paralophid that is fused with the anterior cingulids. The protolophid extends anterolingually, forming an obtuse angle (about 100°) with the posterolingually oblique metalophid. The talonid is shorter and wider than the trigonid. The entoconid is low and small. The entolophid tapers lingually and joins the hypolophid at nearly a right angle. The buccal cingulid is weak but continuous. The lingual cingulid surrounds the trigonid and talonid but is interrupted at the base of the metaconid.

The p4 has a rounded rectangular outline in crown view. This tooth differs from p3 in being larger, and in having a longer paralophid, a more distinct hypoconid and entolophid, and an acute angle (about 75°) between the protolophid and metalophid. The hypolophid extends anterolingually, at the highest level in all teeth, and contacts the metalophid at a point about one third of the way from the buccal end of the metalophid to the lingual end. The cingulids are similar to those of p3, but the buccal cingulids are interrupted at the bases of the protoconid and the hypoconid.

The m1 is heavily worn, and its anterobuccal part is damaged. It is similar to p4 in morphology, but differs from p3-p4 in having a more strongly developed entoconid and entolophid, a transversely aligned metalophid and entolophid, and a weak lingual cingulid that is only present in the valleys of the talonid.

The m2 is larger than m1. The paralophid is short, and its lingual part is slightly damaged. The protolophid extends anterolingually from the protoconid to the midpoint of the anterior border of the tooth. The metalophid extends anterorbuccally and forms an acute angle (ca. 70°) with the protolophid. The hypolophid contacts the metalophid at a point about one quarter of the way from the buccal end of the metalophid to the lingual end. The cingulids are similar to those of m1.

The m3 is slightly longer than m2. The trigonid is very morphologically similar to that of m2. The tooth has a high paralophid and a deep valley. In the trigonid, the protolophid and metalophid form an angle that is only slightly acute (about 80°). The anterior end of the hypolophid reaches the metalophid, and the point of contact is low on the latter structure.

Comparison and discussion GNV-001 resembles previous described eggysodontids in having an anterolingually oblique protolophid, an acute angle (about 70°–80°) between the protolophid and the metalophid, a nearly V-shaped trigonid, the anteriorly subdued hypolophid contacting the metalophid at a low point on m3, and buccal cingulids that are interrupted at the bases of the protoconids and the hypoconids on the lower molars. These morphological features indicate that GNV-001 is referable to Eggysodontidae, which contains three previously described genera: *Proeggysodon*, *Eggysodon* and *Allacerops* (Bai and Wang, 2012).

Some intergeneric differences are known between *Eggysodon* and *Allacerops*. Four morphological differences have been postulated to distinguish *Eggysodon* from *Allacerops*: 1) *Allacerops* has three pairs of lower incisors while *Eggysodon* had two; 2) p1 is present in *Allacerops* but absent in *Eggysodon*; 3) the lower cheek teeth of *Eggysodon* are labiolingually narrower than those of *Allacerops*; 4) the lower cheek teeth have pronounced and continuous buccal cingulids in *Eggysodon*, but rarely in *Allacerops*. The first two purported differences were proposed by Reshetov et al. (1993), and the last two were added by Qiu and Wang (1999).

However, intrageneric variations affect all four suggested points of morphological difference between *Eggysodon* and *Allacerops*, and make the two genera less readily distinguishable from each other. Regarding the first point, Borsuk-Bialynicka (1968) erected *Allacerops minor*, which differs from the previously described species *A. turgaica* in having only two pairs of lower incisors. Furthermore, Antoine et al. (2011) reported that *E. gaudryi* from Moissac, southwest France, had three pairs of lower incisors. The fact that p1 is present in some *Eggysodon* specimens weakens the second point (de Bonis and Brunet, 1995). Data from *A. turgaica* specimens from Tort-Mola and Chelkar-Tenis (Reshetov et al., 1993) show the width/length ratios of the lower cheek teeth are more variable in *Allacerops* than in *Eggysodon* (Fig. 2). Regarding the last point, the buccal cingulids of the lower cheek teeth of *Eggysodon* osborni may be either weak and discontinuous (Uhlig, 1999), or distinct (de Bonis and Brunet, 1995), while in *Allacerops turgaica* the lower premolars have well developed buccal cingulids and the lower molars have moderately developed ones (Reshetov et al., 1993). However, all above variations happen only in a few cases and are probably at the intrageneric level. Here we consider both genera valid, and compare them separately with GNV-001.

The European Oligocene genus *Eggysodon* includes four species: *E. osborni*, *E. gaudryi*, *E. rechenaui* and *E. pomeli*. *Eggysodon* is more derived than GNV-001 in having more strongly developed entoconids and complete entolophids on p3-p4. In addition, the trigonid of m3 is V-shaped in GNV-001, resembling the trigonid of m2, but U-shaped in *Eggysodon*. Of the four species of *Eggysodon*, GNV-001 is most similar to *E. osborni*, resembling this species in size and in the presence of short paralophids and discontinuous buccal cingulids. However, *E. osborni* differs from GNV-001 in sharing the derived features of p3-p4 that are characteristic of *Eggysodon*. GNV-001 differs from *E. gaudryi* in being smaller and in having weaker, discontinuous buccal cingulids, shorter paralophids and V-shaped trigonids on m2-m3. *E. rechenaui* differs from GNV-001 in having remarkably long paralophids. Although the lower cheek teeth of E. pomeli are unknown, GNV-001 is markedly smaller than this species, which is the largest species of the genus *Eggysodon*. These comparisons suggest that GNV-001 represents an eggysodontid that is more primitive than the Oligocene *Eggysodon*.

Previously known Asian eggysodontids include the late Eocene *Proeggysodon* and the Oligocene *Allacerops*. GNV-001 is more derived than *Proeggysodon* in being larger and in having more extensively molarized lower premolars with relatively complete entolophids on p3-p4. In addition, GNV-001 can be readily distinguished from *Proeggysodon* based on the presence in m2-m3 of shorter paralophids, protolophids extending further lingually, more oblique entolophids, and distinct buccal cingulids at bases of the trigonids. *Allacerops* includes *A. turgaica* and *A. minor*. The lower cheek teeth of *Allacerops* are morphologically rather similar to those of *Eggysodon*, and p3-p4 appear more primitive in GNV-001 than in *Allacerops*. GNV-001 differs from a specimen of *A. turgaica* from Tort-Mola (Reshetov et al., 1993) in being smaller, in having shorter talonids on p3-p4, and in that m2 and m3 are subequal in size. GNV-001 differs from *A. minor* in being smaller, in having hypolophids that extend further lingually on p4 and m2, and in having more distinct buccal cingulids.

The lower molars of GNV-001 are evidently characteristic of Eggysodontidae in their overall morphology. However, GNV-001 differs from all three reliably established genera in the family in having moderately molarized lower premolars (p3-p4). GNV-001 appears to be an eggysodontid of intermediate evolutionary grade, more derived than *Proeggysodon* and more primitive than *Eggysodon* and *Allacerops*. Therefore, we erect a new genus and species (*Guangnanodon youngi* gen. et sp. nov.) for GNV-001.

The age of *Guangnanodon* and the Yanshan Formation The moderately molarized lower premolars of *Guangnanodon* suggest that this taxon is probably intermediate in age between *Proeggysodon* on the one hand and *Eggysodon* and *Allacerops* on the other. In Asia, *Proeggysodon* was unearthed in Upper Eocene sediments (Bai and Wang, 2012), while *Allacerops* is from the Lower Oligocene (Daxner-Höck et al., 2010). The oldest specimens of *Eggysodon* are from the lowermost Oligocene (MP1) of Europe (Uhlig, 1999). Accordingly, *Guangnanodon* is probably latest Eocene in age, although more evidence will be needed to confirm this.

Zhang (1981) mentioned several fossils from the Yanshan Formation of the Guangnan Basin, *Urtinotherium* cf. *U. intermedium* unearthed from Lianfeng, and *Prohyracodon* sp. and

Caenolophus sp. unearthed from Xiaoguangnan Village. The bed containing *Urtinotherium* cf. *U. intermedium* probably correlates with a level within the middle to Upper Eocene Caijiachong Formation, which yielded the *Urtinotherium intermedium* (= *Indricotherium intermedium*) material described by Chiu (1962)(Tong et al., 1995; Wang, 1997; Qiu and Wang, 2007). *Prohyracodon* is one of the diagnostic taxa of the middle Eocene Sharamurunian Land Mammal Age (Tong et al., 1995), while the type of *Caenolophus* is from the Shara Murun Formation of North China (Radinsky, 1967). GNV-001 is probably latest Eocene in age, making it younger than the other specimens from the Guangnan Basin. Accordingly, the Yanshan Formation, at least, contains sediments of ages that range from late middle Eocene to latest Eocene.

云南广南古近纪紧齿犀类新材料

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摘要：记述了云南广南盆地古近纪砚山组紧齿犀科(Eggysodontidae)一新属种：杨氏广南犀*Guangnanodon youngi* gen. et sp. nov., 标本为一破损的带p3-m3的左下颌骨。新属种的特征为下前臼齿的臼齿化程度低，p3-p4的下内脊弱，向内收缩呈尖叶状，p4和m2的下次脊略偏向内侧倾斜，m3的下跟座与m2的相近，接近V形，p4-m3外齿带在下原尖和下次尖基部消失。这些特征表明广南犀明显比晚始新世的*Proeggysodon*进步，而比渐新世的其他紧齿犀类原始，其时代很可能为晚始新世最晚期。新标本的发现结合以前报道过的哺乳动物化石材料表明，广南盆地砚山组包含了中始新世晚期至晚始新世晚期的沉积。

关键词：云南广南，始新世，砚山组，紧齿犀科，地层时代

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1　研究历史

犀类是古近纪陆生哺乳动物中较为繁盛的一个类群，在中国南方古近系中有不少化石记录。自20世纪50年代起，以周明镇先生为代表的古生物学家对云南古近纪哺乳动物化石的研究取得了较为丰富的成果。研究区域以滇东地区(石林和曲靖等地)为主，还包括横断山区的丽江等地。

石林(原名路南)地区是云南古近纪哺乳动物化石发现较多、研究程度较高的地区之

一，犀类化石丰富，其中两栖犀类的属种相对较多，还包括貘犀类、蹄齿犀类、巨犀类以及柯氏犀类。化石主要产自中始新世路美邑组，已经发表的奇蹄类属种包括：两栖犀类*Caenolophus medius*, *Caenolophus* sp., *Amynodon lunanensis*, *A. altidens*, cf. *Paramynodon* sp., *Teilhardia pretiosa*, ?*Teilhardia* sp., ?*Paracadurcodon* sp. (Chow, 1957; 周明镇等，1964; 徐余瑄，1966; 郑家坚等，1978; Russell and Zhai, 1987); 貘犀类*Hyrachyus lunanensis*, *H. minor* (黄学诗、齐陶，1982); 蹄齿犀类(当时归入真犀类) *Prohyracodon meridionale*, *P. progressa*, *Ilianodon lunanensis* (周明镇、徐余瑄，1961); 巨犀类*Juxia* sp., *Urtinotherium parvum* (= *Indricotherium parvum*)(周明镇，1958; 徐余瑄、邱占祥，1962; 郑家坚等，1978); 柯氏犀类*Forstercooperia shiwopuensis* (周明镇等，1974)。晚始新世小屯组产奇蹄类化石Hyracodontidae indet., cf. *Gigantamynodon giganteus* (Russell and Zhai, 1987)。曲靖地区古近纪哺乳动物化石也较丰富，犀类化石包括：*Urtinotherium intermedium*, *U. parvum*, *Cadurcodon ardynensis*, *Cadurcodon* sp., *Gigantamynodon* sp., *G. giganteus*, cf. *Metamynodon* sp., Amynodontidae indet.以及*Prohyracodon* sp. (徐余瑄，1961; 邱占祥，1962; 汤英俊，1978; 张玉萍等，1978; 郑家坚等，1978; 王伴月、张玉萍，1983; Russell and Zhai, 1987)。在滇西北丽江盆地和格木寺盆地，发现的古近纪犀类化石有*Sianodon* sp., Amynodontidae gen. et sp. indet., *Prohyracodon major*, *P. meridionale*, *Caenolophus proficiens*, *Lijiangia zhangi* (宗冠福等，1996)。此外，张兴永(1981)以消息的形式记录了广南地区古近纪的犀类化石，包括：*Urtinotherium* cf. *U. intermedium* (= *Indricotherium* cf. *I. intermedium*), *Prohyracodon* sp., *Caenolophus* sp.。丰富的化石记录为云南地区的古近纪生物地层研究提供了较好的材料基础。

20世纪80年代在云南广南县小广南古近纪地层(砚山组)中发现了一段不完整的紧齿犀类下颌，现收藏于云南省广南县博物馆。这是在广南盆地发现的为数不多的哺乳动物化石之一，同时也是中国南方首次发现的紧齿犀类材料。本文对该标本进行描记报道，犀超科的分类以及牙齿描述所用术语依邱占祥、王伴月(2007)。

2 系统古生物学

奇蹄目 Perissodactyla Owen, 1758

犀超科 Rhinocerotoidea Gray, 1825

紧齿犀科 Eggysodontidae Breuning, 1923

广南犀(新属) *Guangnanodon* gen. nov.

属型种 杨氏广南犀(Guangnanodon youngi gen. et sp. nov.)。

包括种 仅属型种。

特征 同属型种的特征。

属名来源 属名源自化石发现地点所在县——广南(Guangnan)。

杨氏广南犀(新属新种) *Guangnanodon youngi* gen. et sp. nov.

(图1)

正型标本 左下颌具p3-m3, m1的颊侧前端部分破损，冠面磨蚀严重。云南省广南

县博物馆标本编号：GNV-001。

产地及时代 云南广南县莲城镇小广南村，砚山组。

特征 小型紧齿犀类。下前臼齿臼齿化程度低，p3-p4的下内尖低于下次尖，二者连成弱的下内脊；p4和m2的下次脊向前内侧延伸；m3下三角座与m2的相近，接近V形。齿带中等发育，前、后侧齿带明显，p3的外齿带弱而连续；p4-m3的外齿带在下原尖和下次尖基部消失；p3-p4内齿带在下后尖基部消失，下臼齿内齿带仅在下跟座开口处有微弱分布。

种名来源 种本名献给最早开展云南古近纪地层研究的杨钟健院士，以纪念他对云南地区古近纪生物地层学研究所做的贡献。

标本描述 标本为一件保存了p3-m3的破损下颌，p3前缘下方可见一颏孔。GNV-001的下臼齿列长度为85.5 mm, 颊齿测量数据见表1。

图 1 杨氏广南犀(新属新种)左下颌骨(GNV-001)

Fig. 1 Fragmentary left mandible of *Guangnanodon youngi* gen. et sp. nov. (GNV-001)

A. 颊侧视 buccal view; B. 冠面视 crown view; C. 舌侧视 lingual view p3: 冠面为前窄后宽的梯形。下三角座长大于宽，由前往后变宽。下前尖呈圆锥状，下前脊短，与前齿带融合，下原脊从下原尖向前延伸，稍向内倾斜；下后脊向内后方倾斜，与下原脊交角约100°，与牙齿长轴交角约50°，是横脊中斜度最大的。下跟座为L形，长度小于下三角座，宽度大于下三角座。下内尖弱，位置比下次尖低，下内脊弱，从下次尖到下内尖逐渐收缩成尖角状；下次脊近似与齿列长轴平行，下次中凹不明显。外齿带弱而连续，内齿带包围下三角座和下跟座，在下后尖基部消失。

p4: 基部呈近似圆角的长方形，前后近似等宽，比p3长、宽。下三角座呈U形，宽稍大于长。下前脊比p3的长，下原脊更向内侧延伸，与下前脊的交角约120°，与下后脊的交角约75°。下后脊比下原脊长，向后的斜度小于p3。下次脊向内倾斜，相交于下后脊的外1/3处。下内尖和下内脊比p3的发育。齿带与p3的相似，但外齿带在下原尖和下次尖的基部消失。

m1: 磨蚀程度较高，下三角座外侧破损，长度大于下跟座。下内尖和下内脊比下前臼齿的发育，下内脊近似与齿列长轴垂直，下次脊与下内脊近于直角相交。外齿带发育状况与p4相近，但内齿带仅在下跟座开口处有微弱分布。

m2: 长、宽都大于m1, 前后宽度相同。下前脊短，前内侧部分轻微破损，下原脊从下原尖向前内方延伸至牙齿前缘中点附近，与下后脊交角70°，下后脊向内后方倾斜，倾斜程度与p4的相近。下次脊向内倾斜程度小于下原脊，相交于下后脊的外1/4处。下内尖和下内脊发育，下内脊由下内尖向前外侧延伸，与下后脊平行；下次脊长度约为下内脊的一半，二者以较圆滑的角连接，下跟座的冠面轮廓呈V形。齿带与m1的相同。

m3: 与m2相似，但比m2稍长。下前脊的位置较高，使下三角座形成比较深的凹坑，下原脊与下后脊交角约为80°，下三角座整体近似V形。下后尖有微弱收缩的迹象，下次脊向前延伸与下三角座接触的位置较低，且比m2的略偏向外侧。齿带发育状况与m2相同。

比较和讨论 GNV-001的下颊齿与两栖犀类的区别明显，后者下颊齿明显窄长，外壁几乎平直，横脊短且向后倾斜显著(Wall, 1989)。貘犀类(如*Hyrachyus*)与蹄齿犀类原始类群(如*Triplopus*)的下颊齿形态相似(邱占祥、王伴月，2007), 它们以个体较小，下前臼齿的下次尖孤立，下内尖不发育，无下内脊等特征与新标本相区别。蹄齿犀类后期进步类型(如*Hyracodon*, *Triplopides*, *Epitriplopus*和*Ardynia*)的p3-p4下内脊发育接近完整，下颊齿的下前脊相对较长，下原脊与下后脊交角近似直角(*Ardynia*除外，其下三角座呈V形), 齿冠有变高的趋势(Radinsky, 1967; 邱占祥、王伴月，2007), 也与新标本不同。巨犀类的p3-p4下跟座长，下颊齿下原脊向内倾斜不明显，m2的下次脊向前侧延伸，m3的下三角座呈U形，个体较大(Lucas and Sobus, 1989), 与GNV-001区别明显。

新材料下颊齿形态与真犀类典型的“U, L”型有明显的差别。广南犀p4和m2的下次脊都向内倾斜，尤其是m2和m3的下三角座，下原尖的位置靠内侧，且下前脊短，下三角座呈V形。此外，目前欧亚大陆以及北美地区已知的晚始新世至早渐新世的真犀类群和广南犀也明显不同(Antoine et al., 2003): 如*Teletaceras*的下前臼齿臼齿化程度较低，p3和p4的下内尖小，下内脊不完整，下臼齿内、外侧无齿带，m3的后齿带很弱或缺失(Hanson, 1989); *Guixia*的下颊齿呈长方形，下原脊与下后脊、下次脊与下内脊的交角约为直角，下三角座长、宽都大于下跟座，齿带不发育(尤玉柱，1977); *Subhyracodon*

的p3尚未完全臼齿化，下内尖不发育，下跟座窄，但p4已完全臼齿化(Scott, 1941); *Epiaceratherium*的p3和p4下原脊与下后脊交角近似呈直角，p4的下内脊稍向后倾斜，下颊齿无内侧齿带(Uhlig, 1999); *Ronzotherium*的p3下次脊较弱，p4接近完全臼齿化，下颊齿内齿带通常发育且连续(Dashzeveg, 1991); *Trigonias*的p4臼齿化程度较高，形态与下臼齿接近，为典型的真犀类“U, L”型，个体也明显比GNV-001大(Scott, 1941)。

根据个体大小和形态特征，与新标本最接近的类群有柯氏犀亚科(Forstercooperinae)、原蹄齿犀属(*Prohyracodon*)和紧齿犀科(Eggysodontidae); 而柯氏犀类、原蹄齿犀属以及宜良犀属(*Ilianodon*)也被一些学者归入到紧齿犀大类中(Heissig, 1989; Dashzeveg, 1996)。柯氏犀类的*Pappaceras*下前臼齿形态相对原始，p3和p4的下后脊向后倾斜明显，下跟座短，下内脊几乎不发育，下臼齿下原脊与下后脊交角约为直角，与GNV-001容易区分。原蹄齿犀的下颊齿材料不多，但该属的个体较小，下前臼齿臼齿化程度低，下前脊中等长度或较长，下原脊几乎不向内侧延伸(Dashzeveg, 1991), 与GNV-001区别明显。宜良犀下前臼齿较为原始，下颊齿整体窄长，向后急剧变大，m3下三角座呈U形，与新标本差别较大(周明镇、徐余瑄，1961)。GNV-001下颊齿的下前脊短，下原脊向内倾斜明显，下原脊与下后脊交角70° ~80° ,下次脊与下后脊相交的位置较低；p3的外齿带弱而连续，内齿带在下后尖基部消失，p4-m3的外齿带在下原尖和下次尖基部消失，这些特征与紧齿犀类相似。

表 1 *Guangnanodon*, *Eggysodon*, *Allacerops*和*Proeggysodon*的下颊齿(p3-m3)测量数据比较

Table 1 Measurements of lower cheek teeth (p3-m3) of *Guangnanodon*, *Eggysodon*, Allacerops and Proeggysodon (mm)

	p3			p4			m1			m2			m3		
	L	W	W/L (%)	L	W	W/L (%)	L	W	W/L (%)	L	W	W/L (%)	L	W	W/L (%)
Guangnanodon youngi	21.5	15.8	73.5	22.8	17.4	76.3	24.0	18.6	77.5	28.8	21.0	73.0	29.8	21.5	72.1
Eggysodon osborni (Möhren)	19.0	13.0	68.4	21.0	14.5	69.0	23.0	16.5	71.7	25.0	17.0	68.0	25.0	17.0	68.0
E. osborni (Kleinblauen)	21.0	16.0	76.2	23.0	17.0	73.9	24.0	18.0	75.0	29.0	20.0	69.0	29.0	19.0	65.5
E. gaudryi (Latou)	25.5	17.0	66.7	26.0	18.5	71.1	28.0	21.0	75.0	30.5	22.0	72.1	30.0	21.5	71.7
E. gaudryi (Puylaurens)	26.5	18.5	69.8	28.0	20.0	71.4	28.5	19.0	66.7	32.0	22.5	70.3	33.5	22.0	65.7
E. reichenaui							25.0	17.5	70.0	28.0	19.0	67.9			
Allacerops turgaica (Tort-Mola)	24.8	20.8	83.9	24.0	21.7	90.4	29.9	26.4	88.3	33.2	26.3	79.2	33.0	23.8	72.1
A. turgaica (Chelkar-Tenis)-min	21.5	16.5	70.0	23.0	17.0	70.8	22.0	22.0	73.3	34.0	24.0	72.0	35.0	22.0	62.8
A. turgaica (Chelkar-Tenis)-max	25.0	17.5	80.0	26.5	20.0	87.0	32.5	25.0	100.0	35.0	25.0	83.0	37.5	24.5	78.0
A. minor	21.5	17.0	79.1	27.0	22.0	81.5	31.0	23.0	74.2						
Proeggysodon qiui	17.1	10.3	60.2	18.1	14.6	80.7	21.4	17.7	82.7	27.7	18.7	67.5	29.1	20.3	69.8

Note: Data for *Eggysodon* from Uhlig (1999): *E. osborni* (Möhren) from tables 116 and 118, *E. osborni* (Kleinblauen) from table 124, *E. gaudryi* (Latou) from table 142, *E. gaudryi* (Puylaurens) from table 143, and *E. reichenaui* from table 148; Data for *Allacerops turgaica* from Reshetov et al. (1993: table 1), with minimum (min) and maximum (max) values given for measurements of specimens from Chelkar-Tenis instead of values for single tooth; Data for *A. minor* from Beliajeva (1954: table II); Data for *Proeggysodon qiui* from Bai and Wang (2012).

目前，公认的紧齿犀类有3个属，分别是*Eggysodon*, *Allacerops*和*Proeggysodon* (Bai and Wang, 2012)。关于*Eggysodon*与*Allacerops*在牙齿特征上的差别，前人的研究共提及以下4点：1) *Eggysodon*有两对下门齿，而*Allacerops*有3对下门齿；2) 前者p1退失，后者具p1; 3) 前者的下颊齿明显比后者的更细长；4) 前者下颊齿外齿带连续而显著，后者的齿带较弱。其中前两点是Reshetov et al. (1993)提出的，后两点由邱占祥、王伴月(1999)补充。事实上，这两个属下门齿数目以及下颊齿特征的差别并不严格而稳定存在，但这些变异仅发生于少量的材料中。比如法国Moissac的*E. gaudryi*化石是目前该属中仅有的具3对下门齿的材料；而*Allacerops*中仅Ulan Ganga的*A. minor*材料具两对下门齿。De Bonis and Brunet (1995)新发现的*Eggysodon*材料具有p1, 这与*Allacerops*的相同。如果依据下颊齿的宽长比值来判断下颊齿整体形态，那么*Allacerops*的比值变化范围比*Eggysodon*的大(图2); 其中采自Chelkar-Tenis的Allacerops材料中比值最小的那部分(*A. turgaica* (Chelkar-Tenis)-min), 其比值与*Eggysodon*的相当(表1; 图2), 这表明二者下颊齿的整体宽窄程度接近。此外，两个属在齿带特征上的差异也不明显，因为*E. osborni*的下颊齿外齿带通常薄且不连续(Uhlig, 1999), 也有部分材料的外齿带较为发育(de Bonis and Brunet, 1995); 而*A. turgaica*下前臼齿的外齿带是较为明显的，只是在下臼齿中弱一些(Reshetov et al., 1993)。以上提及的这些变异确实需要在处理这两个属的归并问题时加以考虑。与*Eggysodon*相比，*Allacerops*的材料相对有限，古生物学家对它的研究程度不高。McKenna and Bell (1997)将*Allacerops*作为*Eggysodon*的同物异名。目前来看，两个属在下门齿数目和p1状态上的变异仅发生于少量标本中，而*Allacerops*在下颊齿的整体形态上变化范围相对较宽，*Eggysodon*齿带发育状况变化相对丰富，这些差异一方面与化石材料的局限性有关，另一方面，它们更可能是属内变异的结果，而非属间差异。因此，建议目前将这些变异作为属内变异来看待，同意邱占祥、王伴月(1999)的观点，仍将二者作为独立的属看待，更为详细的讨论有待新材料的发现。

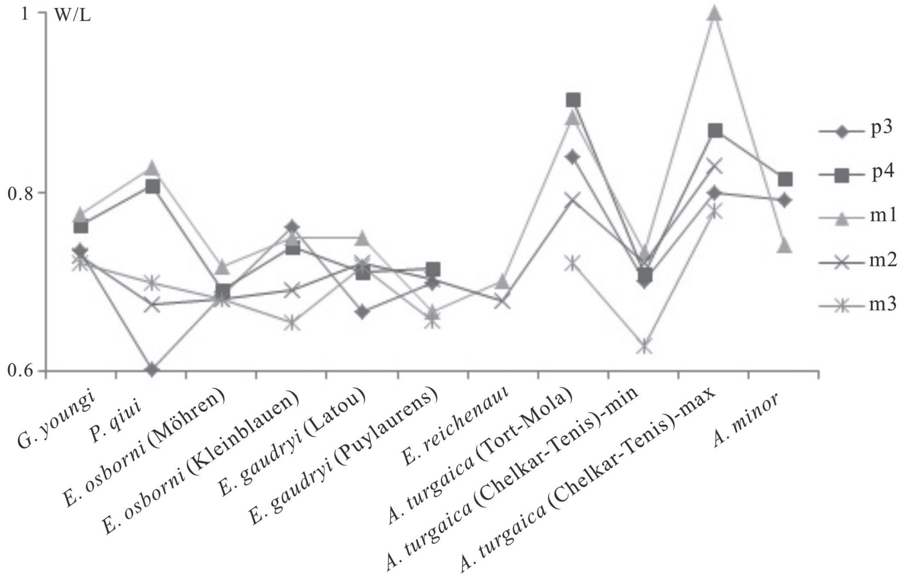

图 2　紧齿犀类下颊齿(p3-m3)宽长比值折线图

Fig. 2　Width to length ratio for p3-m3 in four eggysodontid

欧洲的紧齿犀类材料均被归入*Eggysodon*, 包括*E. osborni*, *E. gaudryi*, *E. reichenaui*和*E. pomeli* (Uhlig, 1999)。Uhlig (1999)对该属的特征进行了较为全面的订正。此后，Becker (2009)报道过采自Kleinblauen的一段*E. osborni*未成年个体的不完整下颌。Antonie et al. (2011)报道了采自法国Moissac的*E. gaudryi*材料。尽管在个体大小上接近(表1; 图3), 但GNV-001与*Eggysodon*已知各种最重要的区别在于下前臼齿的特征：前者p3的下后脊向后倾斜显著，下内尖较低，下内脊弱，从下次尖向下内尖收缩，冠面呈向内收缩的尖叶状，p4下内尖和下内脊均比p3的发育，但下内脊仍不完整；而*Eggysodon*的p3的下内尖更明显，p3和p4的下内脊完整，其下前臼齿臼齿化程度明显高于GNV-001的，这些特征表明GNV-001比*Eggysodon*更为原始。同时，在下臼齿中，GNV-001的m3下三角座形态近似V形，而*Eggysodon*的m3下三角座的下原脊与下后脊交角更大，整体呈U形；GNV-001的m2的下次脊向内倾斜，这也与*Eggysodon*的各个种不同。此外，GNV-001与该属各种还有以下异同点：*E. gaudryi*最为明显的特征是p2-m2有发育而连续的外齿带，在m3中则通常没有，而GNV-001除p3外，下颊齿的外齿带不连续，在下原尖和下次尖基部中断，二者差别明显(Uhlig, 1999; Antoine et al., 2011)。*E. reichenaui*由于缺少下前臼齿材料，可与GNV-001直接对比的仅为下臼齿，其典型特征是下前脊较长，这与下前脊较短的GNV-001有明显区别(Uhlig, 1999); 此外，*E. reichenaui*下原脊与下后脊的交角与*E. gaudryi*的相近，都比GNV-001的大。*E. pomeli*尚未发现下颊齿材料，不能与GNV-001直接对比，但其个体为该属中最大的，从大小上可与GNV-001相区别(Uhlig, 1999)。GNV-001的部分形态特征与*E. osborni*相近, 二者大小相当(表1), 下颊齿(p3-m3)下前脊较短，下前臼齿的外齿带连续，内齿带在下后尖基部消失，下臼齿的外齿带在下原尖和下次尖基部消失，内齿带弱，仅分布于下跟座开口处(Uhlig, 1999); 但二者的下前臼齿特征区别明显。

亚洲的紧齿犀类包括*Allacerops*和*Proeggysodon*两个属(Bai and Wang, 2012)。*Proeggysodon qiui*是依据内蒙古四子王旗额尔登敖包的不完整下颌创建的，Bai and Wang (2012)认为*Proeggsodon*与欧洲渐新世的*Eggysodon*有较近的亲缘关系。GNV-001与*Proeggysodon*的p4下次脊都向内倾斜，但二者的下三角座、跟座形态差异明显：GNV-001下前臼齿化程度相对较高，p3和p4都已形成了下内脊，而*Proeggsodon*的下前臼齿臼齿化程度低，p4的下内脊较弱，较为原始；GNV-001的下原脊向内倾斜明显，下前脊短，m2-m3的下内脊向后倾斜明显，而*Proeggsodon*的m2下内脊几乎不倾斜；GNV-001下臼齿中有中等发育、不连续的外齿带，后侧齿带明显，而*Proeggsodon*的外齿带较弱，后齿带仅m3的较为显著；GNV-001下臼齿中下次脊与下内脊的交角较为圆滑，而*Proeggysodon*的较为尖锐；此外，GNV-001下颊齿的尺寸比*Proeggysodon*的稍大(图3)。

*Allacerops*包括*A. turgaica*和*A. minor*。Borissiak (1915)依据采自哈萨克斯坦Chelkar-Tenis的不完整头骨、下颌以及头后骨骼材料命名了新种*Epiaceratherium turgaica*; Wood (1932)以该种作为新属*Allacerops*的属型种：*Allacerops turgaica*。Beliajeva (1954)将少量采自蒙古Tatal-Gol的材料定为*Allacerops turgaica minor*; Borsuk-Bialynicka (1968)依据蒙古Ulan Ganga发现的新材料建立新种*Allacerops minor*, 与*A. turgaica*相比，其特征为个体小，外脊发育，下颌联合部和犬齿向上弯曲的幅度小，下门齿为两对。Birjukov (1961)和Reshetov et al. (1993)分别在哈萨克斯坦的Myneske-Suyek和Tort-Mola地区报道过这个

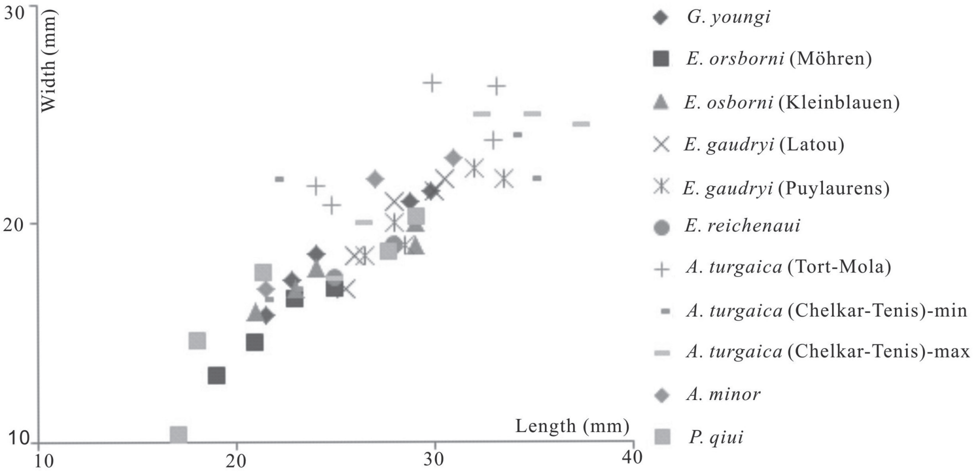

图 3　紧齿犀类下颊齿(p3-m3)测量散点图
Fig. 3　Proportions of p3-m3 in four eggysodontid genera

种的材料。与*Allacerops*两个种相比，GNV-001的个体较小(图3), p3和p4下内尖位置较低，下内脊弱、不完整，下跟座较短。Reshetov et al. (1993)认为Tort-Mola的标本几乎与正型标本一样，与Tort-Mola的标本相比，GNV-001的下颌水平支更为纤细，前者的m2大于m3, 是下颊齿中最大的，而GNV-001的 m2与m3近似等大。Tort-Mola的标本外齿带在下前臼齿中相对发育, 而在下臼齿中较弱，这似乎与GNV-001的接近，但从Reshetov et al. (1993:fig 2)中很难判断下臼齿外齿带是否连续，以及前后齿带的发育状况。邱占祥、王伴月(1999)在甘肃兰州盆地发现过*Allacerops* cf. *A. turgaica,* 由于材料是幼年个体，恒齿中仅保存了m1。尽管GNV-001的m1前外侧有破损，下三角座部分无法与兰州的材料直接对比，但GNV-001的m1比兰州标本的小，下跟座明显较短，下内脊近似与齿列长轴垂直。*A. minor*与*A. turgaica*的下颊齿形态特征区别不大。与*A. minor*相比，GNV-001的p4和m2下次脊向内侧倾斜明显，下颊齿外齿带相对发育，个体较小(Beliajeva, 1954)。此外，Dashzeveg (1991)在蒙古Khoer-Dzan地区发现过*Allacerops* sp.的材料，由于保存状况不理想，尺寸也明显偏小，其分类还存在争议(邱占祥、王伴月，1999; Bai and Wang, 2012)。王伴月、邱占祥(2004)在甘肃地区发现的Allacerops sp., 材料为幼年个体的左下颌骨具m1, m1还未完全长出，且GNV-001的m1三角座外侧破损，难于直接对比，但其尺寸明显比GNV-001的大。

综上所述，新标本和目前已知的紧齿犀类3个属*Eggysodon*, *Allacerops*和*Proeggysodon*都有显著区别，无法归入到任何已知属种。因此，以GNV-001为正型标本建立新属种——杨氏广南犀(*Guangnanodon youngi* gen. et sp. nov.)。

3　*Guangnanodon*和砚山组的时代

已报道过的分类较为可靠的紧齿犀类目前有3个属，产自额尔登敖包剖面乌兰戈楚组(?)“中白层”的*Proeggysodon*, 时代明显晚于沙拉木伦动物群(Bai and Wang, 2012),

很可能为晚始新世。欧洲的*Eggysodon*最早出现的种是*E. osborni*, 于渐新世最早期(MP21)的动物群中出现(Uhlig, 1999); 此前亚洲发现*Allacerops*的地层，时代最早为早渐新世(Daxner-Höck et al., 2010); 从下前臼齿臼齿化水平来判断，*Guangnanodon*应该比*Proeggysodon*进步，而比渐新世的*Eggysodon*和*Allacerops*原始，其时代很可能为晚始新世最晚期。

广南地区的古近系仅张兴永(1981)以消息的形式报道了莲峰十三队及小广南两地的一批哺乳动物，前一地点的化石被鉴定为*Urtinotherium* cf. *U. intermedium*, 当时将时代定为渐新世；后一地点的化石为*Prohyracodon* sp.以及*Caenolophus* sp., 时代为始新世。在云南古近纪其他化石地点中，邱占祥(1962)报道过师宗发现的*Urtinotherium intermedium* (= *Indricotherium intermedium*), 含化石层位为蔡家冲组(云南省地质矿产局，1990), 目前认为其时代为晚始新世中晚期(童永生等，1995; 王伴月，1997; 邱占祥、王伴月，2007)。云南罗平古近纪地层中报道过巨犀的材料(Chiu, 1962), 如果张兴永(1981)对化石的鉴定是准确的，那么广南莲峰发现*Urtinotherium* cf. *U. intermedium*的地层层位最有可能与之相当，时代也为晚始新世中晚期。在云南路南盆地“下路南组上部”发现有*Prohyracodon meridionale*和*P. progressa* (周明镇、徐余瑄，1961), 这套地层后被划归路美邑组上部(郑家坚等，1978); 路美邑组上部动物群的年代与沙拉木伦动物群相当，时代为中始新世晚期(童永生等，1995; 邱占祥、王伴月，2007)。宗冠福等(1996)描记了云南丽江象山组的新种*Prohyracodon major*, 当时认为其时代为晚始新世，目前普遍认为应该为中始新世(童永生等，1995; 王伴月，1997)。因此，小广南产*Prohyracodon* sp.的层位很可能与沙拉木伦组相当，时代为中始新世晚期。*Caenolophus*是沙拉木伦期动物群的典型代表，其时代应当与沙拉木伦期相当(童永生等，1995)。因此小广南产*Caenolophus* sp.的地层层位也很可能与沙拉木伦组相当，时代为中始新世晚期。

由此可见，广南盆地小广南至少包含两个化石层，一是层位相当于沙拉木伦组的*Prohyracodon-Caenolophus*层，时代为中始新世晚期；另一个是晚始新世最晚期的*Guangnanodon*。而莲峰发现*Urtinotherium* cf. *U. intermedium*的地层层位应与蔡家冲组相当，时代为晚始新世中晚期。所以广南盆地砚山组包含了中始新世晚期至晚始新世晚期的沉积。

4 结论

尽管GNV-001的门齿和犬齿信息缺失，但其下颊齿的形态特征和齿带的发育情况与紧齿犀类最为接近。鉴于GNV-001的下前臼齿特征，尤其是下前臼齿的臼齿化程度，与紧齿犀类目前已知的3个属*Eggysodon*, *Allacerops*和*Proeggysodon*区别明显，因此将其作为新属新种——杨氏广南犀(*Guangnanodon youngi* gen. et sp. nov.)归入紧齿犀科。前人提及的区别*Eggysodon*与*Allacerops*的4个特征，下门齿数目、p1的差异、下颊齿宽窄程度和外齿带发育状况，适用于大多数材料，而在有限的化石中发生了变异，因此更为合理的做法是认同二者为独立的属，将这些差异作为属内变异，并在将来的分类鉴定工作中加以注意。对二者差别更为深入的讨论还有待更多更好的化石材料的发现。从紧齿犀类下前臼齿臼齿化程度的差异来判断，新标本为晚始新世相对原始的*Proeggysodon*和

渐新世较为进步的*Eggysodon*和*Allacerops*之间的过渡类型，其时代很可能为晚始新世最晚期。新标本是中国南方首次发现的紧齿犀类化石，为紧齿犀类的古地理分布和系统发育研究提供了新的证据。新标本的发现结合广南地区曾经报道过的一些哺乳动物化石表明，砚山组包含了中始新世晚期到晚始新世最晚期的沉积，其时代不晚于晚始新世晚期，但该结论还需要更多的标本和方法来印证。

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Allacerops and Proeggysodon (mm)