

Restudy of “*Ictitherium hyaenoides*” in the Lagrelius Collection

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All the material of “*Ictitherium hyaenoides*” Zdansky, 1924, kept in the Paleontological Museum of the University of Uppsala, is here restudied. It reveals that the species in question is a composite one and should be attributed separately to three known species: *Palinhyaena reperta* Qiu *et al.*, 1979 (15 individuals), *Thalassictis hyaenoides* Zdansky, 1924 (*s.str.*, 15 individuals) and *Thalassictis wongii*, Zdansky, 1924 (seven individuals). Despite overlapping in size and, partly, morphology, the last two species could be separated and represent two successive evolutionary levels of one lineage. *Palinhyaena reperta* represents a lineage quite different from *Thalassictis*, with characters strongly reminiscent of recent *Crocuta*.

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Introduction

Over the last ten years with steadily growing interest in the intercontinental correlation of Neogene continental deposits, the icthere hyaenids, as one of the most frequently encountered groups of fossils in these strata, have been attracting more and more attention from palaeontologists. “*Ictitherium hyaenoides*”, being the most advanced member of the group in question, has been discussed and debated whenever the general problem of hyaenid evolution has arisen. However, it seems to me that the true nature of this important species has never been clear, and may differ considerably from author to author. The original specimens described by Zdansky in 1924 are so different in size and morphology, which can be easily recognized when the pictures of the four specimens given by Zdansky (1924) in his plates XVI–XIX are compared, that Zdansky could do no more than separate them into two “series”, representing male and female, respectively. While dealing with the hyaenid material of the Qingyang *Hipparion* fauna in 1979, Qiu *et al.* pointed out that part of the material attributed by Zdansky to his “*Ictitherium hyaenoides*” (at least Ex. 7) is quite different from the remainder of the material, and were inclined to include that part in the new genus of the Qingyang fauna, *Palinhyaena*. But at that time it was impossible to do more than merely touch on the problem.

Taken as a whole, three problems are involved

here. The first is whether the material, on which Zdansky based his “*Ictitherium hyaenoides*” is sufficiently homogeneous to be confined in one species, or is it to be considered as representing sexual dimorphism, as Zdansky thought. The second is its taxonomic rank. Recently there has been repeated discussion of Kretzoi’s suggestion in 1938 that a new generic name, *Hyaenictitherium* should be given to it. The third is the problem of its phylogenetic position in the Family Hyaenidae. Although these problems are mutually connected, the first of them is evidently the crucial one. Therefore, a detailed restudy of the original material, which is predominantly housed in the Paleontological Museum of Uppsala University, is greatly needed, and may prove important in the future in understanding hyaenid evolution.

Material Studied

In order to check Zdansky’s concept of the species in question against the original specimens, the present study has been restricted to the material in the Lagrelius Collection. This contains altogether 40 specimens labelled as “*Ictitherium hyaenoides*”; they belong to 32 individuals. The specimens described and measured (but not figured) by Zdansky as Ex. 3, 4, 9, 10, 11, 16 and 18 are absent. Two of them, Ex. 9 and 16 were returned to China by the Sino-Swedish Expedition and are now in the collection of the Institute of Vertebrate Paleontology and

Paleoanthropology, China. They are also included in the present study. The other five "lost" specimens may also be (at least some of them) in China, but are now unavailable to the author. Zdansky gave no exact indication about the number of the original specimens (he noted about 30 individuals were studied).

During the checking of the ictithere part of the Lagrelius collection, the author succeeded in finding seven specimens belonging to five individuals, originally assigned to other species. According to my present opinion, they are to be associated with the group in question. On the other hand, one specimen labelled as "*Ictitherium hyaenoides*" is to be transferred to *Lycyaena*. So, altogether 48 specimens belonging to 38 individuals have been checked and restudied. Among them are eleven more or less completely preserved skulls, five of them with associated lower jaws. Consequently the material restudied can be considered fully representative of the species in question. All the specimens kept in Uppsala were recatalogued and are designated by M, the two in the IVPP are designated by V.

Reidentification of the Specimens

After careful study of the material it became apparent that, except for one palate, which should be attributed to *Lycyaena* and will be discussed separately, Zdansky lumped three different forms into one species, under his two "series" representing male and female individuals of the same species. They are: (1) The specimens evidently belonging to a new form differing considerably from all the other known "*Ictitherium*" species, for which a new genus, *Palinhaena*, was previously established (Qiu *et al.* 1979). Most of Zdansky's female individuals belong to this form. (2) The "*Ictitherium hyaenoides s. str.*" These are mainly Zdansky's male individuals. (3) The remainder represents a form transitional between "*I. hyaenoides s. str.*" and "*I. wongi*". Inasmuch as morphological gaps exist between these two forms, it is better to consider these specimens only as larger individuals of "*I. wongi*", from which the specimens of this last group could hardly be separated morphologically. The reasons underlying Zdansky's approach seem to lie with the fact that he failed to recognize the peculiar nature of the new form, *Palinhaena*, which shows intermediate characters between "*I. hyaenoides s. str.*" and the larger individuals of "*I. wongi*" (for instance, the robustness of the cheek teeth, the reduction of molars, etc.). Thus, Zdansky wrongly considered the specimens of *Palinhaena* as individuals linking the other two groups, and, hence,

made his "*I. hyaenoides*" extremely variable in morphology and in size. In reality, once the specimens of *Palinhaena* are removed, the differences between the two remaining groups become apparent.

In the following description I follow Solounias (1981) and Kurtén (1982) and use *Thalassictis* as the generic name for "*I. wongi*" and "*I. hyaenoides*". For further details regarding the *Thalassictis* problem the reader is referred to the above mentioned papers.

Palinhaena reperta Qiu *et al.*, 1979.

Pl. 1, Pl. 2, Figs. 1-4, Pl. 3, Fig. 1. See also Zdansky (1924, Pl. 18, Figs. 1-2).

MATERIAL: A total of 19 specimens belonging to 15 individuals are attributed to this group:

1. M.41-42, skull with lower jaw, Zdansky, Ex. 2, loc. 30 (Pl.1)
2. M.36, skull, Zdansky, Ex. 5, loc. 30 (2) (Pl. 3, Fig. 1)
3. M.37-39, skull with lower jaw, Zdansky, Ex. 7, loc. 30 (Zd.Pl. 18, Figs. 1-2)
4. M.7169, right horizontal ramus, Zdansky, Ex. 20, loc. 30 (Pl. 2, Figs. 1-2)
5. M.7107, left mandibular fragment with P₄, labelled originally as "*I. wongi*", loc. 30
6. M.7130, left half of snout, labelled originally as "*I.*" sp., loc. 30
7. M.7148, left half of a middle part of associated skull and lower jaw, loc. 49
8. M.7158, lower jaw, labelled originally as *I. sinense*, loc. 49 (Pl. 2, Figs. 3-4)
9. M.7167, mandibular fragment with P₄-M₁, loc. 30 (2)
10. M.7168, mandibular fragment with I₂-P₃, loc. 30
11. M.7184, almost complete right mandible, loc. 116
12. 7187-88, two mandibular fragments, probably of the same individual, loc. 116
13. M.7190, right mandibular fragment with P₃-M₁, loc. 30 (5)
14. M.7191, anterior half of a skull of very old individual, loc. 30
15. M.7192 left mandibular fragment with P₂-M₁, labelled originally as "*I.*?" *hyaenoides*, loc. 30

CHARACTERISTICS: A detailed description and a diagnosis based on ten specimens from the Qingyang Hipparion fauna were given by Qiu *et al.* (1979). It is important here to point out that almost in every point the description and the diagnosis above mentioned hold good in the present case. It is regrettable that the description of the new genus

Table I. Lengths and widths of some skulls.

| SPECIMEN | | L (prothion-basion in mm) | max. width (in mm) | W/L % |
|---------------------|--|------------------------------|-----------------------|-------|
| <i>Palinhyæna</i> | THP 03838 (Qiu <i>et al.</i> , 1979, Pl. 3) | 162 | 108 | 66.6 |
| <i>reperta</i> | M 41 (Zdansky, 1924, "I. <i>hyaenoides</i> ", Ex. 2) | 163 | 107 | 65.6 |
| <i>Thalassictis</i> | M 3710 (Zdansky, 1924, "I." <i>wongi</i> , Ex. 12) ^a | 174 | 120 | 68.9 |
| <i>wongii</i> | M 3853 (Zdansky, 1924, "I." <i>hyaenoides</i> , Ex. 1, Pl. 17, Figs. 1-2) d | 177 | 96 ^c | 54.2 |
| | M 3707 (Zdansky, 1924, "I." <i>wongi</i> , Ex. 14) ^b | 152 | 72 ^c | 47.4 |
| <i>Thalassictis</i> | M 3849 (Zdansky, 1924, Ex. 8, Pl. 19, Figs. 1-2) | 208 | 146 | 70.1 |
| <i>hyaenoides</i> | | | | |

^a large form^b small form^c skulls compressed^d lectotype of "T. *hyaenoides*" designated by Solounias (1981)

and species and the discussions about it were only in the Chinese text and could be overlooked by other authors. In order to remedy this, a detailed description, with new observations, is given below:

(1) The overall size of this genus is about the same as that of a large individual of *Thalassictis wongi*, but definitely smaller than that of *T. hyaenoides s. str.* Table 1 shows this point clearly. The width-length indices (around 65) differ considerably from the typical small-sized *T. wongi*. The same index of a not very strongly compressed skull of *T. wongi* (M.3707, Zdansky 1924, Ex. 14, Pl. 15, Fig. 2) is only 47.4. On the other hand, there is no principal difference in skull proportion between the larger individuals of *T. wongi*, *T. hyaenoides s. str.* and *Palinhyæna*. They are all proportionally wider than *T. wongi* of smaller size. However, it is necessary to point out that this was achieved in different ways. While it was arrived at in both species of *Thalassictis* through widening of the zygomatic arches during the process of gradual lengthening of the skull, in *Palinhyæna* it was achieved through the "shortening" of the skull. The evidence to support the foregoing viewpoint is: The snout in *Palinhyæna* is shortened; accordingly, the diastemata between C and P¹, and between P¹ and P² are also shortened, or even lacking (see Qiu *et al.*, 1979, p. 209, Fig. 1). Further, the form of the temporal opening formed by the zygomatic arches and the vertical walls of the palate and pterygoid bones in *Palinhyæna*, seen from the ventral side, is shortened longitudinally, with its length equal to or even shorter than its width (Pl. 1, Fig. 1; Zdansky, 1924, Pl. 18, Figs. 1-2), whereas in *Thalassictis*, its length is longer than its width (Zdansky, 1924, Pl. 16, Figs. 1-2, Pl. 17 Figs. 1-2 and Pl. 19, Figs. 1-2). On the basicranium of *Palinhyæna* the foramen rotundum is very close to the anterior margin

of the bulla and the postglenoid process lies behind the anterior margin of the bulla, whereas in *Thalassictis* these elements are more separated from each other (see the same Plate). In conclusion, *Palinhyæna* could be characterized as "brachycephalic".

(2) Apart from the differences in size and proportion of the skull, there also exist differences in relative positions of certain elements and morphology.

(a) As already pointed out in 1979, the posterior palatine foramen is situated at the level of the first half of P², and the infraorbital foramen is above the middle of P³, just between the two roots of that tooth in *Palinhyæna*. In all specimens of either *Ictitherium* or *Thalassictis* which I have compared, the former foramen lies posterior to the middle of P², and the latter foramen lies just before the anterior edge of the anterior root of P⁴. It was rather unexpected that the above mentioned positions of these two foramina proved very characteristic for the genus. In every case, it has never failed when using them as criteria to distinguish the genus *Palinhyæna* from the other two genera.

(b) The positions of the posterior border of the bony palate. In *Palinhyæna* it is at the level of the posterior border of M², whereas in the other two mentioned genera it is, in most cases, far behind this level. The distance between the posterior border of the palate and that of M² varies from 5 to 10 mm. If we compare the posterior border of the palate relative to P⁴, instead of M², the difference between *Palinhyæna* and the other two genera appears even more conspicuous because the molars in the first genus are also more reduced than in the other two. From all the available specimens of *Ictitherium* and *Thalassictis* in Uppsala, that is about 20 skulls, only one (M. 34, Zdansky, Ex. 16 of "I." *wongi*) has an anteriorly situated posterior bor-

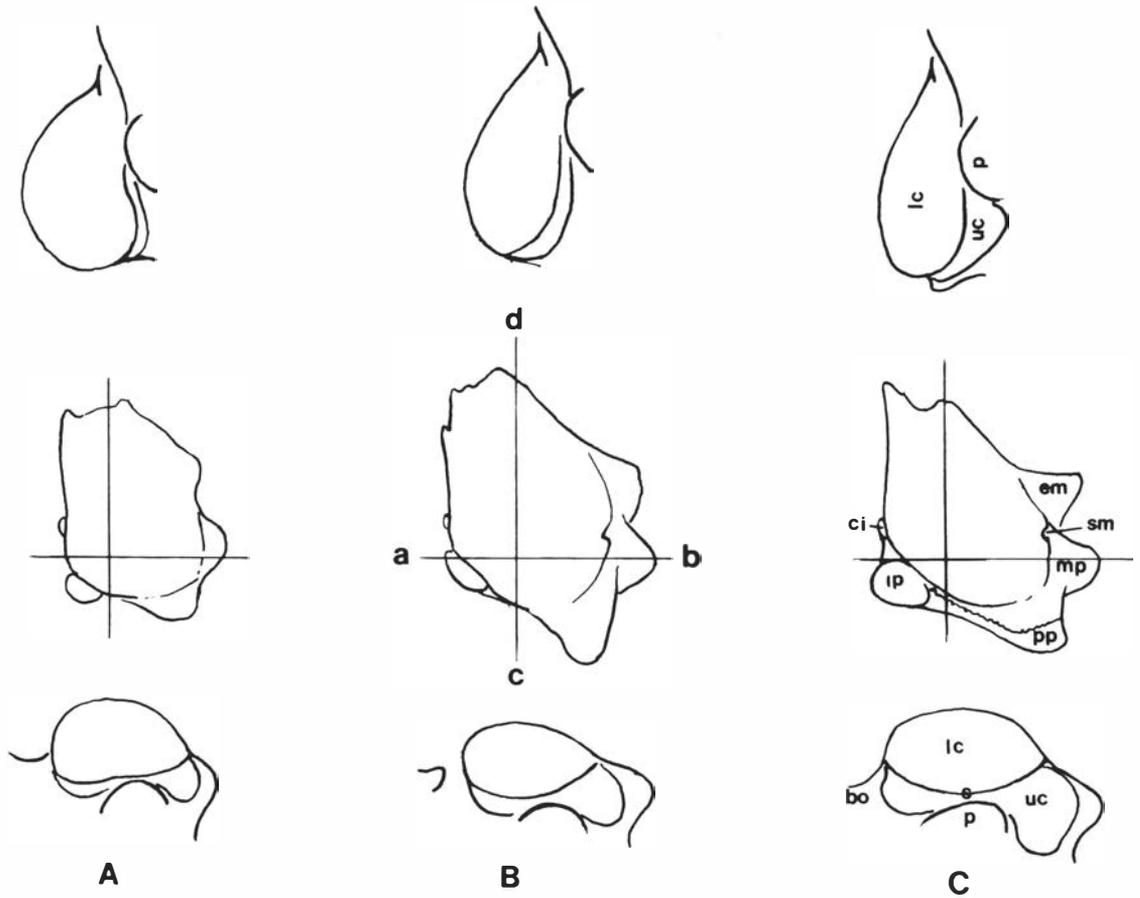


Fig. 1 Left ear-regions. A, *Palinhyana reperta*, M. 36, B, *T. hyaenoides* s. str., M. 3849, C, *Hyaena brunnea*, S. 205, Inst. für Geowiss., Mainz Univ. Middle: Ventral view, Lower: section through a-b, Upper: section through c-d. bo: basioccipital, ci: canal for the internal carotid artery, em: external meatus, lc: lower (ectotympanic) chamber, lp: posterior lacerate foramen, mp: mastoid process, p: petrosal, pp: paroccipital process, s: septum, sm: stylomastoid foramen, uc: upper ("endotympanic") chamber.

der of the palate. But even in this skull, it is still more posterior to that in *Palinhyana*

(c) The ear-region shows also a series of interesting differences. First of all, the bulla in *Palinhyana* is very swollen (Qui *et al.*, 1979, Pl. 3, Fig. 1; Zdansky 1924, Pl. 18, Fig. 2). Seen from the lateral side, it is well below the occipital condyles. The distance between the lowest point of the bulla and the basioccipital surface is about 16–18 mm. The inner wall of the bulla is very steep and strongly convex medially. The septum within the bulla is generally horizontal, but considerably higher (dorsally toward the cranium) than the basioccipital surface (Fig. 1). Perhaps because of the high position of the septum, the canal for the inner carotid artery is salient on the lower surface of the septum in the

form of a ridge (Pl. 3, Fig. 1). The lower, or the ectotympanic chamber, is very large and wide transversely. The upper, or the "endotympanic" chamber, on the contrary, is very limited in size. In fact, it is only developed in the posteroexternal corner of the bulla. The tympanic bullae of the other two species are also different from each other, but they are both less swollen with smaller ectotympanic chambers (Fig. 1).

(d) Zdansky mentioned two types of nasal bones in his "*I. Hyaenoides*": one with a pointed posterior end, and the other with a blunt one. The present study reveals that the first type is principally confined to the specimens listed here as *Palinhyana reperta*. But this difference is only one of relative significance. In several specimens of *Thalassictis* the

nasal bones do have posteriorly pointed ends, but they are never so pointed as in the former.

(e) In *Palinhyæna*, on the outer wall of the vertical plate formed by the palate and the pterygoid bones, there is a very prominent, horizontally situated plate-like ridge. This ridge is present in *T. wongi* and the forms more primitive and smaller than *T. wongi*, but absent in later forms, such as *T. hyaenoides s. str.* and more advanced forms.

(3) The lower jaw of *Palinhyæna* is also characterized by its shortness. There is only one nearly complete lower jaw of *Palinhyæna* in the Lagrelius Collection on which the total length can be measured. This is the jaw of M. 7184, labelled originally as "*I. hyaenoides*". The total length from the prosthion to the posterior margin of the condyle is 131 mm; the height of the mandible taken between P_4 and M_1 is 26 mm. The height/length index is 19.9. The same measurements for a smaller individual of *T. wongi* (M. 3709, Zdansky 1924, Ex. 14 of "*I.*" *wongi*, Pl. 15, Figs. 1–2) are 127 mm, 18 mm and 14.2, respectively. Those for a larger individual of *T. wongi* (M. 3854, Zdansky 1924, Ex. 1 of "*I. hyaenoides*", Pl. 16, Figs. 3–4) are: 141 mm, 26 mm and 19.1. For all the specimens of *T. wongi*, irrespective of small or large individuals, the lower border of the horizontal ramus slopes down from the symphysis to the point beneath M_1 ; therefore the height of the lower jaw differs considerably. In *Palinhyæna* the lower border of the jaw is almost parallel to the alveolar border. For *T. hyaenoides s. str.* there is no complete lower jaw. The best specimen in the Lagrelius Collection is M. 40 (Zdansky, 1924, Ex. 13, Pl. 17, Figs. 3–4), the angle and condyle of which were restored with plaster. Approximately, it might be estimated as a little longer than 160 mm. The height of the mandible is 32 mm. Hence, the height/length index is about 20, which is about the same as in *Palinhyæna*. Its lower border is also almost horizontal and also similar to *Palinhyæna*. But it is much stouter and larger in size, so it is easily distinguished from the latter.

(4) The characteristics of the dentition, based on the original description of the genus and the additional observations during the present study, may be listed as follows:

(a) Zdansky (1924, p. 85–87) gave a precise description of the incisors to which the readers are referred in order to avoid unnecessary repetition. Zdansky based his description upon only part of his specimens, namely those belonging to *Palinhyæna*. The cusps and ridges on the posterior sides of the incisors described by Zdansky are clearly demonstrated in M. 41–42 (Zdansky, Ex. 2, Plate 1 in this paper), M. 7180 and 7184, but no clearly separated cusps on the posterior sides of the upper incisors

and prominent ridges on the lower ones have been observed on the specimens referable to *T. wongi* (M. 3853–55, Zdansky, 1924, Ex. 1 of "*I. hyaenoides*", Pl. 16, Figs 3–4 and Pl. 17, Figs. 1–2) and to *T. hyaenoides s. str.* (M. 3849, Zdansky, Ex. 8 of "*I. hyaenoides*", Pl. 19, Figs. 1–2). This is in full agreement with the observations on the specimens from Qingyang (Qiu *et al.*, 1979, p. 208, Fig. 1).

(b) Both upper and lower P1 in this genus are situated very close to P2, often without diastemata between them. The diastema between P1 and C is, in general, also very short. Furthermore, P_1 is always situated internal to the tooth-row, close at the anterointernal corner of P_2 . In all observed specimens of *T. wongi*, the diastemata between P1 and C, and between P1 and P2, are always comparatively longer. Also, P_1 is in front of P_2 . *T. hyaenoides* is similar to *T. wongi*, but P_1 is here completely reduced.

(c) As already partly pointed out (Qiu *et al.*, 1979), the cheek teeth of *Palinhyæna* are in general robust, high-crowned, with reduced accessory cusps, and the size of the teeth at both extremities of the tooth-row is reduced considerably (expressed by the strong reduction of P2 and M2). The difference in robustness between *T. wongi* and *Palinhyæna* was previously illustrated by the present author (Qiu *et al.*, 1979, Table 8, Fig. 3, p. 213) and partly again in Table 2 and Fig. 2. For example, the robustness indices of *Palinhyæna*, for P_2 and P_3 , are around 60 (the index of M. 7169 is not exact), while these for *T. wongi* are around 50. The difference between *Palinhyæna* and *T. hyaenoides s. str.* is less prominent, since the cheek

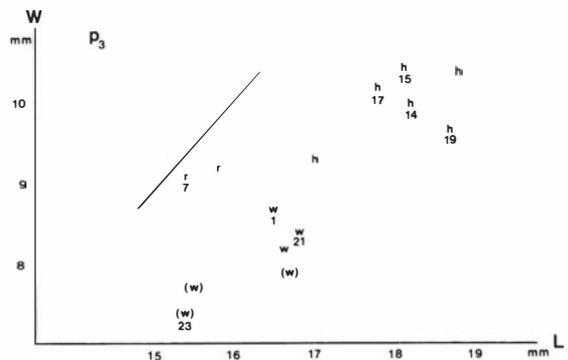


Fig. 2 Lengths and widths of P_3 . r: *Palinhyæna reperta*; w: *Thalassictis wongi*, originally labelled as "*I. hyaenoides*"; (w): *T. wongi*, identified by Zdansky as "*I.*" *wongi*; h: *Thalassictis hyaenoides s. str.*; 1–23: Zd. Ex.; straight line – a line connecting the minimum and maximum measurements of *P. reperta* from Qingyang (Qiu *et al.*, 1979).

Table II. Measurements of P₂ - P₄ (mm.)

| | <i>Palinityaena reperta</i> | | | | <i>Thalassictis wongi</i> | | | | | <i>Thalassictis hyaenoides</i> | | | | | | | | |
|----------------|-----------------------------|-------------------|---------------------|----------------------|---------------------------|---------------------|----------------------|--------|--------|--------------------------------|--------|--------------------|--------------------|----------------------|----------------------|----------------------|----------------------|------|
| | M 42 Zd. Ex. 2 | M 39 Zd. Ex. 2 | M 7169 Zd. Ex. 7 | M 7158 Zd. Ex. 20 | (Qiu et al., 1979) | M 3854 Zd. Ex. 1 | M 7166 Zd. Ex. 21 | M 7132 | M 7205 | M 8188- 89 | M 8201 | M 40 Zd. Ex. 13 | M 44 Zd. Ex. 14 | M 7173 Zd. Ex. 15 | V 7273 Zd. Ex. 16 | M 7183 Zd. Ex. 17 | M 7186 Zd. Ex. 19 | |
| P ₂ | L. | 13.2 | 12.0 | 12.4 | 12.1 | 11.7-12.7 | 13.8 | 13.5 | 12.4 | 13.4 | 13.1 | 12.5 | 13.5 | 14.5 | 14.4 | 14.8 | 16.5 | 16.2 |
| | W. | 8.3 | 7.4 | 7.7 | 7.6 | 6.9-8.3 | 7.7 | 6.8 | 5.9 | 6.4 | 6.6 | 6.2 | 7.6 | 7.6 | 7.7 | 8.0 | 7.6 | 8.8 |
| P ₃ | W/L | 62.9 | 61.6 | 62.1 | 62.8 | 58.6-69.1 (62.7) | 55.8 | 50.4 | 47.6 | 47.8 | 50.4 | 49.6 | 56.2 | 52.4 | 53.5 | 54.1 | 46.6 | 54.3 |
| | L. | | 15.8 | 14.0 | 15.4 | 14.8-16.3 | 16.5 | 16.8 | 15.5 | 16.6 | 16.7 | 15.4 | 15.5 | 18.2 | 18.1 | 17.0 | 18.7 | 18.8 |
| P ₄ | W. | | 9.2 | 9.6 | 9.1 | 8.7-10.4 | 8.7 | 8.4 | 7.7 | 8.2 | 7.9 | 7.4 | 9.3 | 10.0 | 9.3 | 10.2 | 9.7 | 10.4 |
| | W/L | | 58.2 | 68.6 | 59.1 | 54.5-65.3 (60.9) | 52.7 | 50.0 | 49.7 | 49.4 | 47.3 | 48.1 | 60.0 | 54.9 | 57.5 | 57.3 | 51.9 | 55.3 |
| P ₄ | L. | 18.1 | 17.0 | | 17.2 | 16.1-18.0 | 18.7 | | | | 18.5 | 17.3 | | 21.7 | 19.1 | 20.6 | 22.1 | 21.7 |
| | L _{pr} | 9.6 | 9.0 | | 8.6 | | 8.8 | | | | 8.4 | 8.1 | | 10.6 | 9.0 | 9.6 | 10.1 | 9.1 |
| | H. | 14.3 | 12.8 | | 13.1 | 13.3 | 12.6 | | | | 12.0 | 11.6 | | 15.5 | 13.0 | 14.5 | 15.0 | 15.5 |
| | W. | 10.4 | 9.6 | | 10.0 | 9.0-10.3 | 9.6 | | | | 8.6 | 8.4 | | 10.6 | 9.6 | 10.7 | 10.0 | 10.9 |
| P ₄ | L _{pr} /L | 53.0 | 52.9 | | 50.0 | | 47.1 | | | 45.4 | 46.8 | | 48.8 | 45.9 | 47.1 | 46.6 | 45.7 | 41.9 |
| | H/L | 79.0 | 75.3 | | 76.2 | 80.0 | 67.4 | | | 64.9 | 67.1 | | 71.4 | 67.0 | 68.1 | 70.4 | 67.9 | 71.4 |

L_{pr} - lengths of the main cusps.

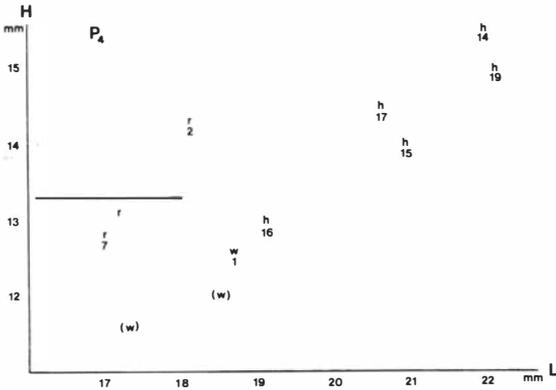


Fig. 3 Heights and lengths of P₄. Symbols as in Fig. 2.

teeth in the latter species also became robust. But, in *T. hyaenoides* s. str. there is practically no tendency to reduce its P₂ length, so the difference of robustness between them in terms of this tooth still remains prominent. Table 2 and Fig. 2 demonstrate this clearly. M 40 and M. 7169 were intentionally excluded from Fig. 2 because the wear of these teeth was too strong to warrant useful measurements.

It is about the same with the differences in hypsodonty in these three forms. Except the pictures in the plates of the present paper, which demonstrate the hypsodonty differences clearly, P₄ is chosen to illustrate this in particular (Table 2 and Fig. 3).

One of the most important features of the cheek teeth of *Palinhyæna* is the reduction of the accessory cusps. In fact, it is this reduction that renders the teeth very robust in appearance. The reduction can be seen in almost all the cheek-teeth, but is especially clearly shown on P₃ and P₄, and is better expressed by the index of the length of the main cusp to the total length of the tooth. As can be seen from Table 2 and Fig. 4, the differences for the three forms are quite prominent and diagnostic.

It is also quite diagnostic that both extremities of the tooth row in *Palinhyæna* are strongly reduced in size. This concerns mainly P₂ and M₂, which are more reduced than in the other two forms, but partly also the talonid of M₁ and M¹. In *Palinhyæna*, M¹ is generally more slender anteroposteriorly, with a more reduced metacone; the talonid of M₁ is proportionally and absolutely smaller than those in all the observed specimens of *Thalassictis*. In connection with this we have the difference in the angle between the external borders of the premolars and the molars. Zdansky wrote that the angle is 80°, except Ex. 11, in which it is only 60°. Ex 11 is now unavailable, but for the remainder, some differ-

ences between the specimens here attributed to *Palinhyæna* and those to *Thalassictis* can also be observed. In fact, in the first group the angle is 80° or more, while in the second it is smaller, around 75°.

Thalassictis hyaenoides (Zdansky)

Pl. 2, Fig. 5, Pl. 3, Figs.2-3 and Pl. 4, fig. 1. See also Zdansky (1924, Pl. 17, Figs. 3-4 and 19, Figs. 1-2).

MATERIAL: 15 specimens representing the same number of individuals are here included:

1. M.3849, skull, Zdansky 1924, Ex. 8, Pl. 19, Figs. 1-2, loc. 49.
2. M.7182, left maxilla, Zdansky, Ex. 12, loc. 109.
3. M.40, left mandible, Zdansky, Ex. 13, loc. 49 (Zdansky 1924, Pl. 17, Figs. 3-4).
4. M.44, left horizontal ramus, Zdansky, Ex. 14, loc. 108 (Pl. 3, Figs. 2-3).
5. M.7173, left horizontal ramus, Zdansky, Ex. 15, loc. 49 (Pl. 2, Fig. 5).
6. M.7183, left horizontal ramus, Zdansky, Ex. 17, loc. 49.
7. M. ?, right horizontal ramus, Zdansky, Ex. 19, loc. 49.
8. M.45, anterior part of right mandible, loc. 49.
9. M.7179, anterior part of left mandible, loc. 49.
10. M.7181, left maxilla, loc. 49.
11. M.7186, right horizontal ramus, loc. 116.
12. M.7193, lower C, loc. 49.
13. M.7194, left p⁴ and C, Nan-ting, Wu-hsiang, Shanxi.
14. V.7272, palate, Zdansky, Ex. 9, loc. 49, kept in IVPP.
15. V.7273, left horizontal ramus, Zdansky, Ex 16, loc. 49, kept in IVPP.

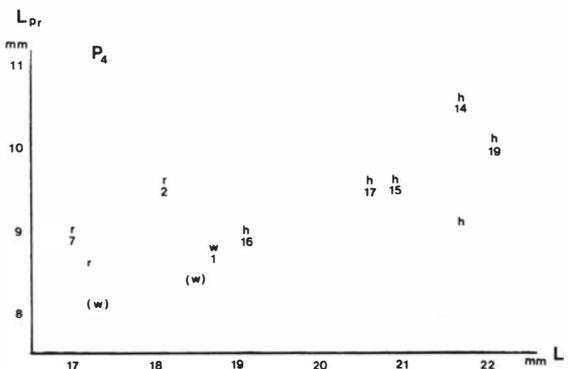


Fig. 4 Total lengths and the lengths of the main cusps (L_{pr}) of P₄. Symbols as in Fig. 2.

CHARACTERISTICS: From the foregoing comparative description of *Palinhyæna* it is evident that the distinction between the latter and *T. hyænoïdes s. str.* is well defined. Unfortunately, there is only one well preserved skull, M. 3849. Judging from this material, it differs widely from that of *Palinhyæna*. It is characterized by larger size (about 1/4 longer, see Table 1), comparatively dolicocephalic proportions and the positions of the preorbital and the posterior palatine foramina and the posterior border of the bony palate characteristic for the genus *Thalassictis* (*vide supra*). What is peculiar and worthy of special mention is the ear-region (Pl. 4, Fig. 1 and Fig. 1). The external meatus is already prolonged, forming a laterally stretched shelf on the dorso-anterior corner of the meatus. The bulla itself is also a little widened and swollen, in comparison with that of *T. wongi*, but still less so than in *Palinhyæna*. The posterior portion of the septum observed through the hole on the surface of the right bulla, turns steeply downwards, so that a downward extension of the upper, or the "endotympanic" chamber is formed between the septum and the posterior wall of the bulla. The paroccipital process is well separated from the bulla and stretches downwards. A very prominent, bulbiform mastoid process is developed behind the external meatus. In general, the ear-region of *T. hyænoïdes* seems more advanced in comparison with the other two forms.

The lower jaw is distinguished by its "hyaenoid" appearance: stout, thick, with high horizontal ramus and straight lower border parallel to its alveolar border. The mental foramen may be single or double. One is often much enlarged in size, and seemingly moved gradually forward, because on all the specimens, except one (M. ?, Zdansky 1924, Ex. 19), the larger foramen lies always under the first half of P_2 , or even anterior to it.

The teeth are in general of the type of *T. wongi*, although they are much larger in size: incisors without remarkable cusps and ridges, dentition not imbricated, cheek teeth with larger accessory cusps, the main cusps comparatively smaller and no evident size-reduction at the extremities of the tooth row. As already pointed out, the cheek teeth are comparatively high-crowned, and in this respect, except P_2 , they could hardly be separated from those of *Palinhyæna*.

Zdansky, Ex. 13 (M. 40, Zdansky, 1924, Pl. 17, Figs. 3–4) is otherwise quite characteristic for the species in question, except its teeth, which are much smaller owing to the fact that they are much worn. The teeth of M. 44 (Zdansky, Ex. 14) are more representative of the species, and reproduced here in Plate 3, Figs. 2–3.

Thalassictis wongi (Zdansky) (large form)

Pl. 4, Fig. 2, See also Zdansky (1924, Pls. 16, Figs. 3–4 and 17, Figs. 1–2)

MATERIAL: 12 specimens belonging to seven individuals are referable to the present species:

1. M.3853–55 skull with lower jaw, Zdansky, Ex. 1, loc. 44 (Zdansky 1924, Pls. 16, Figs. 3–4 and 17, figs 1–2) (lectotype: Solounias, 1981).
2. M. ?, middle part of skull, Zdansky, Ex. 6, loc. 30.
3. M.7166, left horizontal ramus, Zdansky, Ex. 21, loc. 110.
4. M.7180, anterior part of skull with only right dentition, partly damaged, loc. 115.
5. M.7189, right horizontal ramus with P_3 – M_1 , most probably belongs to the same individual as M. 7166, loc. 110.
6. M.7200–02, skull with lower jaw, teeth rather damaged, loc. 30.
7. M.7204–05, skull with lower jaw, much damaged, labelled originally as "*Ictitherium*" sp., loc. 115.
8. M.7215, skull, badly damaged, loc. 115.

CHARACTERISTICS: The above-listed specimens are morphologically inseparable from those of typical *Thalassictis wongi*. The features listed by Zdansky as characteristic for his "*I. hyænoïdes*" *s. l.* seem to be based mainly on the specimens referable here either to *T. hyænoïdes s. str.*, or to *Palinhyæna*, and could not be applied to the above-listed specimens. Even in size they are hardly separable from the larger specimens identified by Zdansky himself as belonging to "*I.*" *wongi*. For example, M.2801 (Zdansky, Ex. 23 of "*I.*" *wongi*, Pl. 4, Fig. 2 in this paper), M. 7132 and M. 8188-90 are almost identical to M.7200–02, which were labelled as "*I. hyænoïdes*" and now included in *T. wongi* by the present author, are only a little larger than M.7200–02. The reader is referred to Pl. 4, Fig. 2 to compare, side by side, the two specimens referred by Zdansky respectively to "*I.*" *wongi* and "*I. hyænoïdes*". Although P_1 of M.3854 is not preserved, its alveolus is present.

On the other hand, there are gaps between *T. hyænoïdes s. str.* and the larger form of *T. wongi*. As an example, Tables 1 and 2 show the differences in overall size and in P_2 – P_4 between these two groups. Figures 2–4 show this graphically. As noted above, the form of the mandible of *T. hyænoïdes* also differs considerably from that in *T. wongi*: in the former it is much stouter, with lower border parallel to the alveolar border and large and anteriorly moved mental foramen. The constant absence of P_1 in *T. hyænoïdes* is also characteristic.

The canine is crocoid in appearance; I did not see the skull of M.3853 (Zdansky, Ex. 1 of "*I. hyaenoides*") during my visit to Uppsala, but according to the picture given by Zdansky (1924 Pl. 17, Fig. 2), it is the same as in other specimens of typical *T. wongi* and thus quite different from that of *T. hyaenoides*. Although there are some morphological gaps between them, *T. wongi* and *T. hyaenoides*, taken as a whole, are morphologically transitional: neither could be placed with *Palinhyena*.

Nomenclatural Problem

If Zdansky's "*Ictitherium hyaenoides*" is really a composite and should be further segregated, which group of specimens should bear the species name *hyaenoides*? In principle, according to page or number priority, it should be Zdansky's Ex. 1, as in Solounias (1981). But the following difficulty arises. Zdansky, Ex. 1, according to my point of view, belongs to *T. wongii*. Further, the next in order numbers, Zdansky's Exs. 2, 5 and 7 prove now quite different from the remainder of Zdansky's "*I. hyaenoides* (*s. l.*)" at the generic level. Zdansky's Ex. 6 is also to be associated with *T. wongi*. Zdansky's Ex 3 and 4 "lost", but according to their size, as given by Zdansky, they may belong either to *T. wongi* or are to be associated with Zdansky's Ex. 2, 5 and 7. While studying some new material from Qingyang, Gansu, Qiu *et al.* (1979) noticed that some specimens among Zdansky's "*Ictitherium hyaenoides*" (*s. l.*), at least Exs. 7 and 20 (Qiu *et al.*, 1979, p. 213), could be conspecific with some specimens from Qingyang, Gansu. However, at that time a conclusive identification of the two forms and a thorough revision of Zdansky's "*I. hyaenoides*" was impossible. As a result, based chiefly on the material from Qingyang, Qiu *et al.* (1979) erected a new genus, *Palinhyena*. The present study has proved the point of view expressed in 1979: not only isolated specimens, but as many as 15 among the specimens of "*I. hyaenoides*", are almost identical to the specimens of *Palinhyena* from Qingyang. Now the problem is if, according to number priority, the species name of *hyaenoides* belongs to Zdansky's Exs. 2 or 5 or 7, the species name *reperta* should be abandoned. On the other hand, a new species name is needed for the remainder of Zdansky's "*I. hyaenoides*". It also is a fact that the species *hyaenoides* has been long and very often considered as the species successive to *T. wongi*. Therefore, it would be extremely inconvenient to use the species name in another lineage of Hyaenidae.

In connexion with the validity of *Palinhyena* as a genus, some words should be added regarding the

relationship between it and *Miohyaena*. The latter genus shows similar specialization in dentition. It might be close to *Palinhyena* phylogenetically, but morphologically they can hardly be congeneric. The type species of *Miohyaena* is *M. certa* from St. Alban. It is too primitive and too old to be congeneric with *Palinhyena*. A number of specimens of Vallesian age from Spain and Turkey (Crusafont-Pairo and Petter, 1969; Schmidt-Kittler, 1976) were attributed to *Miohyaena*. A detailed revision of these specimens is needed, but it goes beyond the topic of the present paper.

After all the specimens in the Lagrelius Collection which belong to *Palinhyena* have been studied, the present author is convinced that the differences between the two species, *P. imbricata* and *P. reperta*, expressed chiefly in the degree of imbrication of the cheek teeth, are not tenable, and seem too slight to warrant a species distinction. Therefore, there is only one species of the genus in China, and this is, according to page priority, *Palinhyena reperta*.

Locality Distribution in Paote Area

According to Zdansky's record, his "*I. hyaenoides*" (*s. l.*) were as widespread as his "*I. wongi*": both were found at the same localities: 30, 43, 44, 49, 108, and 109, with the exception of loc. 110, where only the first species was recorded. After "*I. hyaenoides*" (*s. l.*) splits into three species, the distribution pattern also changes. The results are: *Palinhyena reperta* is restricted to only locs. 30 and 49; *T. hyaenoides* is found mainly at loc. 49, only in rare cases at locs. 108 and 109 and the large form of *T. wongi* occurs at locs. 44, 110, and 30. When the relative positions of the localities are considered (Zdansky, 1923, Table 5), these can be subdivided into three sub-areas: the northern: 44 and 110; the middle: 49 and 108; and the southern: 30 and 109. Accordingly, *Palinhyena* is restricted to the middle and southern sub-areas, *T. hyaenoides* is predominantly in the middle, only occasionally in the south (loc. 109) and *T. wongi* (here only the large form) is mainly found in the north, only one specimen is found at loc. 30. As is known, the Paote fossil-bearing area is only about 30 km², so the species may not be geographical ones. Thus, the localized distribution of these species led me to ask whether there are differences in age. Some facts seem meaningful in this connexion. For example, loc. 30 yields no *T. hyaenoides*. What was originally considered by Zdansky as "*I. hyaenoides*" at loc. 30 is to be re-assigned to *Palinhyena*. In fact, at loc. 30, except *Adcrocuta*, the predominant forms of

hyaenids are only *T. wongi* (the small form) and *Palinhyaena*. Loc. 49 contains all kinds of both large and small forms: *Ictitherium gaudryi*, *I. sinense*, *Thalassictis wongi*, *T. hyaenoides* and *Lycyaena*. It seems possible that loc. 49 might contain deposits of a higher level than that of loc. 30. On the other hand, in the northern sub-area there is no *T. hyaenoides*, nor is there typical small *T. wongi*. Here, the hyaenids are mainly represented by large forms of *T. wongi* and a very small-sized *I. gaudryi*. Can it therefore be postulated that this locality is stratigraphically intermediate between the level of loc. 30 and the higher level of loc. 49?

The *Lycyaena* Problem

The *Lycyaena* problem is a very difficult one and complexly entangled with specimens, the nature of which is still not clear, even now. As to *Lycyaena dubia*, Zdansky himself admitted that it was very difficult to separate it from "*I. hyaenoides*", except for the absence of M^2 . Kurtén considered it an aberrant individual of *T. hyaenoides*.

Specimen M. 7155, a palate from loc. 49, was labelled as "*I. hyaenoides*", but actually also belongs to *Lycyaena dubia*. It is almost identical to the type specimen of the species. Perhaps because of its young age, M. 7155 seems more similar to the type specimen of the genus described by Gaudry 1862–67).

A closer comparison reveals that the difference between *Lycyaena* and *T. hyaenoides* is not only restricted to the absence or the presence of the M^2 . *Lycyaena dubia* differs also in: (1) The cheek teeth are proportionally longer, especially the P^2 ; (2) The posterior accessory cusps are also proportionally longer, this can be seen from the lateral side; (3) M^1 is more reduced, anteroposteriorly shorter, with reduced metacone. Although these differences are small indeed, they seem real, and could not be considered as belonging to an aberrant individual. The discovery of the second specimen, which is almost completely identical to the first specimen described by Zdansky, is evidence against the aberrant-individual proposition. What is more meaningful is the fact that these seemingly slight differences are strongly reminiscent of the specialization of the latter *Chasmaporthetes*. However, the tiny differences between the two forms do render the status of *Lycyaena dubia* as a species of a separate genus rather questionable. Would it not be better if it were placed in the genus *Thalassictis*, but under the subgeneric name of *Lycyaena*, i.e. *Thalassictis (Lycyaena) dubia*?

Conclusion

Evolutionary Roles of *Thalassictis* and *Palinhyaena*

During the Turolian stage, *Thalassictis* was the main and most successful lineage among the small and medium-sized hyaenids. *T. robusta*, *T. wongi* and *T. hipparionum* are only slightly different species in different areas of the Old World. *T. hyaenoides s. str.*, as here understood by me, represents the culminating stage of the phylogenetic lineage. The basic structure of this lineage, as evidenced by the skull and teeth, is highly constant. The skulls are always comparatively dolicocephalic, the preorbital foramen lies above and in front of the anterior root of P^4 , the posterior palatine foramen lies behind the middle line of P^2 , the posterior border of the bony palate extends far back to M^2 , the incisors are without prominent accessory cusps and ridges, diastemata are always present before and behind P^1 , cheek teeth are weakly imbricated (with longer accessory cusps) and the upper molars and the talonid of M_1 are less reduced. The most striking thing is that the ear-region of *Thalassictis hyaenoides s. str.*, especially the protrusive and bulbiform mastoid process, is similar to that of recent *Hyaena brunnea*. So far as we know, the bulbiform mastoid process is characteristic of *Hyaena brunnea*. So it also seems probable that *T. hyaenoides*, or its like, may have given rise to the recent *Hyaena brunnea*. *Thalassictis (Lycyaena) dubia* or *T. (L.) chaereticis* might be separated from the same lineage somewhere after the stage of *T. wongii* and specialized in a different way. It lost its M^2 precociously and all the teeth became thinner. It gave rise to the specialized group of *Chasmaporthetes*.

The other phylogenetic lineage, which was not so successful at that time, but more promising in the later period, is *Palinhyaena*. As already pointed out by the author several times, this lineage showed a series of features reminiscent of the recent genus *Crocota*. These characters are: the brachycephalic skull, narrow and long palatine fossa pierced by a small anterior palatine foramen, preorbital foramen above the middle of P^3 , posterior palatine foramen before the middle of P^2 , forward position of the posterior border of the bony palate, strongly developed secondary structures on the posterior side of incisors, precocious reduction in size of the extremities of the tooth row and strong main cusps of the cheek teeth with weak accessory cusps, etc. Perhaps it is not superfluous to mention here that there is a rather good sample of Ruscinian-Villafranchian hyaenids from Licent's collection, which shows that the intermediate forms between the recent *Crocota* and *Palinhyaena* might be the forms now designated

as species of *Hyaenictis*, "*Hyaena*" *donnezani* and *Lycyaena*.

If *Hyaena brunnea* is really derived from *T. hyaenoides*, *Crocota* and *Hyaena* must stem from different lineages and they may have diverged as early as the end of the St. Alban stage. *Chasmaportetes*, although its teeth are more similar to *Crocota*, nevertheless, came from the *Thalassictis* lineage. The other alternative is that all the recent hyaenids, *Hyaena* and *Crocota*, derive from *Palinhyaena*, as supposed by Qiu *et al.* (1979), and *Thalassictis* is only a side branch in the Family Hyaenidae.

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PLATES

Plate 1

Palinhyana reperta, M. 41-42 (Zdansky Ex. 2 of
“*I. hyaenoides*”) (All figures natural size).

- Fig. 1 Ventral view of skull;
- Fig. 2 Crown view of lower jaws;
- Fig. 3 Lateral view of lower jaw.



Plate 2

- Fig. 1 *Palinhyena reperta*, M. 7169 (Zdansky Ex. 20 of "*I. hyaenoides*"), right horizontal ramus, lateral view;
- Fig. 2 The same, crown view;
- Fig. 3 *Palinhyena reperta*, M. 7158 (originally labelled as "*I. sinense*") lower jaw, crown view;
- Fig. 4 the same, lateral view;
- Fig. 5 *Thalassictis hyaenoides s. str.*, M. 7173 (Zdansky Ex. 15 of "*I. hyaenoides*"), left horizontal ramus with P₂ – M₁, crown view. (All figures natural size.)



Plate 3

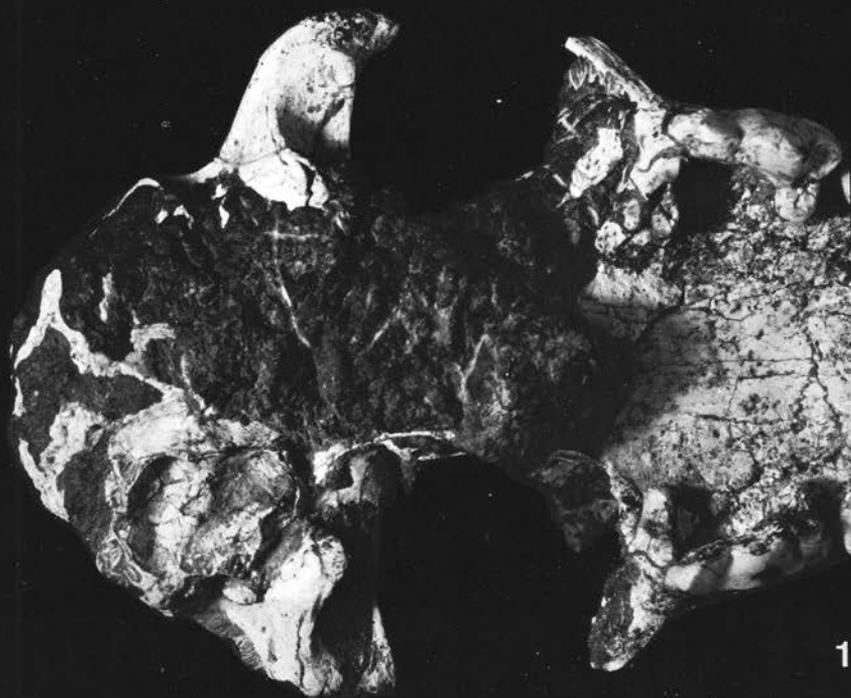
- Fig. 1 *Palinhyana reperta*, M. 36 (Zdansky Ex. 5 of "*I. hyaenoides*"), basicranium, shows the opened bulla and the septum;
- Fig. 2 *Thalassictis hyaenoides* s. str., M. 44 (Zdansky Ex. 14 of "*I. hyaenoides*"), left horizontal ramus, lateral views;
- Fig. 3 The same, crown view. (All figures natural size.)



3



2



1

Plate 4

- Fig. 1 *Thalassictis hyaenoides* s. str., M. 2849 (Zdansky Ex. 8 of "*I. hyaenoides*"), Basicranium;
- Fig. 2 *Thalassictis wongi*, left mandibles, crown view: (lower of the two) M. 3854 (Zdansky Ex. 1 of "*I. hyaenoides*"); (upper of the two) M. 8201 (Zdansky Ex. 23 of "*I. wongi*");
- Fig. 3 *Thalassictis (Lycyaena) dubia*, M. 7155 (originally labelled as "*I. hyaenoides*"), palate, ventral view. (All figures natural size.)



