Thalassictis wongii (Mammalia: Hyaenidae) and Related Forms from China and Europe.

BJÖRN KURTÉN

Kurtén, Björn. 1985 10 01: *Thalassictis wongii* (Mammalia: Hyaenidae) and related forms from China and Europe. *Studies of Chinese Fossil Vertebrates.* S.G. Lucas and N.J. Mateer (eds.). *Bulletin of the Geological Institutions of the University of Uppsala,* N.S. Vol. 11 pp. 79–90. ISSN 0302-2749.

A number of *Thalassictis* taxa from the late Miocene of China are characterised and compared with contemporary material from Samos (Greece) by odontometric analysis, employing Simpson's ratio diagram as the main instrument. The taxa are *T. w. wongii* (Zdansky) (localities 30, 43, 108, 109), *T. w. atalanta,* new subspecies (locality 49) and *T. mesotes,* new species (localities 110, 115). The Samos hyaenid is *T. wongii* ssp. Useful odontometric characters include absolute size, relative width of premolars, reduction of upper molars, and relative length of M_1 trigonid. Implications for relative dating are mostly uncertain, but the *T. w. wongii* localities are probably close in age to each other and to the Samos bone-bed (8.5 – 9.0 MA).

Björn Kurtén, Department of Geology, University of Helsinki, Snellmaninkatu 5, 00170 Helsinki 17, Finland. October 10th, 1983.

Introduction

Small Hyaenidae, often referred to as "ictitheres", are common in the late Miocene (Vallesian and Turolian) *Hipparion* faunas of Asia and Europe, and may occur in large numbers at certain localities (Zdansky 1924; Kurtén 1952, 1953; Solounias 1981). Due to various misidentifications, to the proposal of superfluous genera and species, and to the lack of consistent quantitative studies, their taxonomy is in a chaotic state. Although many students have continued to lump them in *"Ictitherium"*, it was shown by Kurtén (1957a, 1976, 1982) that the genera *Icititherium* and *Thalassictis* are distinct and indeed widely divergent. Crusafont and Petter (1969) and Solounias (1981) concur in this opinion. The genus *Ictitherium* Wagner comprises *I. viverrinum* Roth and Wagner and a small group of related, small species, whereas *Thalassictis* Gervais *ex* Nordmann includes a wider range of species from fox-sized to wolf-sized (see Kurtén, 1982 and Solounias (1981) for further discussion).

To lay the foundation for a more satisfactory taxonomy of the admittedly "difficult" genus *Thalassictis,* in which the morphology is relatively stereotyped, careful metric analysis beginning at the local population level is recommended. The following procedure is suggested:

(1) The minimum number of populations represented in each local fauna is determined and their variate means calculated. The ratio diagram of Simpson (1941) is an excellent instrument for this purpose.

(2) Mean characters of such populations are compared between local faunas of the same region.

(3) Analogous comparisons are extended to more distant geographic areas (e.g. China with Europe). Again, the ratio diagram is highly useful in pinpointing resemblances and differences which may be further evaluated by univariate or multivariate comparison, in steps (2–3).

In the present paper, this method has been applied to *Ictitherium* and *Thalassictis* in the Lagrelius Collection, Department of Historical Geology and Palaeontology, University of Uppsala, with special reference to the medium-sized forms generally referred to *"Ictitherium"* (=*Thalassictis*) *wongii.* They are then compared with European material. The intent has been to arrive at, and characterize, the minimum number of taxa represented in the Chinese material (steps 1–2) and to resolve which of them, if any, are identical with European taxa (step 3). Problems of geographic and temporal variation will obviously intrude and are dealt with by the use of the subspecies category. At the present day, China and Europe are in the same biogeographical province, and have numerous species in common; there is every reason to assume the same for the late Miocene (Kurtén, 1957a). Thus heterogeneity, not homogeneity, is saddled with the burden of proof, and a provincial taxonomy is *a priori* suspect.

Chinese small Hyaenidae: historical note

In 1903, Schlosser described a few teeth of small hyaenids in Richthofen's "drugstore collection", tentatively identifying the material as *"Ictitherium" hipparionum* (Gervais), a European species. A firm basis for further work was laid by Zdansky (1924, 1927) in his detailed and well-illustrated description of the material which had been collected by the Sino-Swedish Expedition, and which is kept in the Lagrelius Collection. Zdansky erected four species of *Ictitherium,* two of which are now referred to *Thalassictis: I. gaudryi, I. sinense, T. wongii,* and *T. hyaenoides*.

In later work, the species distinguished by Zdansky have generally been accepted, although Kurtén (1953, 1954) suggested that *I. sinense* might be merged with *I. gaudryi,* a possibility also noted by Zdansky. Additional material in the Frick Collection, American Museum of Natural History, however, confirms the specific distinction of *I. sinense* (Solounias, personal communication). There have been suggestions that the Chinese species may represent the eastern wings of continuous Palaearctic populations also known from Europe. Thus, *I. gaudryi* appears to be conspecific with the European *I. viverrinum* (Kurtén, 1954; 1982). Solounias (1981) and Kurtén (1982) have identified *T. wongii* at Samos. Qiu *et al.* (1979) considered *T. hyaenoides* conspecific with the European *T. hipparionum.* Solounias (1981), however, in my opinion correctly, maintains that these two species are distinct; on the other hand, he identified certain larger *Thalassictis* at Samos with *T. hyaenoides.* As a result of preliminary analysis, it may be noted that the Chinese material in the Lagrelius collection which has been referred to *T. hyaenoides* is heterogeneous and that the Samos hyaenid is not the same taxon as *T. hyaenoides s.str.* from Locs. 30 and 44 (the latter is the type locality). It may yet prove to be conspecific with some one of the larger forms originally lumped in *T. hyaenoides*.

From the above account, it will be evident that the only way to reach a reliable taxonomic grouping of *Thalassictis* will be by detailed, first-hand cross-comparison of the entire Palaearctic material.

Material

The principal material for the present study is in the Lagrelius Collection of the Department of Historical Geology and Palaeontology, University of Uppsala (PMU). It was described by Zdansky (1924, 1927) *q.v.* for lists of localities and specimens. A few of Zdansky's specimens were used in exchange; these have been studied in the Senckenberg Museum, Frankfurt am Main, and the American Museum of Natural History, New York. Also, the Lagrelius Collection comprises some additional specimens which evidently were not at hand when Zdansky wrote his memoir.

The Chinese material of *T. wongii* and related forms was compared with a sample of *T. wongii* from Samos, Greece (see Solounias, 1981); the material is scattered in various museums.

Methods

The study focuses on the cheek teeth. I have measured dimensions which have been found to be (1) easily defined and reproducible and (2) informative as to taxonomic characters. The following measurements have been used: (1) Upper canine width (transverse at base), lower canine length (anteroposterior – mesiodistal at base). These measurements were chosen because they happened to be obtainable for most specimens. (2) Premolars, P^{2-3} and P_{2-4}, length and width (mesiodistal and buccolingual, the former always taken so as to give the greatest diameter, the latter transverse to it). In addition, the notch-to-notch length of the protoconid or main cusp of P_4 was measured. For P^1, only the length was used. (3) Premolar, P^4, length, width, blade width, and paracone and metastyle lengths. The length was measured externally in the plane of the blade, the width includes the protocone. Blade-width is taken at the junction of the paracone and the metastyle. Cusp-length was measured internally; note that the length of the metastyle was taken obliquely, from the internal notch between the paracone and the metastyle, to the posterior end of the tooth. (4) Molar, M_1, length, width, and trigonid length. Length and width as for P_{2-4}. The length of the trigonid, which (together with the total length) gives information on the development of the shearing blade, relative to the talonid, is measured from the front end of the tooth to the hind-edge of the protoconid. (5) Molars, M^{1-2}, width (greatest buccolingual diameter) and length (anteroposterior, transverse to width). (6) Molar, M_2. Length and width.

Measurements were generally taken to the nearest tenth of a millimetre. Consistency, tested by repeated measurements, is adequate. All measurements are given in millimetres. In Table 1, N = number of individuals (for associated left and right specimens, the mean was used), M = mean (with standard error if $N \geq 3$), $S.D.$ = standard deviation and V = Pearson's coefficient of variation (both given if $N \geq 4$), *O.R.* = observed range of variation.

Of the total 28 variates (see Table 1), a selection of 20 were treated by means of Simpson's (1941) well-known ratio-diagram method. This was done in preference of, for instance, multivariate analysis for the following reasons: (1) much of the material is fragmentary and association of upper and lower jaws scarce, which would make it impossible to use more than a small fraction of the material at hand, (2) the ratio-diagram immediately reveals the kind of differentiation encountered. It was found that populations form easily identified "bundles" in the diagrams and virtually every specimen can be determined in the first step of the analysis. In the comparison of populations from different sites (the second and third steps in the analysis as outlined in the Introduction), the visual patterns in the ratio diagram are similarly easy to evaluate. Statistical differences could then be evaluated by means of univariate and bivariate analyses.

Taxonomy

Family HYAENIDAE Gray, 1869

Genus THALASSICTIS Gervais, 1850, *ex* Nordmann

TYPE SPECIES: *Thalassictis robusta* Gervais 1850 ex Nordmann, designated by Palmer (1904).

INCLUDED SPECIES: *T. hipparionum* (Gervais), *T. wongii* (Zdansky), *T. mesotes* Kurtén, new species, *T. hyaenoides* (Zdansky), *T. certa* (Forsyth Major) and several other species of mostly uncertain status.

DISTRIBUTION: Palaearctic and Indian regions; in Europe, Astaracian, Vallesian and Turolian Land Mammal Ages.

REMARKS: The generic distinction between *Thalassictis* and *Ictitherium* Wagner was demonstrated in Kurtén (1982), *q.v.* for a discussion. It was shown that *Thalassictis* includes *Palhyaena* Gervais and *Miohyaena* Kretzoi; for further synonymy see Solounias (1981: 66–67). I follow Solounias in including *Hyaenictitherium* Kretzoi and *Hyaenalopex* Kretzoi in *Thalassictis* but wish to reserve comments on his proposed inclusion of *Lycyaena* Hensel.

Thalassictis wongii (Zdansky)
1924 *Ictitherium wongii* Zdansky, p. 73

TYPE: (lectotype: Solounias 1981). PMU 3708-3709, associated skull and mandible (Zdansky's Ex. 14); figured by Zdansky (1924, Pl. 15); from locality 109, Shansi, China.

DIAGNOSIS: (emended from Solounias, 1981). Smaller than *T. hyaenoides*, larger than *T. robusta*. Also differs from *T. hyaenoides* in: skull less deep; sagittal crest less developed; P^{2-3}, P_{2-4} more compressed; M^2 less reduced, triangular; M_1 talonid less reduced; masseteric fossa shallower; angular process longer; coronoid process relatively larger.

REFERRED SPECIMENS: See under subspecies and discussion.

Thalassictis wongii wongii (Zdansky)

REMARKS: The nominate subspecies includes type and referred material from localities 30, 43, 108 and 109 all in Shansi, China (including Zdansky's Ex. 1-3, 5-22, 24, 26, 28). For measurements see Table 1. See also Fig. 1 (right) and Fig. 2 (centre).

Thalassictis wongii atalanta Kurtén, new subspecies

Ictitherium wongii Zdansky, 1924, p. 81 (*pars*)

HOLOTYPE: PMU not listed, right mandible fragment with M_1 in situ and P_4 emerging (Fig. 2, bottom); from locality 49, Shansi, China.

DERIVATIO NOMINIS: Greek *atalantos*, of equal weight.

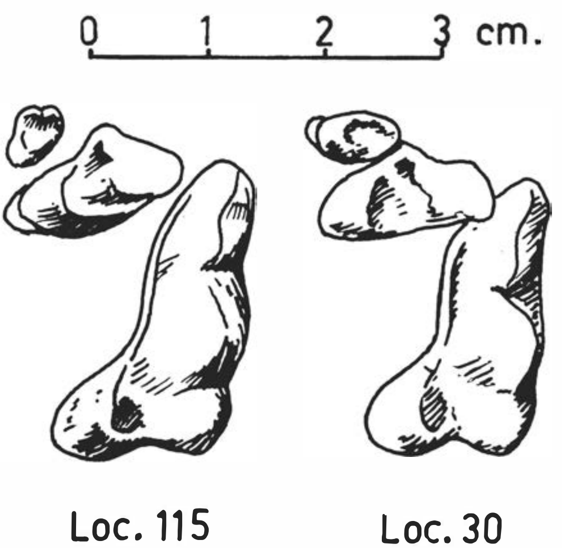

Fig. 1 Thalassictis, right P^4–M^2, occlusal views. Left, *T. mesotes,* new species, holotype, Loc. 115; right, *T. wongii wongii* (Zdansky), Zdansky's Ex. 11, Loc. 30. Both in PMU Uppsala.

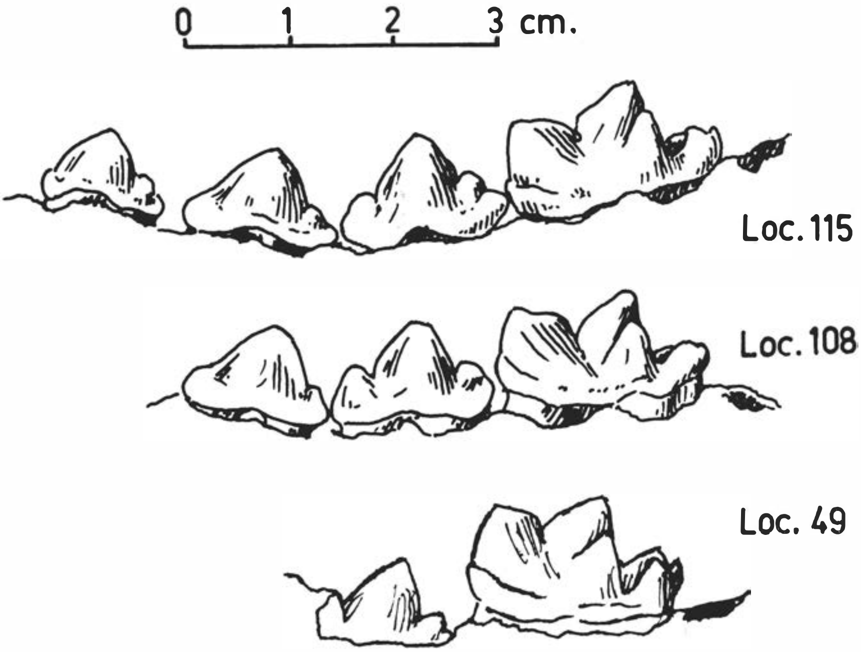

Fig. 2. Thalassictis, right lower dentitions, lingual views. Top, *T. mesotes,* new species, holotype, Loc. 115; middle, *T. wongii wongii* (Zdansky), Zdansky's Ex. 22, Loc. 108; bottom, *T. wongii atalanta,* new subspecies, holotype, Loc. 49. Top figure reversed from left dentition. All in PMU Uppsala.

DIAGNOSIS: Slightly larger, with markedly larger canine teeth than nominate subspecies; M^2 more reduced in relation to P^4. For measurements see Table 1.

REFERRED SPECIMENS: Zdansky's Ex. 4 (a skull) and Ex. 23 (a mandible) of "*I. wongii*", and additional material (snout fragment, palate, left upper and lower jaws *in situ,* skull fragment, isolated M^2, mandible) from locality 49, Shansi, China.

REMARKS ON SUBSPECIES OF *T. WONGII:* Several taxa of "*Ictitherium*"in the *T. wongii* size range have been erected for hyaenids from Europe and Asia minor. It is possible that the subspecies of *T. wongii* present at Samos (see Solounias, 1981) may be referable to one of these.

Thalassictis mesotes sp. nov.

1924 Ictitherium hyaenoides Zdansky, p. 90 (*pars*).

HOLOTYPE: PMU, partial skull with right mandible (Fig. 1, left; Fig. 2, top); from locality 115, Kansu, China.

DERIVATIO NOMINIS: Greek *mesotes,* mean.

DIAGNOSIS: Size near *T. hyaenoides;* lower premolars compressed as in *T. wongii,* upper P^{2-3} slightly broader, all much narrower than in *T. hyaenoides:* M^1 more reduced and more compressed anteroposteriorly, and M^2 much more reduced than in *T. wongii:* M^{1-2} less reduced than in *T. hyaenoides;* M_1 talonid more reduced than in *T. wongii,* less than in *T. hyaenoides.* For measurements see Table 1.

REFERRED SPECIMENS: Skull with rami, associated upper and lower dentitions, two upper dentitions, one isolated P^2, two isolated P^4, two mandibles, all in PMU collections from locality 115, Kansu, China; two mandibles (one of which is Zdansky's Ex. 21 of "*I. hyaenoides*"), from locality 110, Shansi, China.

Chinese local faunas

The Chinese *Hipparion* fauna is represented in the Lagrelius Collection by numerous local faunas or faunules from the provinces of Honan, Chihli, Kansu, Shansi and Shensi. Most of the sites are close to the river Hwang-Ho or major tributaries. The geographic distribution of the herbivorous mammals indicates the existence of two distinct palaeoenvironments: an eastern forest biotope with a preponderance of brachydont browsers and a northern and western steppe or savanna area with hypsodont grazers in the majority (Kurtén, 1952). These were named the *gaudryi* and *dorcadoides* faunas respectively, after two characteristic *Gazella* species. Some local faunas, notably that of locality 49 near Paote, Shansi, show a mixture of elements, and presumably existed at a time when the boundary of the two palaeoenvironments traversed the area.

Material from the following sites is treated in the present paper: (1) *Dorcadoides* fauna: Localities 30, 108, 110 (near Paote, Shansi; locality 115 (near Kingyang, Kansu). (2) Mixed fauna: Localities 43, 49, 109 (near Paote, Shansi).

Populations in local faunas

Local populations of smaller Hyaenidae were studied by use of the ratio-diagram method, recording data for each specimen separately (see Figs. 3-5). Twenty variates were used, and the standard of comparison (vertical line at zero of the log difference scale) is the same in each case: mean values for the Samos sample of *T. wongii.*

The minimum number of populations represented at each locality is generally evident from the bundling of the patterns in the diagram, and varies between one and four.

LOCALITY 30 (Fig. 3): This locality, which lies in the Paote area, in addition to being particularly rich in small Hyaenidae, is also one of the most typical *dorcadoides* fauna sites. It yielded mass occurrences of the hypsodont bovids *Urmiatherium* and *Gazella dorcadoides,* the hypsodont giraffid *Samotherium,* and the rhinocerotid *Chilotherium.* The extremely hypsodont rhinocerotid *Sinotherium* is also present. On the other hand, the brachydont giraffid *Palaeotragus* is scarce, and there are only single specimens of a suid and a cervid.

The hyaenids, apart from the ubiquitous *Adcrocuta eximia* ("*Hyaena variabilis*"), are represented in the ratio diagram (Fig. 3). In spite of the large number of specimens, the data dissociate readily into two contrasting patterns, indicating the presence of two populations. One of the "bundles" tends to cluster around the standard, indicating absolute and relative proportions close to the latter. This material is referred to *Thalassictis w. wongii.*

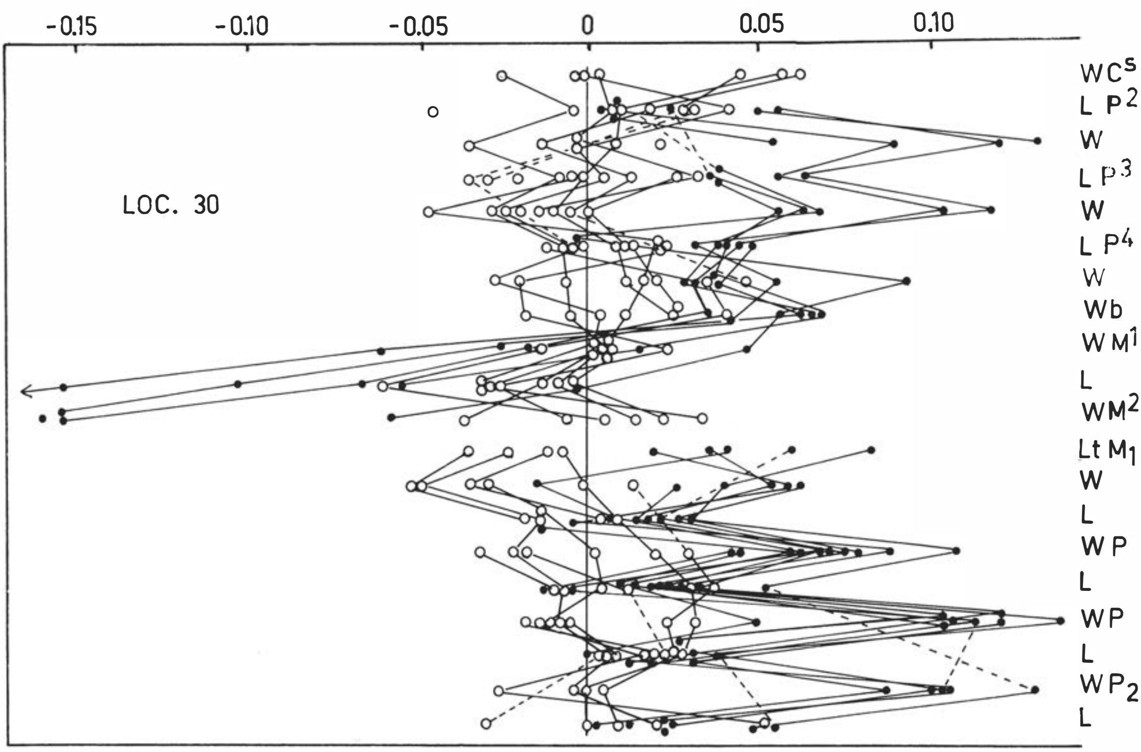

Fig. 3. Ratio-diagram, showing individual measurements for small Hyaenidae at locality 30 (Paote, Shansi), compared with means for *Thalassictis wongii* from Samos, Greece (standard). The scale shows log difference from standard. Two populations are represented (*T. w. wongii,* open circles; *T. hyaenoides,* filled circles). Variates indicated at right margin; L length, Lt trigonid length (in M_1), W width, Wb blade width (in P^4). See text for discussion.

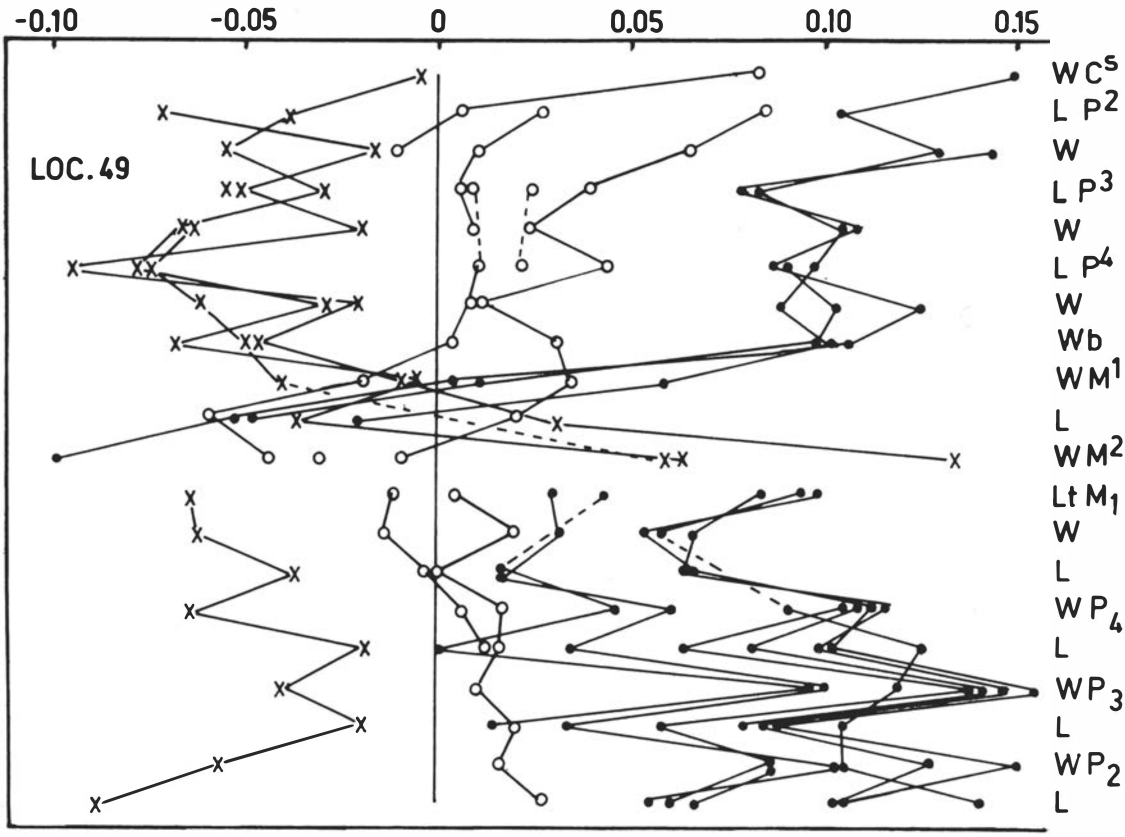

Fig. 4. Ratio-diagram, locality 49 (Paote, Shansi). Represented are *Ictitherium* (X), *Thalassictis w. atalanta* (open circles, *T.* cf. *hyaenoides* ssp. (filled circles). For other explanations and discussion see Fig. 3 and text.

Hyaenid material which exhibited similar clustering at the standard occurs at localities 43, 108, and 109, and includes the lectotype (Solounias, 1981) of *T. wongii*. Detailed univariate and bivariate comparisons failed to disclose any significant differences between these and the Loc. 30 *T. wongii* and ensuing mean ratio diagram patterns were nearly identical. Thus, all of these samples may be referred to the same subspecies.

The second "bundle" in Fig. 3 shows a strikingly different pattern. It deviates from the standard, and from *T. w. wongii,* in the following characters:

(1) Length measurements of tooth-crowns average sligthly greater, although there is considerable overlap except in the cases of P^3 and P^4.

(2) Widths of precarnassial premolars are much greater, absolutely and also in relation to crown lengths; this is reflected in the marked zigzag pattern.

(3) While the width of M^1 is approximately the same as in *T. w. wongii,* the length of this tooth is smaller, and M^2 is more reduced. Both upper molars are more variable in size.

(4) The trigonid of M_1 is absolutely and relatively longer, and M_1 also tends to be broader.

The sample is referred to *T. hyaenoides* s.str., because the lectotype (Solounias, 1981) from Loc. 44 is similar, and fits perfectly in the same "bundle".

LOCALITY 49 (Fig. 4): This is again a Paote site with a diverse (more than 40 taxa) fauna, but in contrast with locality 30 there is a mixture of forest and steppe elements, the former actually being in the majority. Almost two-thirds of the herbivores (number of individuals) are suids and deer, but there is also a fair number of grazing bovids (see Kurtén, 1952).

At first glance it appears that there are three populations of hyaenids – a small form, a medium-sized and a large one. However, the small form shows two contrasting patterns in the upper denti-

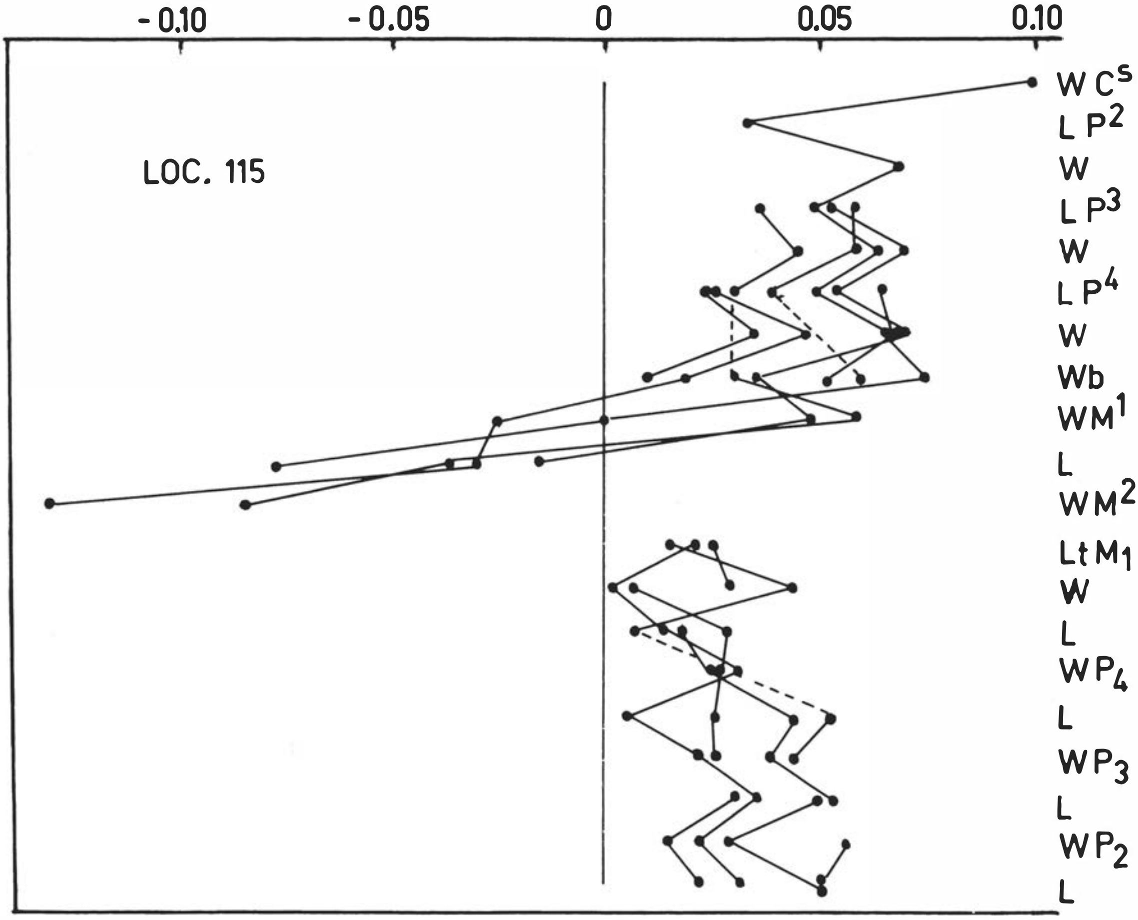

Fig. 5. Ratio-diagram, locality 115 (Kingyang, Kansu). The single population represented is *Thalassictis mesotes*. See text and Fig. 3 for other explanations and discussion.

tion, one specimen having much broader P^2 and P^3 than the others. That specimen is the type of *Ictitherium sinense,* while the other group includes the type of *I. gaudryi.* As a whole, the *Ictitherium* specimens differ from the standard (*T. wongii,* Samos) in (1) smaller size, (2) relatively large canines, (3) short càrnassials, (4) thick upper carnassial blades, (5) relatively much larger upper molars.

The medium-sized form is fairly close to the standard but differs from it in (1) slightly larger size, (2) larger canine, (3) longer P^2, (4) somewhat more reduced upper molars, (5) shorter M_1 relative to $P_{2\text{-}4}$. This material includes the type of *Thalassictis wongii atalanta* subsp. nov.

The large form, finally, deviates in the general manner of *T. hyaenoides* but tends to exceed the Loc. 30 form of that species in size. It may represent a distinct subspecies of *T. hyaenoides.*

LOCALITY 115 (Fig. 5): This Kansu site, at Kingyang by the King-Ho river, a tributary of the Hwang-Ho, and the nearby locality 116, are the westernmost localities in the group, and have a grazer-dominated *dorcadoides* fauna. The ratio diagram (Fig. 5) reveals the presence of a single population. It is well distinguished from the standard by larger average size, very large canines, and reduction of the upper molars. On the other hand, there is no trace of the broadening of the premolars so typical of *T. hyaenoides,* except in P^2. Thus, the locality 115 hyaenid takes an intermediate position between *T. wongii* and *T. hyaenoides,* sharing some characters with the former and some with the latter, while others are intermediate (e.g. overall size and the development of the M_1 trigonid). The material includes the type of *Thalassictis mesotes* sp.nov.

LOCALITIES 43, 108, 109, 119: In addition to locality 30, localities 43, 108 and 109 have yielded additional material of *T. w. wongii;* the two latter samples are fairly large. Of these, localities 43 and 109 include some forest forms in addition to the predominant grazers, while locality 108 appears to have a "pure" *dorcadoides* fauna. All are in the Paote area.

Two specimens of *T. mesotes,* indistinguishable from the topotype material, are from locality 110, a Paote site with a *dorcadoides* fauna.

Interpopulation Comparisons

When means for local samples were compared, by means of ratio diagrams and univeriate and bivariate analysis, it was found that the samples of *T. w. wongii* from localities 30, 43, 108 and 109 agreed in every respect. In the same way, the samples of *T. mesotes* from localities 110 and 115 could be united. The sample of *T. w. atalanta* from locality 49 was found to be unique.

The ratio-diagram in Fig. 6 summarizes the results, based on grand means for *T. w. wongii, T. w. atalanta* and *T. mesotes,* related to the standard (*T. wongii* from Samos). For comparison, means for *T. hyaenoides* (loc. 30) have also been plotted. Most of the differences which may be noted have already been commented upon.

UNIVARIATE COMPARISON: A series of *t* tests, based on Table 1, gave the following results: (1) *Thalassictis w. wongii* and *T. w. atalanta.* – The material of *T. w. atalanta* is small and the statistical significance of the difference is doubtful for most variates. However, the TWA C^s width is 2.39 standard deviations from the TWW mean ($P{\sim}0.05$) and values approaching $P = 0.05$ were also found for other variates (lengths of P^3 and P^4). The difference is probably significant. (2) *Thalassictis w. wongii* and *T. mesotes.* – High significance levels (P < 0,01) were found for most variates. The difference is certainly significant. (3) *Thalassictis w. atalanta* and *T. mesotes.* – The material of both taxa is re-

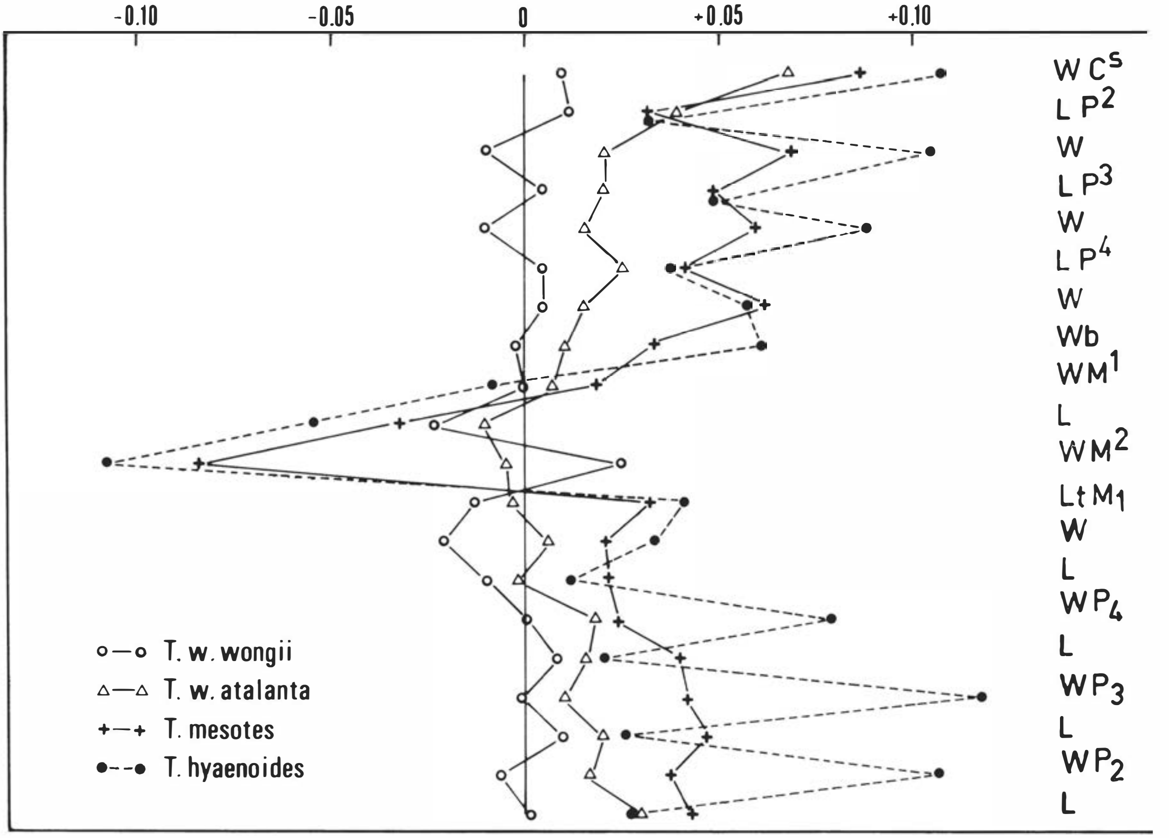

Fig. 6. Ratio-diagram for means of Chinese taxa of *Thalassictis* as labelled, compared with standard (*T. wongii,* Samos, Greece). The means for *T. hyaenoides* are based on the sample from locality 30. See text and Fig. 3 for other explanations and discussion.

Table 1. Dental dimensions in *Thalassictis wongii*, Samos (TWS), *T. w. wongii*, China Locs. 30, 43, 108, 109 (TWW), *T. w. atalanta*, China Loc. 49 (TWA), and *T. mesotes*, China Locs. 110, 115 (TM).

	N	M	S.D.	V	O.R.
C^s Width					
TWS	6	7.03±0.20	0.48	6.8	6.5– 7.9
TWW	14	7.17±0.11	0.43	6.0	6.4– 7.8
TWA	1	8.2	–	–	–
TM	1	8.6	–	–	–
P^1 Length					
TWS	8	5.56±0.28	0.80	14.4	4.7– 6.7
TWW	12	5.35±0.14	0.50	9.4	4.8– 6.5
TWA	–	–	–	–	–
TM	2	6.0	–	–	–
P^2 Length					
TWS	19	12.83±0.16	0.68	5.3	11.9–14.4
TWW	18	13.19±0.11	0.45	3.4	12.6–14.0
TWA	3	14.00±0.78	–	–	12.9–15.5
TM	1	13.8	–	–	–
P^2 Width					
TWS	18	6.48±0.10	0.44	6.8	5.8– 7.6
TWW	15	6.36±0.08	0.32	5.0	6.0– 6.9
TWA	3	6.80±0.36	–	–	6.3– 7.5
TM	1	7.6	–	–	–
P^3 Length					
TWS	22	16.21±0.14	0.67	4.1	14.9–17.4
TWW	23	16.35±0.19	0.91	5.6	14.8–18.5
TWA	4	17.03±0.30	0.60	3.5	16.5–17.8
TM	4	18.15±0.15	0.31	1.7	17.7–18.4
P^3 Width					
TWS	22	9.01±0.13	0.59	6.6	8.1– 9.9
TWW	19	8.79±0.11	0.49	5.6	8.1–10.0
TWA	2	9.35	–	–	9.2– 9.5
TM	4	10.35±0.13	0.26	2.5	10.0–10.6
P^4 Length					
TWS	23	24.90±0.20	0.96	3.9	22.8–26.4
TWW	21	25.18±0.23	1.04	4.1	23.4–27.0
TWA	3	26.37±0.55	–	–	25.5–27.4
TM	7	27.41±0.39	1.03	3.8	26.3–29.0
P^4 Width, anterior					
TWS	21	13.72±0.18	0.84	6.1	12.0–15.2
TWW	20	13.86±0.28	1.27	9.2	10.9–16.9
TWA	2	14.2	–	–	–
TM	5	15.80±0.25	0.57	3.6	15.0–16.3
P^4 Width, blade					
TWS	23	7.86±0.12	0.58	7.4	6.6– 8.8
TWW	19	7.81±0.10	0.43	5.5	7.2– 8.7
TWA	2	8.05	–	–	7.8– 8.3
TM	7	8.50±0.17	0.46	5.4	7.9– 9.2
P^4 Length, paracone					
TWS	17	9.12±0.09	0.38	4.2	8.6–10.0
TWW	18	9.36±0.11	0.48	5.1	8.3–10.0
TWA	1	9.8	–	–	–
TM	6	10.25±0.17	0.41	4.0	9.7–10.7
P^4 Length, metastyle					
TWS	19	9.68±0.11	0.49	5.1	8.8–10.7
TWW	16	10.03±0.14	0.56	5.6	9.2–11.0
TWA	1	10.6	–	–	–
TM	6	10.67±0.16	0.40	3.8	10.3–11.3
M^1 Width					
TWS	23	15.55±0.17	0.82	5.3	14.3–17.7
TWW	17	15.53±0.17	0.72	4.6	14.0–17.1
TWA	2	15.8	–	–	14.8–16.8
TM	4	16.23±0.70	1.41	8.7	14.6–17.5
M^1 Length					
TWS	18	8.33±0.12	0.51	6.1	7.5– 9.0
TWW	18	7.91±0.12	0.49	6.2	6.8– 8.5
TWA	2	8.15	–	–	7.4– 8.9
TM	4	7.75±0.23	0.47	6.1	7.1– 8.2
M^2 Width					
TWS	15	7.02±0.14	0.55	7.8	6.1– 8.4
TWW	15	7.42±0.11	0.44	5.9	6.8– 8.2
TWA	3	6.95±0.16	–	–	6.7– 7.2
TM	2	5.8	–	–	5.5– 6.1

	N	M	S.D.	V	O.R.
M^2 Length					
TWS	11	4.45±0.10	0.34	7.6	4.0– 4.9
TWW	15	4.62±0.08	0.31	6.7	4.2– 5.4
TWA	2	4.65	–	–	4.3– 5.0
TM	2	3.9	–	–	3.6– 4.2
C_i Length					
TWS	4	10.06±0.33	0.66	6.6	9.7–11.0
TWW	8	10.88±0.28	0.80	7.4	9.6–11.8
TWA	1	11.5	–	–	–
TM	3	11.93±0.23	–	–	11.7–12.4
P_2 Length					
TWS	11	11.98±0.27	0.88	7.4	10.5–13.3
TWW	19	12.01±0.13	0.56	4.7	11.2–13.5
TWA	1	12.8	–	–	–
TM	5	13.22±0.20	0.44	3.3	12.6–13.6
P_2 Width					
TWS	9	5.96±0.09	0.28	4.7	5.5– 6.3
TWW	16	5.88±0.08	0.33	5.6	5.4– 6.8
TWA	1	6.2	–	–	–
TM	5	6.48±0.12	0.26	4.0	6.2– 6.8
P_3 Length					
TWS	11	14.80±0.16	0.54	3.6	14.0–15.7
TWW	20	15.13±0.13	0.57	3.8	14.0–16.1
TWA	1	15.5	–	–	–
TM	6	16.47±0.16	0.38	2.3	15.9–16.9
P_3 Width					
TWS	9	7.21±0.08	0.23	3.2	6.9– 7.5
TWW	17	7.20±0.07	0.30	4.2	6.7– 7.8
TWA	1	7.4	–	–	–
TM	6	7.95±0.11	0.27	3.4	7.6– 8.3
P_4 Length					
TWS	12	16.51±0.18	0.61	3.7	15.6–17.7
TWW	18	16.84±0.19	0.80	4.8	15.1–18.1
TWA	2	17.15	–	–	17.1–17.2
TM	6	18.10±0.31	0.75	4.1	16.8–18.8
P_4 Width					
TWS	11	8.15±0.12	0.39	4.8	7.7– 8.7
TWW	15	8.17±0.12	0.46	5.6	7.4– 9.0
TWA	1	8.5	–	–	–
TM	4	8.63±0.11	0.22	2.6	8.3– 8.8
P_4 Length, protoconid					
TWS	9	7.83±0.11	0.32	4.1	7.3– 8.9
TWW	14	7.86±0.11	0.40	5.1	7.2– 8.5
TWA	2	7.95	–	–	7.7– 8.2
TM	3	8.30±0.06	–	–	8.2– 8.4
M_1 Length					
TWS	10	20.22±0.30	0.96	4.8	18.4–21.9
TWW	17	19.76±0.18	0.74	3.7	18.1–20.7
TWA	2	20.15	–	–	20.1–20.2
TM	6	21.27±0.19	0.47	2.2	20.6–21.7
M_1 Width					
TWS	11	8.62±0.12	0.41	4.8	7.8– 9.2
TWW	17	8.20±0.13	0.52	6.3	7.4– 9.1
TWA	2	8.75	–	–	8.3– 9.0
TM	6	9.05±0.14	0.34	3.8	8.6– 9.5
M_1 Length, trigonid					
TWS	10	14.55±0.20	0.63	4.3	13.6–15.5
TWW	14	14.12±0.14	0.54	3.8	13.0–14.9
TWA	2	14.45	–	–	14.2–14.7
TM	6	15.67±0.18	0.44	2.8	15.1–16.2
M_2 Length					
TWS	4	6.09±0.16	0.33	5.4	5.6– 6.3
TWW	5	5.92±0.38	0.85	14.4	5.0– 7.0
TM	2	5.9	–	–	5.9
M_2 Width					
TWS	2	5.1	–	–	5.1
TWW	5	5.07±0.20	0.45	8.9	4.4– 5.6
TM	2	5.35	–	–	5.1– 5.6

latively small and the resulting t-values are not significant. However, the two diverge widely in some characters and resulting V-values are abnormally high. They are not likely to represent the same population. (4) *Thalassictis w. wongii* and *T. wongii* from Samos. – The ratio-diagram indicates that this is the only meaningful comparison between Chinese and European samples. For the great majority of variates, no significant differences were found, in spite of the fact that both samples are statistically adequate, the combined N exceeding 30 in many instances. The Chinese (TWW) M^1 tend to average shorter anteroposteriorly than the Greek (TWS) ($P < 0,02$); TWW M^2 may be wider than TWS M^2 ($P < 0,05$); and TWW M_1 may be narrower than TWS M_1 ($P < 0,02$). Such differences may be random results in a series of 28 comparisons. On this score, the Chinese and Greek forms are only doubtfully distinct.

BIVARIATE COMPARISON: The ratio-diagram (Fig. 6) is a useful indicator of which variate pairs should be studied for possible differences. They were studied by means of analysis of variance. Six variate pairs were found to merit detailed investigation. For the sake of simplicity, they are treated here as indices of the type 100A/B, where A is (normally) smaller than B. Statistics for these indices (including *T. hyaenoides* for comparison) are given in Table 2, and they are compared in Table 3.

(1) *Thalassictis w. wongii* and *T. w. atalanta*. – The only possibly significant difference is WM^2/LP^4. (2) *Thalassictis w. wongii* and. *T. mesotes*. – Five indices differ significantly. P^2 and P^3 are relatively wider, M^2 more reduced relative to P^4 and M^1, the M_1 trigonid is relatively longer (i.e. the talonid more reduced) in TM. The last-mentioned index (Lt/LM_1) is stable within *T. wongii* as a whole (see Table 2). (3) *Thalassictis w. atalanta* and *T. mesotes*. P^3 is relatively broader in TM. (4) *Thalassictis w. wongii* and *T. wongii* from Samos. – P^2 and P^3 are relatively narrower, M^2 less reduced in relation to M^1 length, and P_4 possibly longer in relation to M_1, in TWW. The differences, although slight, are certainly valid in the three first-mentioned cases. On the other hand, Lt/LM_1 has the typical *wongii* value in both samples. A subspecific difference is indicated.

CONCLUSIONS: Absolute size, relative canine

Table 2. Dental indices for samples of *Thalassictis wongii* and *T. mesotes* (see Table 1 for details) and *T. hyaenoides*, China Locs. 30, 44 (TH).

	N	M	S.D.	O.R.
100 Width/Length P^2				
TWS	18	50.7±0.7	2.9	46.7– 55.8
TWW	14	47.9±0.5	2.0	44.1– 51.2
TWA	1	48.4	–	–
TM	1	55.1	–	–
TH	6	58.9±1.2	3.0	54.7– 62.1
100 Width/Length P^3				
TWS	21	55.6±0.7	3.2	48.2– 61.6
TWW	18	53.0±0.4	1.7	49.7– 56.6
TWA	1	53.4	–	–
TM	4	57.0±0.4	0.7	56.3– 57.7
TH	7	60.7±1.0	2.7	58.2– 65.3
100 Width M^2/Length P^4				
TWS	15	28.3±0.6	2.4	24.0– 31.8
TWW	12	29.2±0.5	1.7	25.6– 31.0
TWA	2	26.4	–	26.3– 26.5
TM	2	21.8	–	20.6– 23.1
TH	6	20.5±1.7	4.2	14.4– 26.3
100 Width M^2/Length M^1				
TWS	12	84.5±1.6	5.6	77.1– 96.0
TWW	13	93.4±1.7	6.0	82.4–101.4
TWA	2	86.0	–	81.5– 90.5
TM	2	73.9	–	70.5– 77.2
TH	6	75.6±3.7	9.1	67.2– 91.9
100 Length P_4/Length M_1				
TWS	9	82.1±1.3	3.8	77.9– 90.8
TWW	13	89.9±0.5	1.7	81.4–87.9
TWA	2	85.1	–	–
TM	6	85.1±1.5	3.6	80.4– 91.3
TH	8	83.8±1.2	3.3	80.6– 90.5
100 Trigonid Length/Length M_1				
TWS	9	71.7±0.5	1.6	68.8– 73.9
TWW	14	71.2±0.4	1.4	69.0– 72.8
TWA	2	71.7	–	70.6– 72.8
TM	6	73.7±0.9	0.6	73.1– 74.7
TH	7	77.6±0.8	2.1	75.2– 81.5

Table 3. Comparison between dental indices (see Table 2) in samples of *Thalassictis wongii* and *T. mesotes* (see Table 1). Table of P (probability); P > 0.10 indicated by dash.

	Samples compared			
Index	TWW–TWS	TWW–TWA	TWW–TM	TWA–TM
100 W/LP^2	<0.01	–	<0.01	–
100 W/LP^3	<0.01	–	<0.01	<0.02
100 WM^2/LP^2	–	<0.10	<0.01	–
100 WM^2/LM^1	<0.01	–	<0.01	–
100 LP_4/LM_1	<0.05	–	–	–
100 Lt/LM_1	–	–	<0.01	–

size, relative width of premolars, degree of reduction of upper molars, especially M^2, and relative length of M_1 trigonid (as an inverse measure of talonid reduction), appear to be the most useful odontometric characters in the taxonomy of *Thalassictis*. *Thalassictis w. atalanta* and the Samos form may be referred to the species *T. wongii* but are subspecifically distinct from the nominate subspecies and probably from each other. *T. mesotes* is distinct and in some respects intermediate between *T. wongii* and *T. hyaenoides*.

Implications for Relative Dating

The close similarity between the *T. wongii* populations of localities 30, 43, 108 and 109 suggests that they are close to each other in age. On the other hand, locality 49, which is in the same region, must be different in age, which is also suggested by its otherwise distinct fauna with a large admixture of forest forms (also present at loc. 109 but to a much lesser extent). Whether it is younger or later cannot be determined. The fact that the subspecies *T. w. atalanta* has derived characters in comparison with *T. w. wongii* (more reduced M^2, larger canine) may, or may not, imply a more recent age.

In the same area (at loc. 110), as well as in Kansu, occurs *T. mesotes*. As far as the Paote localities are concerned, a difference in age is again suggested. This may be a western species which temporarily extended its range into the area. The fact that this species has many derived characters compared to *T. wongii* does not necessarily bear on the relative dates. Both may have existed at the same time as vicarious forms.

Finally, the broad similarity between *T. w. wongii* and the Samos *T. wongii* suggests approximate contemporaneity. The Samos bone-bed is dated at 8.5-9.0 MA (Solounias, 1981).

REFERENCES

Crusafont Pairó, M & G. Petter 1969: Contribution a l'étude des Hyaenidae, la sous-famille des Ictitheriinae. *Ann. Paléontol.* 55, 89–129. Paris.

Kurtén, B. 1952: The Chinese *Hipparion* fauna. *Commentat. biol. Soc. Sci. Fenn. 13,* 1–82. Helsinki.

Kurtén, B. 1953: On the variation and populations. dynamics of fossil and recent mammal populations. *Acta zool. Fenn. 76,* 1–122. Helsinki.

Kurtén, B. 1954: The type collection of *Ictitherium robustum* (Gervais, ex Nordmann) and the radiation of the ictitheres. *Acta zool. Fenn. 86,* 1–26. Helsinki.

Kurtén B. 1957a: Helsingfors University, communicaciones. *Bol. Info. Actividades europeos en Paleo. Vertebr. 8–9,* 37–42. Sabadell.

Kurtén, B. 1957b: Mammal migrations, Cenozoic stratigraphy, and the age of Peking Man and the australopithecines. *J. Paleontol. 31,* 215–227. Tulsa, Oklahoma.

Kurtén, B. 1976: Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes Serv. Géol. Tunis 42,* 177–214. Tunis.

Kurtén, B. 1982: Status of the fossil hyaenids *Ictitherium viverrinum* and *Thalassictis robusta* (Mammalia). Z. Geol. Wiss. 10, 1009–1018. Berlin.

Palmer, T.S. 1904: Index generum mammalium. U.S. Department of Agriculture, Washington D.C.

Qiu Zhan-Xiang, Huang Wei-long & Guo Zhi-hui 1979: Hyaenidae of the Qingyang (K'ingyang) *Hipparion* fauna. *Vertebr. PalAsiatica. 17,* 200–221. Beijing.

Simpson, G. G. 1941: Large Pleistocene felines of North America. *Amer. Mus. Novit. 1136,* 1–27. New York.

Solounias, N. 1981: The Turolian fauna from the island of Samos, Greece. *Contrib. Vertebr. Evol.* 6, 1–232. Basel.

Zdansky, O. 1924: Jungtertiäre Carnivoren Chinas. *Palaeontol. Sin., Ser. C,* $1^{2(\ )}$, 1–146. Peking.

Zdansky, O. 1927: Weitere Bemerkungen über fossile Carnivoren aus China. *Palaeontol. Sin.,* (C) 4 (4), 1–30. Peking.

Printed by Ekenäs Tryckeri Ab, Ekenäs, Finland October 1st, 1985