

CRANIAL AND DENTAL CHARACTERISTICS IN THE SYSTEMATICS
OF OLD WORLD FELIDAE

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Introduction

A recent paper by Hemmer (1978) in this journal uses diverse sources of information to revise the systematics of the Felidae. It is the purpose of the present study to see whether Hemmer's views are supported in any degree by use of traditional skull and tooth characters.

The general skull morphology clearly separates the Felinae (i.e. Felidae excluding *Cryptoprocta*) into two sections. In the first, containing the restricted genus *Felis* as well as *Otocobus* [which, as Mazak (1979) has shown, is not separable even subgenerically from *Felis*], *Lynx* and *Caracal*, the whole skull is shorter and broader, especially the braincase; the face is relatively long; the superior orbital rims have a distinct backward trend as they go laterally; the postglenoid process is wedged up against the bulla (fig. 1, no. 3); the paroccipital process is long and extends down onto the side of the bulla; the interpterygoid space is broad (fig. 2, no. 2); the pterygoid processes end in very elongated points (fig. 3, no. 3); and the palate is short, with a median posterior prominence in many cases. The second section, which includes all other cats including the Pantherines and even, in many respects, *Acinonyx*, has a longer narrower skull with relatively longer braincase and temporal fossa; the superior orbital rims sweep outward with much less backward trend; the postglenoid process is free from the bulla, with a flat plane, of

varying size, postero-medial to it (fig. 1, nos. 1-2); the paroccipital process is very short; the interpterygoid space is much narrower (fig. 2, no. 2); the pterygoid processes are truncated (fig. 1, nos. 1-2); and the palate is longer, roofing over the posterior nares to a greater degree, and ends with a straight or concave posterior edge. There is considerable variation in some of these characters, such that certain species approach the *Felis* group to a greater or lesser extent (see below).

The unvarying nature of the characters of the first group, compared with the variable degree of expression of those of the second, and the diversity of species in the second section, suggest that the characters of the first section are synapomorph. The predominantly transverse pattern of flank markings in the first section (Weigel, 1961) links the members together into a compact group, and this is also Hemmer's interpretation.

An interesting character to consider is the shape of the contracted pupil (Nawa, 1967). In the restricted genus *Felis* this is always slit-like (Nawa's Type A); in the lynxes and the manul, however, it is a pointed oval (his Type C). In Nawa's data the pupil contracts to a spindle-shape (his Type B) in *Prionailurus*, *Profelis temmincki*, *Leopardus pardalis*, and in the Serval, Clouded leopard and Marbled Cat; Imaizumi (1967) figures this type in *Mayailurus*; Blom (1965) notes it in *P. aurata*; and I have observed it additionally in *Ictailurus*, *Oncifelis geoffroyi*

and *O. tigrinus*. Nawa recorded Type D, a circular pupil, in *Herpailurus*, the Pantherines and the Cheetah; I have observed it in *Lynchailurus*.

Within the second group, restricting ourselves to the Old World members in the present instance, a few outstanding problems demand attention. These are:

1. The relationship of the Marbled Cat, *Pardofelis marmorata*. Traditionally associated with *Profelis badia* (Pocock, 1917) or with *Prionailurus* (Weigel, 1961) in a group, Hemmer (1978) claims that it derives from the Pantherine stem.
2. The unity of the genus *Profelis*. Van Mensch & Van Bree (1972) consider, then reject, the possibility that the African species, *P. aurata*, may be closer to the Serval than to the Asian species (*P. temmincki*); Hemmer (1978) separates the Asian and African representatives into two different genera, as representing totally separate lineages.
3. The position of *Mayailurus*. Described as a full genus by Imaizumi (1967), this cat has generally been associated with *Prionailurus* (Hemmer, 1978), but the matter needs to be investigated more closely.

The Marbled Cat

The three competing theories of the relationships of this species can be tested on the basis of skull characters.

It should be mentioned at the outset that Pocock's (1917) description of the skull of his combined *Pardofelis* (including *badia* as well as *marmorata*) is not totally accurate; it fails to take

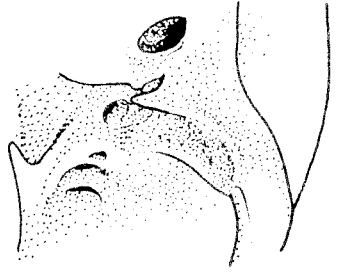
into account, and appears to lean more heavily on *marmorata*. The skull of *badia*, the Bornean Bay Cat, is that of a fairly typical *Profelis*, resembling *P. temmincki*, differing mainly in size-related characters such as the more extensive, often complete, ossification of the post-orbital bar.

As first shown by Mazák (1968), the most striking feature of the pantherine skull is the shape of the malar region. Other Felids, such as *Prionailurus* and *Profelis*, have along the malar-maxillary suture, just lateral to the infraorbital foramen, a strong angulation, causing a "shelf" which overhangs the foramen superolaterally. The Pantherines lack this angulation, and the infraorbital foramen is not sunk in a pit. In *Pardofelis*, as also in *Neofelis*, an angulation does exist but it is not at all marked, and there is no real "shelf", so that the foramen does not lie in a pit (fig. 3). If this feature is correctly interpreted as a derived one in the Pantherines, the hypothesis of a pantherine relationship for the Marbled Cat is supported.

The postglenoid process in *Prionailurus* (fig. 1, no. 2) points anteroinferiorly, leaving a broad flat surface behind it, anterior to the bulla. In *Profelis* the flat area is even broader; in the Pantherines the process is directed less anteriorly, and there is little remnant of the flat surface (a slight approach to *Felis*). In *Pardofelis* (fig. 1, no. 1) the postglenoid process points directly downward, or very slightly forward; there is no flat surface, the pre-bullar foramen lying immediately posteromedial to the process. In this feature also, therefore, the Marbled Cat resembles the Pantherines.

- Figure 1. Pterygoid and glenoid fossa regions (from right side slightly tilted) to show postglenoid process and its relation with bulla, the disposition of the four basal pterygoid foramina, and the shape of the pterygoid process. Above to below:
- 1) *Panthera (Pardofelis) marmorata*. B.M. 61.1277, from Negri Sembilan, W. Malaysia.
 - 2) *Prionailurus (Prionailurus) bengalensis*. B.M. 33.4.1.208, from Quangtri, Vietnam.
 - 3) *Felis (Felis) silvestris*. B.M. 18.8.1.8, from Jerusalem, Israel.
- Figure 2. Posterior palate and pterygoid regions (in basal view) to show shape of posterior border of palate and width of interpterygoid space. Left to right:
- 1) *Prionailurus bengalensis*. B.M. 33.4.1.208
 - 2) *Felis silvestris*. B.M. 18.8.1.8
- Figure 3. Left side of facial skeleton (in dorsal view) to show shape of malar angle and length of posterior nasal suture. Above to below:
- 1) *Prionailurus bengalensis*. B.M. 33.4.1.208
 - 2) *Panthera (Pardofelis) marmorata*. B.M. 61.1277
- Figure 4. Anterior end of palate in basal view to show shape of premaxillary-maxillary suture and postcanine constriction. Left to right:
- 1) *Prionailurus bengalensis*. B.M. 33.11.10.1, from Kashmir, India.
 - 2) *Panthera (Pardofelis) marmorata*. B.M. 42.47, from Malacca, W. Malaysia.
- Figure 5. Snout regions, in lateral view (titled dorsally) to show shape of anterior margin of premaxilla. Above to below:
- 1) *Felis silvestris*. B.M. 18.8.1.8
 - 2) *Prionailurus bengalensis*. B.M. 33.4.1.208
- Figure 6. Left P₃ and P₄, to show details of morphology. Above to below:
- 1) *Panthera (Pardofelis) marmorata*. B.M. 61.1277
 - 2) *Prionailurus bengalensis*. B.M. 33.4.1.208
- Figure 7. Left tooth rows, to show details of morphology. Above to below:
- 1) *Catopuma temmincki*. B.M. 32.3.1.33, from Burma.
 - 2) *Catopuma badia*. B.M. 88.8.13.1, from Borneo.
- Figure 8. Left malar regions, to show shape of malar-maxillary suture. Above to below:
- 1) *Profelis aurata*. B.M. 1938.3.29.1, from Cameroun.
 - 2) *Catopuma temmincki*. B.M. 32.2.1.33.
- Figure 9. Posterior palate and pterygoid regions. Above to below:
- 1) *Profelis aurata*. B.M. 1938.3.29.1
 - 2) *Catopuma temmincki*. B.M. 32.3.1.33

I-1



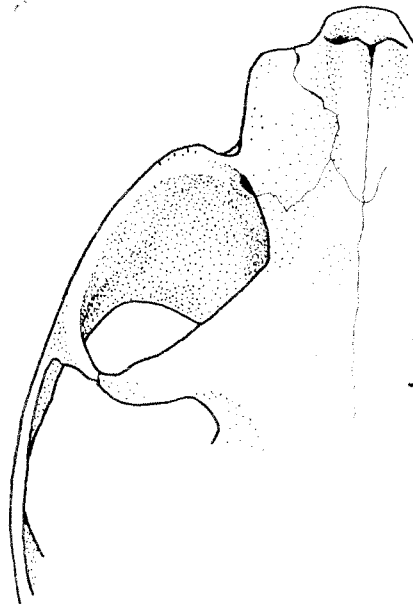
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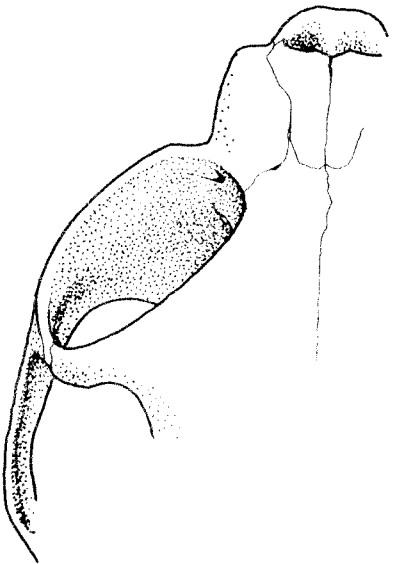
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III-1



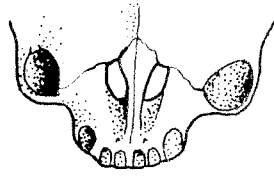
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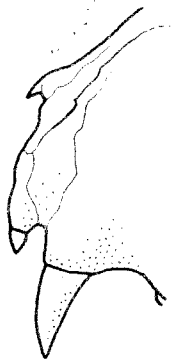
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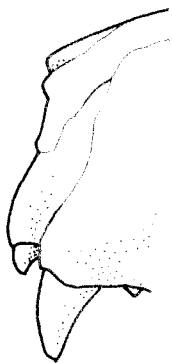
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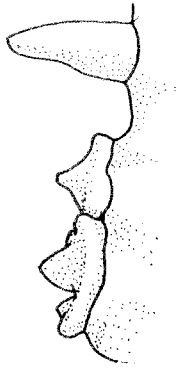
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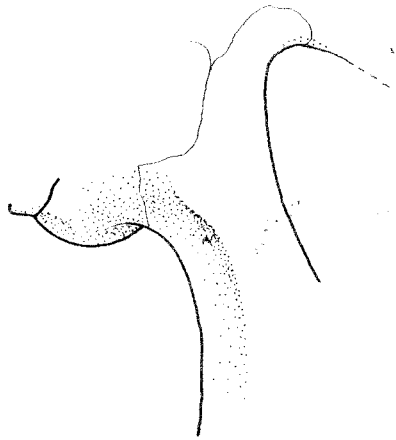
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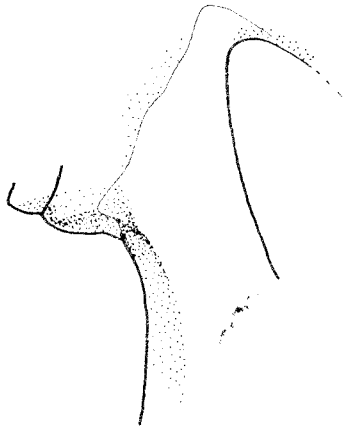
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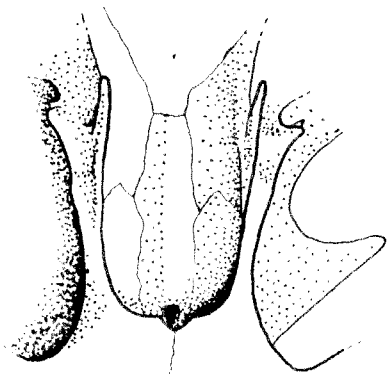
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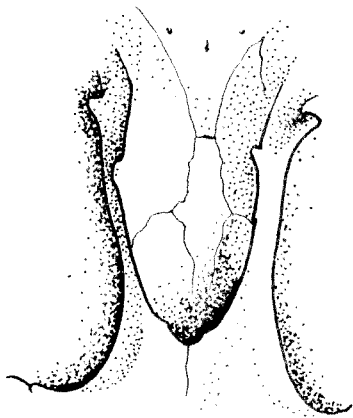
VIII-2



IX-1



IX-2



The four foramina (optic, sphenoid, rotundum and ovale) lying serially along the base of the pterygoid process have some value for taxonomic differentiation (fig. 1). In *Prionailurus* the second of them, the sphenoid foramen, is large and D-shaped and points anteriorly; the third, the foramen rotundum, points laterally, and is commonly separated from the sphenoid by a continuation of the ridge at the base of the pterygoid process; the fourth, the ovale, is elongated and bordered below by a strong ridge. In *Profelis* the sphenoid foramen resembles *Prionailurus*; the rotundum is smaller and directed more medially, and the ridge though bigger fades away before reaching the interforaminal septum; the ovale is more rounded and is not defined inferiorly by a ridge. In the Pantherines the sphenoid foramen points more laterally so is more visible from the side, and is oval in shape; the foramen rotundum is small as in *Profelis* and points more medially, but the ridge is small or tiny and fades rapidly; the foramen ovale is rounded and lacks a ridge, as in *Profelis*. There is thus an overall similarity between *Profelis* and the Pantherines, and *Pardofelis* fits into this group; where the two differ, *Pardofelis* resembles the Pantherines in the oval, laterad sphenoid foramen, and is idiosyncratic in that the basal pterygoid ridge is continued posteriorly to the foramen rotundum.

The shape of the premaxillary-maxillary suture on the palate (fig. 4) differentiates between *Prionailurus* and *Profelis*, on the one hand, and the Pantherines on the other. In the former, it runs tolerably straight from the incisive foramen to the canine alveolus, slanting back slightly; in the latter it curves anteriorly, then runs laterad and finally turns backward toward

the canine. In *Pardofelis* it is intermediate; it runs initially laterally anteriorly, then turns decisively laterad.

The malar-maxillary suture, seen from the side, slopes back and down from the orbital margin then turns up before reaching the zygomatic root, in *Prionailurus*. In *Profelis* it is similar, but is not upturned at the end. In the Pantherines it is nearly straight, so more or less resembles *Profelis*. In the Marbled Cat it is angled in the middle: sloping back and down, then turning down, then turns and runs horizontally. It is thus quite different in shape to any other form.

As pointed out by Imaizumi (1967), the length of the fronto-nasal suture is less than a third the length of the nasals in *Prionailurus*; about one-third in the Pantherines; nearly a half in *Profelis*. In this character, the Marbled Cat resembles *Profelis*.

Another character studied by Imaizumi is the shape of the anterior border of the ascending premaxilla. This is nearly straight in *Prionailurus* (fig. 5, no. 2), and more concave in *Profelis*; it varies in the Pantherines, however. In *Pardofelis* it is somewhat concave. (In none of these, except some Pantherines, is it as markedly concave as is the case in *Felis* (fig. 5, no. 1)).

The ascending ramus of the mandible is low in *Prionailurus*, anteroposteriorly wide; the coronoid process is rounded; the angular process is prominent and slightly upturned. The masseter insertion is deeply scooped out up to the posterior margin immediately below the condyle. A strong ridge along the front edge of the ascending ramus continues as far as M_1 . In *Profelis* the ramus is just somewhat

less low and wide; the angular process is even more prominent but is not upturned; the masseter insertion is deeper, leaving bordering ridges on all sides; and the anterior ridge is just as strong. In the Pantherines the ascending ramus is high and anteroposteriorly narrow, its anterior margin abruptly sweeping up from the corpus; the angular process is not so prominent; the masseter insertion is deep but less sharply outlined, and it slopes back across the ramus so that there is less of a ridge posteriorly; and there is no marked ridge down the anterior margin of the ramus. *Pardofelis* shows a distinctly pantherine form: the ramus is high, thin and abrupt, with a high pointed coronoid; the angular process is not very prominent, and point backward; the masseter insertion slopes, and is not deeply scooped out; and there is no anterior marginal ridge to the ramus.

P₃ in *Prionailurus* (fig. 6, no. 2) is a simple tooth with no marked hypocone, and the parastyle hardly exists; the protocone is very high and dagger-like (most markedly so in *P. planiceps*). In P₄ also the protocone is very long and dagger-like, and straight-edged; the metacone is only very slightly divided into two; and there is a slight development of the natero-buccal cingulum cusp. *Profelis* contrasts with this (fig. 7): the hypocone on P₃ is prominent (more so in *P. temmincki* than in *P. badia*), with a ridge at its base on the buccal side; the parastyle is divided into two; and the protocone is blunter; its posterior edge more nearly horizontal. P₄ has a more rounded posterior blade to the protocone; the metacone is slightly divided and its blade concave; and the cingulum cusp is well formed. The Pantherines tend towards *Prionailurus* in these characters, the main

difference being the even more complete reduction of the parastyle on P₃ and the cingulum cusp on P₄. In all features, *Pardofelis* (fig. 6, no. 1) is pantherine.

A similar picture is seen in the lower cheekteeth. In *Prionailurus* P₃ has a buccal cingulum at the base of the hypoconid which itself forms a cusp posteriorly; and the protoconid is high though rounded. In P₄ the protoconid is broad and the other cusps are well set-off. In M₁ the cusps are upright. *Profelis* differs in its high, dagger-like protoconid on P₄, and the even more upright cusps on M₁. The Pantherines are not entirely like *Profelis*: there is hardly any buccal cingulum on P₃, and the protoconid is lower; the protoconid of P₄ is broader and the others less set-off; the cusps are more divergent on M₁. *Pardofelis* resembles the Pantherines in most of these features except that the protoconid of P₃ is higher, and that of P₄ is narrow and pointed.

The muzzle is narrower in *Pardofelis* than in any other cat except *Neofelis*; and, like the latter, the lower jaw is noticeably constricted behind the canines to accommodate enlarged upper canines. The maxillary (postcanine) diastema is likewise constricted in both forms.

The Marbled Cat, in conclusion, is clearly on the pantherine stem as Hemmer (1978) hypothesized. The skull characters can be added to those of the karyotype and so on to help to define the basal characters of the lineage. *Neofelis* not only belongs to the same lineage, but is almost certainly even a member of the same side-branch as *Pardofelis*; seen in this light, the remarkably similar skin pattern of the two need no longer be seen as convergent, but is derived in common.

The best way of recognising these relationships in taxonomy will be discussed below.

The Golden Cats

As noted by Van Mensch and Van Bree (1969), the African and Asian Golden Cats (*Profelis aurata* and *P. temmincki*) differ in several skull characters, and the latter shows resemblances, presumably symplesiomorph, with the New World genus *Leopardus*. A few extra characters are noted here.

In most skulls of *P. aurata* there is a pit on the metopic suture immediately posterior to the nasal root; *P. temmincki* never has one.

As noted above, in *P. temmincki* (fig. 8, no. 2) the malar-maxillary suture is nearly straight (or has a very slight kink). In *P. aurata* (fig. 8, no. 1) it loops down below the rim of the masseter origin scar, then turns up again; it is more sinuous in its course than *Prionailurus*. This is a very characteristic difference.

The foramen rotundum is very narrow and faces forwards in *P. temmincki*, but rounded and faces laterally in *P. aurata*. The foramen ovale is elongated in *P. temmincki* - for all that it is less so than in *Prionailurus* - but small and round in *P. aurata*. The pterygoid plate itself is more posteriorly extended in the former, but elongated postero-inferiorly in the latter.

In *P. temmincki* (fig. 9, no. 2) there is a "bite" out of the back of the palate; in *P. aurata* (fig. 9, no. 1) the posterior rim is smooth, even though sometimes concave, and occasionally there is a slight prominence as in *Felis*; the

interpterygoid space is broader again as in *Felis*. Finally at the anterior end of the palate the premaxillary-maxillary suture runs backward before turning forward in *P. temmincki* but goes straight from incisive foramen to canine in *P. aurata*.

When fitting two species into Imaizumi's (1968) list - neither of them were analyzed by Imaizumi - a few differences emerge. The anterior border of the ascending premaxilla is more strongly concave in *P. aurata*: resembling *Felis* in this respect. The length of the fronto-nasal suture is less than one-third of the nasals in *P. aurata*, but about one-half in *P. temmincki*. In *P. temmincki* there is a depression enclosing the hypoglossal foramen and foramen lacerum posterius; but none in *P. aurata*.

In most of these features - not all - *P. aurata* resembles *Leptailurus* and so, more distantly, *Felis*. There is thus a slight indication that it may spring from the base of the *Felis* lineage; *P. temmincki* being closer to the *Prionailurus* lineage (unless the resemblances, rather tenuous at best, are symplesiomorph). There is some slight corroboration for this in the skin patterning (Van Mensch and Van Bree, 1969); Weigel, 1961): in *P. aurata* the forehead is only occasionally marked, whereas in *P. temmincki* it is boldly marked with four stripes or spot-rows, in either case recalling the typical condition in *Felis* and *Prionailurus* respectively; the ears are uniformly dark in *P. aurata* as in *Felis*, light at the base in *P. temmincki*; and the belly is boldly spotted in *P. aurata* as in many *Felis*. However, Van Mensch and Van Bree (1969) listed characters that clearly differentiate the skulls of *P. aurata* from *Leptailurus*: general narrowness; short nasals; large teeth; deeper pit for infra-orbital foramen; absence of parastyle on P₃ (these would be primitive characters); relation of bulla and

paroccipital process (in which *P. aurata* is more like *Felis*). On these bases it would certainly be inadvisable to align *P. aurata* with *Felis* if the latter includes *Leptailurus*. It is clear at any rate that the two species of Golden Cats have no direct affiliation, and should as Hemmer (1978) proposes be placed in separate genera. Any similarity between them is likely to be due to independent adaptation to humid forest conditions; there has been no direct forest connection between Africa and Asia for 20 million years.

The little-known Bornean Bay cat, as noted in the previous section, seems to be a highly differentiated form of the Asian Golden Cat, and should constitute a second species of the genus *Catopuma* which, as Hemmer (1968) has shown, is the prior available name for the Asian Golden Cat genus.

The Iriomote Cat

Imaizumi had no specimens of Golden Cats to hand when describing *Mayailurus iriomotensis*; to this extent, therefore, his study was incomplete. Sorting out the characters used by him so as to retain only those with no evident individual variability considerably reduces his list; the remaining characters were assessed for *Profelis/Catopuma*, *Pardofelis*, "*Neofelis*" and the South American forms, and scored in numerous individuals of species for which Imaizumi had only a few specimens. (Unfortunately most of the features elucidated in the previous sections of this paper are not known for *Mayailurus*). It became clear not only that about a dozen characters were highly reliable (his characters 2, 5, 9, 17, 18, 20, 31, 33, 34, 50, 51 and 52 in particular) but that *Mayailurus* itself should be compared carefully not only with

Prionailurus but also with "*Profelis*." Dr. P.J.H. Van Bree (pers. comm.) had reached a similar conclusion on the basis of his own observations.

The length of the fronto-nasal suture in *Mayailurus* is about one-third that of the nasals, much less than this in *Prionailurus*, but about one-half in *Catopuma temmincki*. The anterior border of P₄ is usually strongly concave in both, but nearly flat in *Prionailurus*. There is a fairly sharp angle on the inner border of P₃ in both, though it is less marked in *Catopuma*; but it is absent in *Prionailurus*. On the other hand the ethmoid usually (not always, contra Imaizumi) constitutes part of the upper rim of the sphenopalatine foramen in *Mayailurus* as in some species (*planiceps*) or *Prionailurus*; however, it never does in "*Profelis*" (including *Catopuma*). The nasal branch of the premaxilla is nearly straight in *Mayailurus* and *Prionailurus*, but somewhat concave in *Catopuma*.

The phyletic status of these characters is not easy to determine. If it be assumed, however, that the *Panthera* group, the New World cats, and the *Felis* group are, in whichever order, the earliest groups to branch off from the rest of the family, then characters shared with one or more of them are liable to be symplesiomorph. The character of the fronto-nasal suture is thus evidently symplesiomorph; in fact *Prionailurus* is nearly alone in the shortness of that suture. The variability of the ethmoid character makes this less useful than might otherwise appear, but the potentiality for its inclusion on the upper rim of the sphenopalatine foramen recurs in *Pardofelis* and in the South American cats. The two dental characters however would appear in *Mayailurus* to be intensifications of states in which *Catopuma* is divergent to some degree from the primitive state, in some

degree convergent with the South American forms.

The whole question of this little cat's relationships is complex. Undoubtedly its long-standing isolation on a small island of the Ryuku group has contributed to its distinctness; undoubtedly its relationships lie somewhere between *Catopuma* and *Prionailurus*. In some respects, such as Imaizumi's characters 34 and 50--the relation between the paroccipital processes and the bulla, and the shape of P₃--it is quite unique and evidently specialised; in others it shares characters with a diversity of other cats (character 31, the shape of the bulla, and character 33, the depression postero-medial to the bulla), so may even be phyletically more distinct than *Catopuma* and *Prionailurus*. At present it seems best to retain all these three as separate genera, though as further studies are made it may prove valid to combine them in a single genus.

Conclusions

Taxonomy must be made to serve phyletics; that is to say, forms that are "related" to one another (phyletically: in the only sense which gives real meaning to the term "related") should be placed together in a taxonomic category which excludes forms which are not so related, or cannot be demonstrated to be so. In the case of the Felidae, the current position is that a number of species, or species-clusters, appear to show little or no evidence of linkage to one another; others are quite obviously related by a suite of derived characters. Species showing a clear and obvious relationship would most sensibly be placed together in a genus; separate generic status should be retained for those not

(yet?) shown to be affiliated to one or the other of these groups. If this leaves us with some monotypic genera and others "top-heavy" with species, it cannot be helped; it may be an unavoidable result of the conservatism that is necessary if one is to produce a taxonomy that seeks to show only the present state of understanding--no less, and no more.

I propose the following classification of the Old World members of the subfamily Felinae, in which each genus represents a lineage with its own derived characters, and no close links with any other:

- 1) Genus *Felis* Linnaeus, 1758-- including as subgenera: *Felis* Linnaeus, 1758 (with species *silvestris*, *nigripes*, *bieti*, *chaus*, *margarita* and *manul*) *Leptailurus* Severtzow, 1858 *Lynx* Kerr, 1792 *Caracal* Gray, 1843
- 2) Genus *Prionailurus* Severtzow, 1858 (includes *Ictailurus* as a subgenus)
- 3) Genus *Mayailurus* Imaizumi, 1967
- 4) Genus *Catopuma* Severtzow, 1858
- 5) Genus *Profelis* Severtzow, 1858
- 6) Genus *Panthera* Oken, 1816-- including as subgenera: *Panthera* Oken, 1816 (with species *leo*, *pardus*, *onca*, *tigris* and *uncia*) *Pardofelis* Severtzow, 1858 (with species *marmorata* and *nebulosa*)
- 7) Genus *Acinonyx* Brookes, 1828

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