

A review of fossil Ictonychinae (Mustelidae) from the Plio-Pleistocene of Africa

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ABSTRACT - We here describe one new specimen of Prepocilogale from South Africa whilst reviewing previously published material. African representatives of the subfamily are known from Morocco, Algeria, Kenya, Tanzania, and South Africa. The South African specimens are assigned to Prepocilogale bolti (Petter, 1987). North and East African specimens are referred to the extant genera Ictonyx, Poecilictis, and Poecilogale. The specimens from Laetoli, previously assigned to Prepocilogale, are here reassigned to the new species Ictonyx harrisoni and to an unnamed n. gen. and n. sp.

INTRODUCTION

The carnivore fauna of Africa is exceptionally rich, both in the present day and in the past. Among extant terrestrial carnivorous families only Ursidae, Mephitidae, and Procyonidae are absent from the continent today, and of these, Ursidae were sporadically present in Africa until recently. The families of large carnivores present on the continent (Felidae, Hyaenidae, and Canidae) have been extensively studied, whereas the families of smaller carnivores (Nandiniidae, Viverridae, Herpestidae, and Mustelidae) are generally less well known (Werdelin & Peigné, 2010; Kingdon & Hoffmann, 2013). African Mustelidae includes four subfamilies: Mellivorinae (one African genus, *Mellivora*, the honey badger), Lutrinae (two African genera, *Hydrictis*, the spotted-necked otter, and *Aonyx*, the clawless otter), Ictonychinae (three African genera, as discussed herein) and Mustelinae (one African genus, *Mustela*, the weasels and polecats). Among all extant African carnivora, the Ictonychinae must be considered the least well known, which may be reflected in the absence of a vernacular collective name for the subfamily.

In the present day the Ictonychinae has a diversity and distribution that are clearly relictual. Apart from the three African genera, *Ictonyx* (one species, *I. striatus* [Perry, 1811]) *Poecilictis* (one species, *P. libyca* [Hemprich & Ehrenberg, 1833]) and *Poecilogale* (one species, *P. albinucha* Gray, 1864), Ictonychinae is represented by extant species in Eurasia and South America. The Eurasian taxon is the genus *Vormela* with the single species *V. peregusna* (Güldenstaedt, 1770), which has a wide distribution ranging from the Balkans to eastern China (see www.iucnredlist.org for distribution maps of extant species). South America has two genera: *Galictis*, including two extant species, *G. vittata* (von Schreber, 1778) and *G. cuja* (Molina, 1782), with the former distributed across the northern half of the continent and the latter mainly in the south, and *Lyncodon*, with

the species *L. patagonicus* (de Blainville, 1842) with a southerly distribution. *Galictis* is also known from two extinct species, *G. sorgentinii* Reig, 1957 and *G. hennigi* (Mones, 1986), both of uncertain status. A putative extinct species of *Lyncodon*, *L. bosei* Pascual, 1958, is known from only a single specimen (Prevosti & Forasiepi, 2018).

The pre-Pleistocene evolution of Ictonychinae in Eurasia is complex and contentious and includes a number of poorly known genera such as *Pannonictis* and *Enhydriactis*, in addition to the extant *Vormela*. A recent review of European fossil ictonychines can be found in Bartolini-Lucenti (2018).

MATERIAL AND METHODS

The first mention of an ictonychine from the Plio-Pleistocene of Africa is of a braincase from the Sidi Hakoma Member at Hadar (Howell & Petter, 1976). The specimen, A.L. 131-2, has subsequently been identified as likely pertaining to a rodent.

The first fossil Ictonychinae to be described from Africa is *Ictonyx bolti* Cooke, 1985 from Bolt's Farm, South Africa (Cooke, 1985). The specimen is a nearly complete cranium with P4-M1 on both sides (Fig. 1c; Cooke, 1985: fig. 1). This remains the best-preserved African specimen of Ictonychinae thus far. In his description, Cooke (1985) points to the maxillary dental formula of 3-1-3-1 as the main reason for assigning the specimen to *Ictonyx*. Other features, such as the morphology of P4, size of the cheek teeth, and shape of the bulla are in Cooke's estimation closer to *Poecilogale*.

Cooke noted (1985: p. 619) that Germaine Petter was then in the process of assigning material from Laetoli, Tanzania to the same species. These specimens were later published as *Propoecilogale bolti* (Petter, 1987). However, Petter & Howell (1985) had already published the replacement genus name *Prepoecilogale* for *Ictonyx bolti* and because generic names do not require a description or

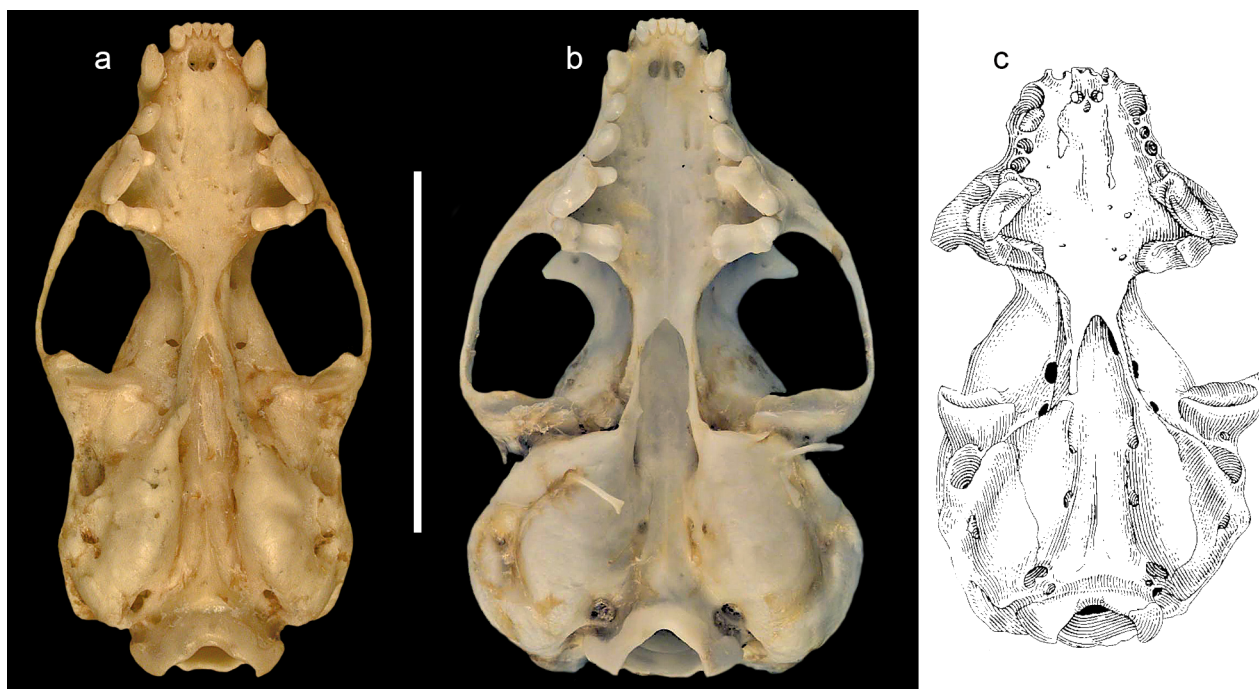


Fig. 1 - (color online) Crania of Ictonychinae in ventral view. a) Extant *Poecilogle albinucha*. b) Extant *Ictonyx striatus*. c) Holotype cranium of *Ictonyx bolti* after Cooke (1985: fig. 1). The figure shows the clear resemblance of *I. bolti* to *Poecilogle* in the shape of the palate and basicranium. Scale bar is 30 mm.

diagnosis but only a designated, valid type species, this is the currently accepted genus name for the Bolt's Farm specimen and any other material considered conspecific or congeneric with it.

The material from Laetoli available to Petter (1987) consists of two numbered specimens. Specimen LAET 75-1358 is an associated left maxilla and mandible fragments with P3-M1 and p4-m1 (Fig. 2a1-a3 and 2b1-b3; Petter, 1987: pl. 7.1, fig. 3; Werdelin & Dehghani, 2011: fig. 8.8). Specimen LAET 74-248 is a left maxilla fragment with C-P2 and associated postcranial elements (Petter, 1987: pl. 7.1, figs 4-7 and fig. 7.2 A-E). Both specimens are from the Upper Laetoli Beds.

The Laetoli material identified by Petter (1987) was redescribed by Werdelin & Dehghani (2011), together with some new specimens. The new material includes a P4 fragment and a calcaneus from the Upper Laetoli Beds, coeval with the material previously described by Petter (1987). An additional craniodental specimen, EP 1140/01, a mandible fragment with m1-m2 (Fig. 2c1-c3), comes from the Upper Ndolanya Beds, dated to the latest Pliocene and is therefore closer in age to the South African material than to the other Laetoli specimens.

Geraads (1997) assigned (but did not figure) a small number of specimens from Ahl al Oughlam, Morocco to *Prepoecilogle* sp. These are dated to the latest Pliocene-earliest Pleistocene. In the same paper, Geraads also identified two craniodental specimens as a new ictonychine subspecies, *Poecilictis libyca minor* Geraads, 1997. Geraads (2016) has later suggested that the Ahl al Oughlam *Prepoecilogle*, as well as the specimens from Laetoli described by Petter (1987), should be reassigned to *Ictonyx*. Geraads (2016) further assigned a few specimens from Tighennif, Algeria (probably late Early Pleistocene)

to *Poecilictis* cf. *libyca*, as well as a single mandibular corpus to the genus *Enhydriactis*, an ictonychine otherwise only known from Eurasia. The latter specimen has subsequently been reassigned to another Eurasian genus, *Pannonictis* (Bartolini-Lucenti, 2018).

Additional specimens from South African sites have been reported in recent years. O'Regan et al. (2013) assigned a right mandibular corpus fragment with m1 from Cooper's D to *P. bolti* (Fig. 3a1-a3). A few years later Fourvel et al. (2016, 2018) reported the presence at Kromdraai Member 2 (recently renamed Unit P) of some specimens assigned to *P. bolti*, including a right mandibular corpus with p2-m1 (Fig. 3b1-b3). This specimen is described below.

Standard methods were applied in this study. Measurements were either taken directly on specimens or, where these were not available, either from published data or from scaled photographs.

Abbreviations: L: length, Lt: length of trigonid; W: width, p/P: premolar; m/M molar. Specimen repositories are given in Supplementary Online Material (SOM).

TAXONOMIC ANALYSIS

Morphological observations

Apart from the holotype cranium of *Ictonyx bolti* and the mandibular corpus from Kromdraai, all the material available consists of mandibular or maxillary fragments with one or two teeth. Therefore, comparisons between specimens are necessarily restricted to limited parts of the dentition, mainly the more diagnostic m1 and P4. The ages of the specimens, although not taxonomic characters per se, can also to some extent inform taxonomic comparisons.

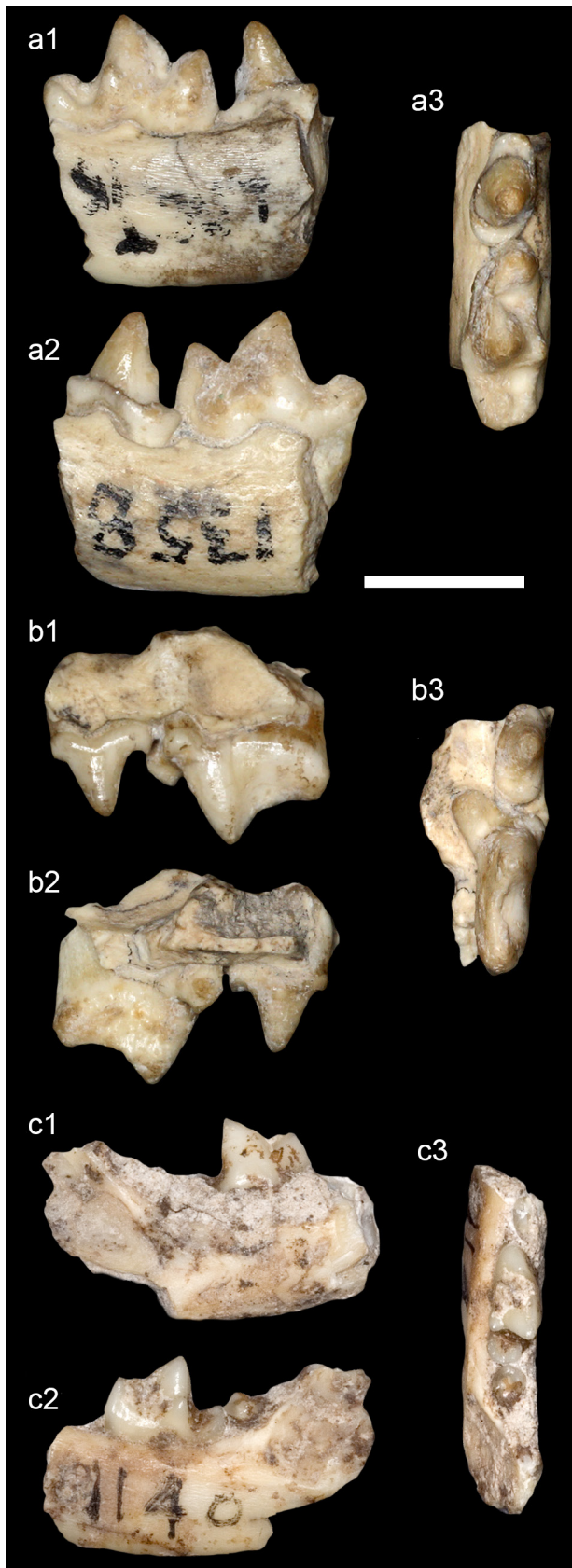


Fig. 2 - (color online) *Ictonyx harrisoni* n. sp. LAET 75-1358 (Holotype) from Laetoli. a) Mandibular fragment in lingual (a1), buccal (a2), and occlusal (a3) views. b) Maxilla fragment in buccal (b1), lingual (b2), and occlusal (b3) views. c) Ictonychinae sp. indet. EP 1140/01 from Laetoli. Mandibular fragment in buccal (c1), lingual (c2), and occlusal (c3) views. Scale bar is 5 mm.

As mentioned above, Cooke (1985) in his original description of *Ictonyx bolti* from Bolt's Farm, South Africa (dated ca. 2.6 Ma), noted that the upper dental formula is identical to that of *Ictonyx* (i.e., 3.1.3.1), whereas in *Poecilogale* it is 3.1.2.1, with the loss of P2. The similarity in this respect to *Ictonyx* is described by Cooke (1985: p. 618) as the main reason for assigning the specimen to that genus, although Cooke also noted that, in many respects, the specimen is intermediate between the two genera. We agree with Cooke on these points although we feel that the P4 protocone as illustrated is closer to that of *Poecilogale* than *Ictonyx* and that the basicranium is quite different from that of *Ictonyx* and similar to *Poecilogale*. This is demonstrated in Fig. 1, where the slender and elongated cranial region posterior to the mandibular articulation in *P. albinucha* and in the fossil contrasts with the shorter, rounded region in *I. striatus*. In particular, *P. albinucha* and the fossil have a narrow, auditory bulla that terminates anterior to the anterior end of the foramen magnum, whereas that of *I. striatus* has a bulla that is very rounded and terminates distal to the foramen magnum.

Petter (1987) used the morphology of P4 of the Bolt's Farm specimen as the primary justification for creating the genus *Prepoecilogale* (Petter & Howell, 1985) and placing it in a sister taxon relationship with *Poecilogale*, with *Ictonyx* plus *Poecilictis* as sister group to those two (Petter, 1987: fig. 7.4). This situation was retained by Werdelin & Dehghani (2011) in their work on the Carnivora of Laetoli. Geraads (2016) noted, however, that the maxilla specimen LAET 75-1358 (one of several associated specimens with this catalogue number) from the Upper Laetoli Beds (dated ca. 3.85-3.63; Deino, 2011), which was assigned by Petter (1987) and Werdelin & Dehghani (2011) to *P. bolti*, has a forwardly directed P4 protocone that is closely similar to that of *Ictonyx* (Fig. 2c3). In view of this, and in view of the approximately one million years separating the Laetoli specimen from the Bolt's Farm one, we agree with Geraads (2016) that the taxonomic identity of the Laetoli specimen is disputable.

As noted above, Laetoli specimen LAET 75-1358, in addition to the maxilla specimen that Petter (1987) considered crucial to her analysis, includes several associated specimens, including mandibular as well as postcranial elements. The most informative of the mandibular specimens is a corpus with p4-m1 (Fig. 2a1-a3). This specimen has a strongly labio-lingually compressed m1 crown with low metaconid and comparatively long talonid, quite similar to that of *Ictonyx*. A second specimen, LAET 74-248, includes an anterior maxilla fragment and several postcranial elements. Noteworthy is the presence of P2 in the maxilla.

The more recently collected Laetoli material includes a second mandibular corpus specimen, EP 1104/01 (Fig. 2c1-c3). This specimen is from the upper unit of the Ndolanya Beds, dated ca. 2.66 Ma (Deino, 2011), i.e., close in time to Bolt's Farm. This specimen resembles LAET 75-1358 in general mustelid characters although it is much smaller than the older specimen. The trigonid of EP 1104/01 differs from that of LAET 75-1358 in several respects, notably that the paraconid makes up slightly more of the mesiodistal length of the trigonid and that the angle between paraconid and protoconid is greater (i.e., the trigonid is more mesiodistally rectilinear). In addition,

there is a greater height difference between paraconid and protoconid in the younger specimen. The m1 talonid of EP 1140/01 also appears considerably smaller and shorter than that of the older specimen (this point is discussed further below).

The first fossil ictonychines from North Africa (Ahl al Oughlam, Morocco) were described as *Prepoecilogale* sp. cf. *P. bolti* by Geraads (1997). The material (not illustrated) includes four mandibular fragments and three P4. In the same publication, Geraads also described an m1 and a P4 as *Poecilictis libyca minor* (Geraads, 1997: fig. 13.3). These two teeth are certainly much more like those of *Ictonyx/Poecilictis* than any of the *Prepoecilogale* specimens, both in morphological features and in being much smaller than the Laetoli and Bolt's Farm specimens assigned to the latter taxon. The *P. libyca minor* m1 is, on the other hand, close in size to Laetoli specimen EP 1140/01. Despite this, the two differ considerably in shape and proportions. The occlusal outline of the Ahl al Oughlam holotype (AaO-2820) is curvilinear whereas that of EP 1140/01 is nearly straight. In addition, the talonid of AaO-2820 is relatively longer than that of EP 1140/01. In these features AaO-2820, like the paratype P4 AaO-2818, is closer to *Ictonyx* and *Poecilictis* than is the Laetoli specimen.

In a later publication Geraads (2016) described additional *Poecilictis* specimens from the early Middle Pleistocene site of Tighennif (Algeria). At the same time, he tentatively reassigned the Ahl al Oughlam *Prepoecilogale* specimens to *Poecilictis* based on the mesially extending P4 protocone. We have not seen these specimens but have no reason to dispute the assessment of Geraads and therefore conclude that *Prepoecilogale* is not at present known from North Africa.

The mandibular corpus fragment from Cooper's D (dated ca. 1.4 Ma), CD 3896 (Fig. 3a1-a3) described by O'Regan et al. (2013) includes an m1 that is very similar to, although somewhat larger than, that of Laetoli specimen LAET 75-1358. O'Regan et al. (2013) note that the m1 metaconid is less well developed than that of LAET 75-1358, which is correct, although the difference is so slight that it may be accounted for by individual variation. The corpus of CD 3896 is short, with alveoli for p3, p4 and m2 in evidence. These teeth were clearly more robust than those of extant *Poecilogale albinucha*. No p2 appears to have been present. Unfortunately, the Cooper's D material does not include the upper dentition, and it is therefore not possible to determine whether the ictonychine from that site had a P4 similar to that of the Bolt's Farm material or was more forward reaching as in LAET 75-1358.

The most recently identified ictonychine specimens from South Africa are from renewed excavations at Kromdraai Member 2 (dated ca. 2.3 ma). These specimens are mentioned in lists and briefly presented in Fourvel et al. (2016, 2018). One of them, KB 7359 (Fig. 3b1-b3), is a mandibular corpus that we describe and illustrate here for the first time.

The right mandibular corpus, KB 7359, is nearly complete, lacking only the part anterior to p2. The canine and incisors are missing, although the canine alveolus is visible on the lingual side and extends to beneath the mesial end of p3. The corpus is robust and deepens only

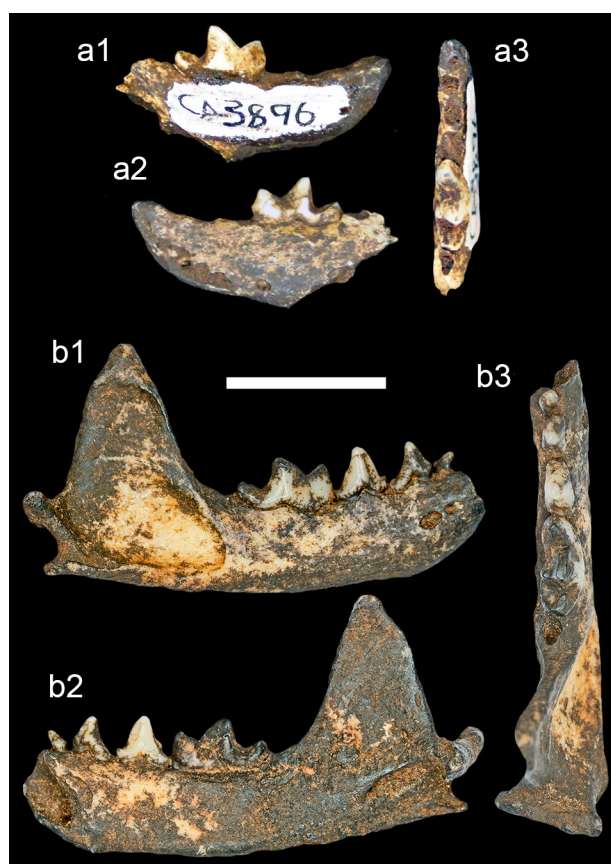


Fig. 3 - (color online) a) *Prepoecilogale bolti* from Cooper's D. Mandibular fragment CD 3896 in buccal (a1), lingual (a2), and occlusal (a3) views. b) *Prepoecilogale bolti* from Kromdraai. Mandibular fragment KB 7359 in buccal (b1), lingual (b2), and occlusal (b3) views. Scale bar is 10 mm.

slightly beneath m1. Two mental foramina are present and placed close together, an anterior one beneath p2 and a posterior one beneath p3. The masseteric fossa extends anteriorly to beneath m2. The fossa is clearly divided into two regions, dorsal and ventral, separated by a low crest. The ascending ramus extends dorsally to reach the masseteric fossa, forming a blunt tip.

The dentition is overall well preserved and includes p2-m1 and the alveolus for m2. The p2 is a small, single-rooted tooth, tallest mesially. The two-rooted p3 is short and tall, with the tallest point beneath the mesial root. The mesial end has a blunt ridge that is nearly vertical, whereas the distal end of the tooth slopes gradually distally without any distinct distal cuspid. The p4 is similar to p3 but larger and with a small mesial cuspid. The mesial crest is nearly vertical and the distal one sloping, with a low bump midway, leading down to a minute distal shelf.

The m1 is low-crowned, with a paraconid that is noticeably shorter and lower than the protoconid. In dorsal view the angle between the two is less than 15°. The metaconid is well-developed and reaches about midway to the protoconid tip, and thus almost as high as the paraconid. It is placed directly lingual to the distal end of the trigonid. The talonid is robust and has a substantial hypoconid but no distinct entoconid. The distal end of the tooth appears to have been worn down by contact with m2, suggesting that the measurement of talonid length is

a slight underestimate. The m2 was small and its alveolus somewhat drop shaped, tapering distally and slightly longer than wide.

Overall, the Kromdraai specimen is, where comparable, very similar to the Cooper's D specimen. Nevertheless, O'Regan et al. (2013) suggest that the Cooper's D specimen is closer to extant *Poecilogle* than the Laetoli specimens. From the above discussion, we know this to be true; however, it can also be said to be true of the difference between the Cooper's D and Kromdraai specimens. Unfortunately, the condition of the specimens precludes drawing any definitive taxonomic conclusions on this basis.

Metric observations

Because of the limited number of fossil specimens, only a few of which have measurement data in common (data available in SOM), there is limited information to be gained from metrics. Figure 4a shows that, overall, m1 width is greater relative to length in *Ictonyx* and *Poecilictis* than in *Poecilogle*. The Kromdraai and Cooper's D specimens align more to *Poecilogle* in this respect. The Laetoli specimens are much smaller than the rest of the specimens and cannot on this account be assigned to a recognised species. Figure 4b shows that the m1 talonid of *Poecilogle* is longer relative to tooth length than in *Ictonyx* and *Poecilictis*. The Kromdraai and Cooper's D specimens follow *Poecilogle* in this respect although they fall near the edge of the distribution of extant specimens. This diagram also shows that the two Laetoli specimens differ considerably from each other. Despite the apparently very short talonid in EP 1140/01 it is in fact longer relative to total tooth length than in LAET 75-1358, contradicting the earlier visual impression. These data suggest that the smaller specimen is closer in proportions to *Poecilogle*, while the larger one is closer to *Ictonyx* or *Poecilictis*.

Molecular observations

There have been only a few publications on the molecular phylogeny of Mustelidae that include Ictonychinae. Koepfli et al. (2008) was the first of these and their study included *Ictonyx*, *Poecilictis* (as *I. libycus*), *Poecilogle*, *Vormela*, and two species of *Galictis*. This study used 22 gene segments totalling ca. 12000 base pairs and analysed this dataset using multiple phylogenetic methods. The results reported herein are from the Bayesian analysis. The analysis indicates that, with *Galictis* and *Vormela* as sequential outgroups to the African taxa, the two putative *Ictonyx* species do not resolve as sister taxa. Instead, *I. striatus* is the sister taxon to *P. albinucha*, with *I. libycus* as sister taxon to this pair. In this analysis, Ictonychinae forms the sister group to Mustelinae plus Lutrinae.

A few years later, Sato et al. (2012) conducted a similar analysis using an overlapping dataset and also employing a variety of analytic methods of which we report the Bayesian analysis. This study added *Lyncodon* to the complement of Ictonychinae, completing the selection of extant taxa of the group. The topology of the Ictonychinae in the Sato et al. (2012) study is identical to that of Koepfli et al. (2008), with the addition of *Lyncodon* as the sister taxon to *Galictis* spp. In Sato et al.

(2012), however, Ictonychinae has switched places with Mustelinae as sister group to Lutrinae, with Mustelinae as sister group to these.

Both Koepfli et al. (2008) and Sato et al. (2012) present Bayesian chronograms of their phylogenetic results. Koepfli et al. (2008) do not provide a complete table of divergence times, but these can be estimated from their fig. 2. In their formulation the date for the divergence of African Ictonychinae from the sister taxon *Vormela* (Node 1) is ca. 4.6 Ma, the divergence of *Poecilictis* from the other two genera (Node 2) ca. 3.5 Ma, and the divergence between *Poecilogle* and *Ictonyx* (Node 3) ca. 2.6 Ma. Ranges are also provided in their fig. 2 but we have not put numbers on them.

Sato et al. (2012) provide explicit dates and ranges for their nodes. For Node 1 they report a date of 8.95 Ma (BEAST) or 9.53 Ma (multidivtime). For Node 2 they report 4.46/4.85 Ma and for Node 3, 3.44/4.27 Ma. The 95% posterior intervals (ranges) are approximately $\pm 20\%$ for these dates. For exact numbers see Sato et al. (2012: fig. 3).

Given the poor fossil record in Africa of Ictonychinae neither of these estimates is implausible. The dates provided by Koepfli et al. (2008) seem slightly young, however, while the date for Node 1 from Sato et al. (2012) is rather old and implies a long stem lineage for the African clade, although this stem lineage may have had an Eurasian origin.

The most important result of these molecular studies is that there is justification for recognising three African genera within Ictonychinae. This may seem implausible from a morphological perspective because the state of the P4 protocone (a key character for *P. boliti*) is similar in *Vormela* and *Poecilogle* and hence potentially plesiomorphic relative to the state in *Ictonyx* and *Poecilictis*. The long stem lineage implied by the results of Sato et al. (2012) suggests, however, that there was plenty of time for hidden change in this and other characters. Testing this hypothesis would require older fossils that could be confidently tied to the African lineage.

DISCUSSION

The very small number of African ictonychine fossils obviously limits the conclusions that can be drawn regarding taxonomy and evolution of the group. Nevertheless, some reasonable suggestions can be made regarding the affinities of the fossil specimens and, by extension, about the evolution of Ictonychinae in Africa.

After Cooke's (1985) initial description of "*Ictonyx*" *boliti* most commentators have attributed this specimen to the genus *Prepoecilogle* and concluded that it is a precursor and possibly direct ancestor of the extant *Poecilogle albinucha* (Geraads, 1997; O'Regan et al., 2013). Based on our study, and in conformity with O'Regan et al. (2013), we assign the Cooper's D mandibular corpus fragment to *P. boliti*. The mandibular corpus from Kromdraai, described herein for the first time, is very similar in most respects to the Cooper's D specimen, and we assign it to *P. boliti* as well.

These three South African specimens span about a million years in age, with Bolt's Farm, similar in age

to the younger Laetoli specimens, being the oldest at ca. 2.6 Ma. This specimen is more similar to the older Laetoli specimens, although O'Regan et al. (2013) note differences between them. The Kromdraai Member 2 and Cooper's D specimens (dated ca. 2.3 Ma and ca. 1.4 Ma, respectively) are quite similar to each other, although demonstrating some differences in dentition that might suggest they belong to a single evolving lineage.

The specimens referred by Geraads (1997) to *Prepoecilogle* sp. cf. *P. bolti*, on the other hand, were reattributed by Geraads (2016) to *Ictonyx* and/or *Poecilictis*, after which no *Prepoecilogle* specimens have been reported from North Africa. The morphology of *P. bolti* as presently known, is plesiomorphic relative to extant *Poecilogle albinucha* but derived relative to *Ictonyx* and *Poecilictis*.

The specimen LAET 75-1358, assigned by Petter (1987) and Werdelin & Dehghani (2011) to *Prepoecilogle bolti* was suggested by Geraads (2016) to be better placed in *Ictonyx* based on the morphology of P4. We concur with this assessment, which is further supported by the presence of P2 in the maxilla of LAET 74-248, which was found at the same stratigraphic level as LAET 75-1358. We suggest that these specimens represent a hitherto unrecognised species of *Ictonyx*, which we herein name *Ictonyx harrisoni* n. sp.

The Laetoli specimen EP 1140/01 deviates from the others in its very small size, proportions of m1, and small, round m2. Despite the limited material we consider this to be a new genus and species of Ictonychinae with affinities to *Poecilogle* based on the morphology of m1. This morphology is quite distinct from that of the Ahl al Oughlam *Poecilictis* specimen AaO-2820 (Geraads, 1997: fig. 4A-B), especially in the smaller angle between paraconid and protoconid, smaller metaconid, and less developed talonid cusp. In these respects, EP 1140/01 is more similar to *Poecilogle*. In view of the limited material, we refrain from naming this genus and species at this time.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821

Family MUSTELIDAE Batsch, 1788

Subfamily ICTONYCHINAE Pocock, 1921

Genus *Ictonyx* Kaup, 1835

Type species. *Ictonyx capensis* (= *Bradypus striatus*) (Perry, 1810)

Ictonyx harrisoni n. sp.
(Fig. 2)

1987 *Prepoecilogle bolti* PETTER, p. 207, Pl. 7.1, figs 3-7.

2011 *Prepoecilogle bolti* Petter - WERDELIN & DEGHANI, p. 204, fig. 8.8a-f.

Derivation of name - For Dr. Terry Harrison, leader of many Laetoli field campaigns.

Type locality - Only known from the Upper Laetoli Member, dated 3.85-3.63 Ma.

Holotype - Associated fragmentary left maxilla (with P3-M) and mandible (with p4-m1) LAET 75-1358.

Referred specimen - Left maxilla fragment with C-P2 and associated postcranial elements LAET 74-248.

Repository - National Museum of Tanzania, Dar es Salaam.

Diagnosis - A species of *Ictonyx* significantly smaller than the extant species, with relatively shorter m1 talonid. Differs from *Poecilictis* in the same characters as from extant *Ictonyx*. Differs from *Poecilogle* and *Prepoecilogle* in having a forwardly directed P4 protocone and shorter m1 talonid.

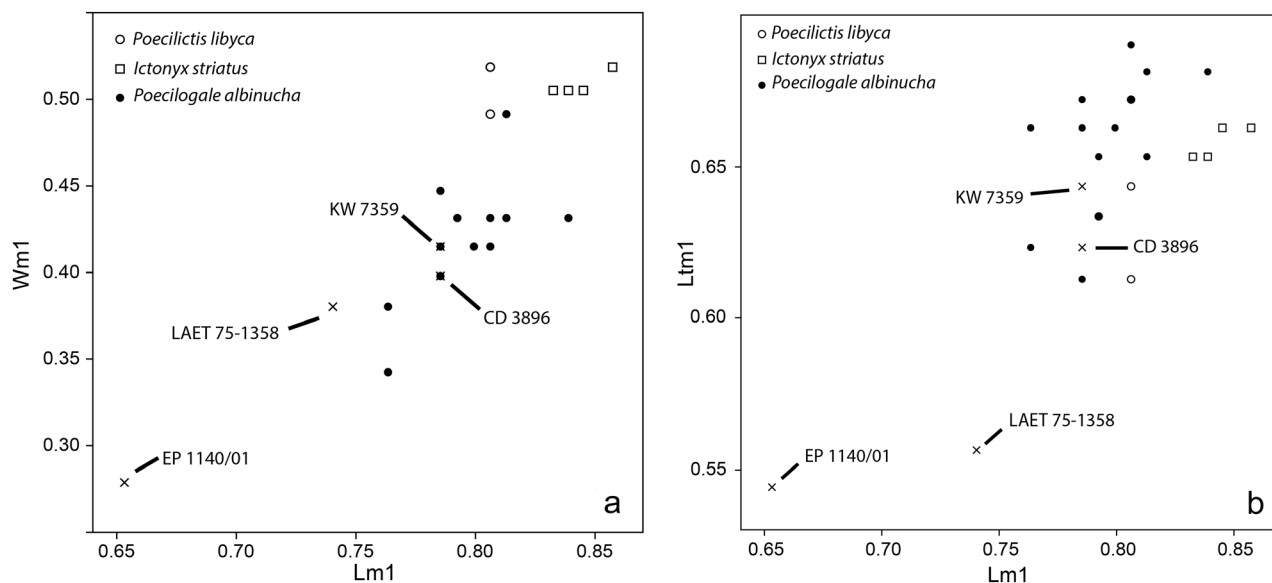


Fig. 4 - a) Bivariate diagram of m1 greatest length versus greatest width. b) Bivariate diagram of m1 greatest length versus trigonid length.

Holotype measurements (in millimetres) - Upper dentition: LP3 3.0; WP3 1.5; LeP4 5.0; WP4 3.0; L M1 2.2; WM1 4.7. Lower dentition: Lp4 3.3; Wp4 1.8; Lm1 5.5; Wm1 2.4; Lt m1 3.6 (for comparative measurements see SOM).

Description and remarks - A comparative description of the material assigned to *Ictonyx harrisoni* n. sp., as well comparative remarks are provided in the above chapters: Morphological observations, Metric observations, and Discussion.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data are available on the BSPI website at: <https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/>

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