Chamaeleo caroliquarti (Chamaeleonidae, Sauria): a new species from the Lower Miocene of central Europe

(1 text-fig., 4 pls.)

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Abstract. *Chamaeleo caroliquarti,* a new species from the Lower Miocene of central Europe, is the oldest fossil referable to the living lizard family *Chamaeleonidae.* Several dentary and maxillary fragments from Dolnice, West Bohemia and Wintershof - West, Bavaria were studied. This material unquestionably has affinity with the extant genus *Chamaeleo* and not with any member of the morphologically similar family *Agamidae.* Shape of the cheek teeth, lack of pleurodont teeth, size of the anterior medial coronoid process, and a nasal arch comprised of maxilla and prefrontal are diagnostic characters. The three older fossil genera *Palaeochamaeleo, Mimeosaurus* and *Tinosaurus* previously considered to be chamaeleons are shown to be agamids. The northern distributional limit of contemporary chamaeleons is the southern Mediterranean area but this new species demonstrates a more northerly distribution during a period of warmer climate.

Abstrakt. *Chamaeleo caroliquarti,* nový druh ze spodního miocénu střední Evropy, je nejstarší fosilní doklad čeledi *Chamaeleonidae.* Práce je založena na fragmentech dentalií a maxil, jež pocházejí z lokality Dolnice v západních Čechách a z lokality Wintershof - West v Bavorsku. Tento materiál jeví nepochybné vztahy k recentnímu rodu *Chamaeleo,* nikoliv však ke kterémukoliv ze zástupců morfologicky podobné čeledi *Agamidae.* Diagnostickými znaky jsou tvar zadních zubů, chybění pleurodontních zubů, velikost předního mediálního výběžku koronoidu a nazální oblouk, který vytváří maxila a prefrontale. Tři starší fosilní rody *Palaeochamaeleo, Mimeosaurus* a *Tinosaurus,* které byly doposud považovány za chameleony, se nyní jeví jako příslušníci čeledi *Agamidae.* Podle nálezu tohoto nového druhu lze konstatovat, že během období teplého klimatu ve spodním miocénu byli chameleoni rozšířeni mnohem dále na sever, než je tomu dnes, kdy s. hranice rozšíření prochází středomořskou oblastí.

Introduction

Chamaeleonid lizards are morphologically unique and easily identifiable owing to possession of evolutionarily derived characters of zygodactylous feet, short prehensile tail, strongly laterally compressed body, highly rotatable independent eyes, projectile tongue, and well developed skull arches. However, little is known about the basic osteological variation of structures which can be compared and

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diagnosed against other lizard families, especially the *Agamidae* which is phylogenetically closest to the *Chamaeleonidae*. The three fossil genera *Palaeochamaeleo* De Stefano, 1903 (Eocene of France), *Tinosaurus* Marsh, 1872 (Eocene of Utah, Wyoming, China and Mongolia), and *Mimeosaurus* Gilmore, 1943 (Upper Cretaceous of Mongolia) were described and assigned to *Chamaeleonidae* only on the basis of acrodont dentition, overlooking the fact that the *Agamidae* also is characterized by acrodont teeth and ignoring the contemporary chamaeleonid geographic distribution of Africa and Madagascar, with one species complex curiously patchily distributed in India, Ceylon, Persia, Arabia and the Mediterranean.

Current study of these fossils by the first author (Moody 1978) has resulted in the discovery of additional characters, notably the presence of the splenial bone and pleurodont anterior teeth which together with similarity to extant agamid species unquestionably indicate assignment to the *Agamidae*. Therefore, no fossils are known for the *Chamaeleonidae*.

While in the process of writing this paper we received a manuscript from Dr. Hillenius of the Zoological Museum in Amsterdam in which he describes a fossil chamaeleon from the Upper Miocene of Kenya, from a horizon estimated to be 12.5 million years old.

The second author in 1976 obtained three tooth-bearing elements of an acrodont lizard from Dr. O. Fejfar of Ústřední ústav geologický, Prague, and the following year excavations at Dolnice near the town Cheb (Eger), Czechoslovakia, resulted in the finding of 9 additional fragments. This material has been deposited in the collections of the Department of Palaeontology, Faculty of Natural Science, Prague (DP-FNSP). Further information on the history and biostratigraphy of this locality may be found in Reuss (1852) and Fejfar (1972a,b). Three similar dentaries from Wintershof-West, Bavaria, F.R.G., were also discovered unidentified in the Bayerische Staatssammlung für Paläontologie und historische Geologie (BSP) in Munich. Dr. Wellnhofer of this institute kindly lent us these specimens. Comparison of this material with some 25 species of chamaeleons, including the genera *Rhampholeon* and *Brookesia* but mostly with species of *Chamaeleo,* and with 35 genera of agamids including over 100 species, allows us to describe this material as a species belonging unequivocably to the genus *Chamaeleo,* the oldest fossil chamaeleon to be described and the first evidence of the occurrence of chamaeleons in central Europe.

Family *Chamaeleonidae*

Genus *Chamaeleo* Laurenti, 1768

Chamaeleo caroliquarti sp. nov.

Pls. I, II, III/1,2

Derivation of name: In honor of King Charles IV, the founder of Prague University in 1348
Type locality: Dolnice near Cheb (Eger), Czechoslovakia.
Type stratum: Ottnang, Dolnice layers 1 and 2, Lower Miocene.
Faunal associates: *Anura*: *Latonia* (Špinar 1978); *Mammalia*: *Heterosorex, Plesiodimylus, Cordylodon, Pseudotheridomys, Ligerimys, Neocometes, Melissiodon, Democricetodon, Cotimus, Myoglis, Peridyromys, Glirudinus, Prolagus, Lagopsis, Piezodus* (Fejfar 1972a); *Teleostei*; *Testudines*; *Lacertilia*; *Ophidia*; *Crocodilia* (unpublished observations).
Holotype: Left dentary, length 15.6 mm, anterior portion including symphysis, most teeth, and impression of anterior medial process of coronoid, pl. I/1,2. DP-FNSP No. 101.

Paratypes: DP-FNSP No. 102, pl. I/3,4. Midsection of right dentary, length 10.5 mm, coronoid process not included, and three posterior-most teeth. DP-FNSP No. 103, pl. II/1,2. Left maxillary, length 8.0 mm, posterior section below orbit, palatine process visible, 5 teeth. DP-FNSP No. 104, pl. II/3,4. Right maxillary, anterior portion including dorsal nasal process and margin of external nares, length of alveolar part 6.8 mm. DP-FNSP No. 105, section of maxillary with 2 teeth, length 4.15 mm. DP-FNSP No. 106, pl. III/1,2. Midsection of left maxillary, 5 teeth, palatine process present, length 10.0 mm. DP-FNSP No. 107, anterior-most section of right dentary with 7 teeth, length 5.5 mm. DP-FNSP No. 108, anterior section of right dentary with 14 teeth and symphysis, length 23.0 mm. DP-FNSP No. 109, section of left maxillary including palatine process and 4 teeth, length 6.5 mm. DP-FNSP No. 110, anterior part of right dentary including symphysis but not coronoid process, length 9.5 mm. DP-FNSP No. 111, midsection of left dentary with 4 teeth, length 8.6 mm. DP-FNSP No. 112, posterior section of left dentary with part of flat syndesmotic facet for coronoid process and 4 teeth, length 6.1 mm.

Diagnosis: *Chamaeleonid* lizard with acrodont dentition and maxillae and dentaries identical with contemporaneous species of chamaeleons belonging to the *Chamaeleo chamaeleon* species group. However, the character combination of a sculptured surface of the dorsal nasal process of the maxilla, a tapering rather than squarish anterior end of the dentary, and the position at which the Meckelian canal anteriorly turns onto the ventral edge of the dentary (text-fig. 1) are unique. *Chamaeleo caroliquarti* is distinct from all agamid lizards by the presence of a strong dorsal nasal process of the maxilla, extensive anterior medial process of the coronoid, teeth with strongly laterally compressed non-contacting bases, and the absence of pleurodont teeth.

Description: Twelve dissociated tooth-bearing elements, 7 dentaries and 5 maxillae. Labially the dentary is angularly convex, with several mental foramina spaced along the anterior two-thirds. Anteriorly the profile is not slender and tapering as in most agamids nor as blunt and squarish as most extant chamaeleons (text-fig. 1). Mandibular symphysis is a simple small oval contact without an extensive area of contact posteriorly (pl. I/2). Medially the dentary has a narrow but distinct groove immediately below the tooth row, from the posterior-most tooth (p. I/2,4) and continuing anteriorly and rounding the anterior end of the dentary above the symphysis (pl. I/2) and becoming slightly visible laterally. Meckelian canal fully open to symphysis, anteriorly turning onto the ventral edge of dentary and thus not visible medially (text-fig. 1). Canal broadens posteriorly but not at the expense of the dentary as dentary depth below the tooth row is approximately equal posteriorly and anteriorly (pl. I/2). Splenial syndesmotic facets not visible and splenial may be assumed absent as in all contemporaneous species. The

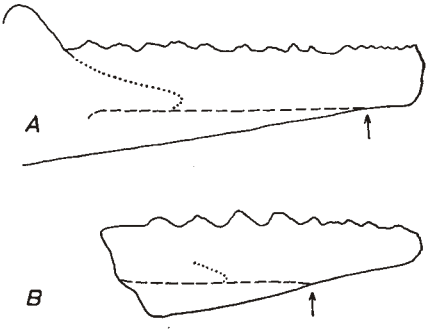

Fig. 1. Mandibles illustrated from lingual side. *A* - typical modern chamaeleon; *B* - *Chamaeleo caroliquarti*. Dashed line - upper margin of Meckelian canal. Dotted line - anterior margin of coronoid [anterior medial process of coronoid (*A*) and preserved margin of syndesmotic facet (*B*)]. Arrows indicate point at which Meckelian canal completely rotates on ventral edge of dentary

extensive anterior medial p ·ess of coronoid is not preserved but is indicated by the flat syndesmotic facet o the dentary (pl. I/2, and specimen DP-FNSP No. 112). All dentaries are broke1 nterior to the coronoid process and contacts with other mandibular elements ca...ot be described.

Dentary dentition is completely acrodont including the anterior-most teeth (pl. I/1,2). Teeth laterally compressed, the lingual side nearly as flat as the labial side, and are situated on the dorsal edge of the dentary. Anterior teeth tiny, gradually becoming larger posteriorly, the midposterior teeth largest, triangular in shape and tricuspid, small cusps present half-way on the edge of the teeth. Distinctive gap between all teeth, except anterior-most. Largest teeth approximately 1.0 mm in height.

Occlusal wear facets between most dentary teeth are oriented downward and slightly obliquely anteriorward (pl. I/1,3). Facets are triangularly cut into the bone and have an acute bottom.

Well-preserved anterior portion of maxilla (pl. II/3,4) demonstrates oval margin of external nares and robust vertically projecting dorsal nasal process of maxilla which arches posteriorly over the external nares. Process has a strongly sculptured surface. Maxilla has a contacting facet for the premaxilla along the anterior inner margin. Distal end tapers to a blunt point anteriorly. Maxillary dentition completely acrodont including anterior extreme (pl. II/3). Teeth are tiny anteriorly, quite large posteriorly, laterally compressed at base, tricuspid, and situated on ventral alveolar margin of maxilla. Tooth bases are not contacting and no occlusal wear facets are present on the labial surface but present in some of the gaps between teeth. A small portion of the palatine process of the maxillary projects horizontally inwards, and is positioned as in extant chamaeleons.

Chamaeleo cf. *C. caroliquarti* sp. nov.

Locality: Wintershof-West, Bavaria, F.R.G.
Stratum: Eggenburg, ±26 million years, Lower Miocene.
Material: BSP 1937 II 19601, pl. III/3, 4. Left dentary, anterior section with symphysis and 12 teeth, length 7.5 mm. BSP 1937 II 19602, pl. IV/1, 2. Left dentary, symphysis and anterior-most teeth lacking, 7 countable teeth, length 7.5 mm. BSP 1937 II 19603, pl. IV/3, 4. Left dentary, anterior section with symphysis and 12 teeth, length 7.2 mm.

Description: Three small dissociated anterior-sections of dentaries. Profile of anterior ends blunt and squarish (text-fig. 1). Meckelian canal turns onto ventral edge of dentary anteriorly but does not attain an extreme position as it is partly visible medially just behind and below symphysis.

Dentition and occlusal wear facets variable. The middle-sized teeth just posterior of the tiny anterior teeth are not as wide in specimens BSP 19601 and 19603 as in specimen BSP 19602. Occlusal wear facets of specimens BSP 19601 and 19602 are quite shallow and have rounded bottoms but BSP 19603 has a deep facet with acute bottom. Facets of specimens BSP 19601 and 19602 are oriented nearly vertically, i.e. perpendicular to the longitudinal axis of the mandible, whereas the anterior facets of BSP 19603 slant obliquely anteriorly and ventrally. Pleurodont teeth are absent.

All dentaries are broken anterior to the coronoid process and the posterior-most teeth are not preserved, preventing assessment of ontogenetic age of the specimens. The flat syndesmotic facet of the anterior medial process of the coronoid is likewise not preserved.

Discussion: These fossil fragments are unquestionably chamaeleonid on the basis of several characters. Although agamid lizards also have acrodont teeth of a type known only to agamids and chamaeleons, chamaeleonid acrodont teeth are distinctive as they are ankylosed exactly on the edge of the dentary or maxilla, not slightly on the lingual surface as in agamids. The larger cheek teeth are also strongly laterally compressed, the lingual surface of the tooth is nearly as flat as the labial surface, unlike agamids which have a swollen lingual tooth surface. Also, the middle and posterior cheek teeth are always separated by a gap measuring 15—25% of tooth width so that tooth bases never contact. In agamids adjacent teeth are contacting, or the gap is insignificant. Wear facets between the dentary teeth caused by occlusion of the maxillary teeth are present in both agamids and chamaeleons.

A major diagnostic character for the chamaeleons is the absence, even in juveniles, of pleurodont teeth in the anterior sections of the dentary and maxilla, and of the premaxilla. Specimens DP-FNSP Nos. 101 and 104 have completely preserved anterior ends demonstrating the presence of only tiny acrodont teeth and the absence of pleurodont teeth and pits from which pleurodont teeth would develop and be replaced. All extant and fossil genera of agamids possess pleurodont teeth anteriorly, which in most taxa are enlarged and caniniform. Only adults of *Uromastyx* lack pleurodont teeth but they are present in the juveniles. Accepting the concurrent opinion that chamaeleons are evolutionarily derived from an early agamid ancestor which probably would have possessed pleurodont teeth in the anterior dentitional quadrant, then the absence of pleurodont teeth in chamaeleons may be a derived character only for recent chamaeleons. The ancestral chamaeleon, cladistically based on other apomorphic characters, may have possessed pleurodont, caniniform teeth.

All species of chamaeleons possess a maxillary process which projects in a vertical plane and arches dorsally-posteriorly forming the anterior and dorsal margin of the external nares. An anterior process of the prefrontal meets this maxillary process and together they form an acute ridge of bone defining the canthus rostralis. Simultaneously this arch restricts the external nares to a completely lateral position, not bounded by the nasal bones. This process is clearly demonstrated by specimen DP-FNSP No. 104 (pl. II/3,4) but is absent in all agamids.

The configuration of the anterior end of the maxilla of *Chamaeleo caroliquarti* clearly indicates that it defined the tip of the snout and that the premaxilla was greatly reduced in size. A groove indicating a syndesmosis with the premaxilla occurs only on the medial margin of the maxilla, a condition identical with extant *Chamaeleo*. The majority of agamids have a broadened alveolar part of the premaxilla and syndesmotic facets are visible on the anterior surface of the maxilla.

The dentary is fairly robust for a small lizard, the labial surface is angularly convex when viewed transversely, a condition found in extant chamaeleons, and the anterior end is rather blunt with a squarish outline. Most small agamids have a weakly convex or flattened labial surface, and the dentaries are proportionally longer and anteriorly more slender and tapering. The Meckelian canal anteriorly rotates onto the ventral edge of the dentary and extends around the anterior end below the symphysis, a condition found in all *Chamaeleo*. However the position at which it changes from medial to ventral sides of the dentary may be taxonomically variable. In agamids the canal does rotate ventrally but the nature of its visibility from a medial view is variable.

The horizontal groove below the tooth row on the lingual side, termed "denta

gutter" by some workers and representing the much larger area of tooth generation and attachment in pleurodont lizards, distinctively continues around the anterior end of the dentary passing through the zone of symphysis (pl. I/1). In agamids this groove is usually shallow, not very distinctive and does not extend around the anterior end because it becomes expanded to support the bases of the pleurodont enlarged caniniform teeth.

Although the coronoid process has not been preserved with any of the fragments, a flat impression representing the syndesmotic facet of the anterior medial process of the coronoid is clearly visible on the dentaries of specimens DP-FNSP Nos. 101, 102 and 112. This process is characteristically extensive and has a straight upper margin obtusely angled towards the Meckelian canal as in extant *Chamaeleo* (text-fig. 1). In agamids, the process is shorter, the upper margin concave or irregular, and the angle less obtuse.

Comparison of *Chamaeleo caroliquarti* with extant species is difficult because of the fragmentary nature of the fossil material, and because there exist no published comparative studies of chamaeleontid osteology. Only on the basis of geographic distribution and overall similarity of the dentaries and maxillae, are we suggesting that *C. caroliquarti* belongs to the *Chamaeleo chamaeleon* species group (Hillenius 1959), a taxon which was defined on the basis of external morphology. *C. chamaeleon* is the nearest living chamaeleon, found in northern Africa and isolated areas of the Mediterranean, but *C. caroliquarti* differs from this species by the more slender dentary at the symphysis. The symphysis of *C. chamaeleon* is deep, which produces a square profile at the anterior end of the dentary, and an abrupt narrowing of the dentary immediately posterior to the symphysis. *C. caroliquarti* has the surface of the dorsal nasal process of the maxilla highly sculptured. Among members of the *C. chamaeleon* species group this sculpturing is variable. We were not able to ascertain if this was sexual or taxonomic variation.

The three dentary fragments from Wintershof-West in Bavaria come from a geological stratum approximately two million years older than the Dolnice locality (Fejfar 1972a). All three are much smaller than the Dolnice form, but not enough of the mandible is intact to determine whether the specimens were juvenile or adult. The profile of the anterior end of the dentary is square, similar to most species of contemporary *Chamaeleo* (text-fig. 1) but unlike the Dolnice *C. caroliquarti*. The Meckelian canal rotates onto the ventral edge of the dentary at a position more anterior than *C. caroliquarti,* and also remains slightly on the medial-ventral edge making it possible to view the canal medially.

As noted in the description of the Bavarian material, tooth size and the nature of the occlusal wear facets are variable. Specimen BSP 19603 has deep, acutely cut wear facets on the dentary which slant obliquely antero-ventrally, similar to *C. caroliquarti* of Dolnice. However the older two specimens have shallow facets with rounded bottoms, and they are oriented vertically.

The nature of the wear facets between the dentary teeth, caused by occlusion with the maxillary teeth, apparently varies both intra- and inter-specifically. A survey of preserved material of several recent species suggests that these facets may be shallow with rounded bottoms or deep with acutely angular bottoms. The facets may also be vertical or obliquely slanted antero-ventrally. Unfortunately not enough material was available to document sexual, ontogenetic and populational variation within species. Hypothetically the facets may be affected by differences in diet, the degree of sand and grit inadvertently entering the mouth,

longevity of adults as the tooth wearing and dentary cutting would be time-dependent, and nature of aggressive combat between individuals.

Possibly the older age and morphological differences justify naming the Bavarian form as a distinct species, but the paucity of material and characters and the lack of information on the intraspecific variation of the observed morphological differences in other species of *Chamaeleo* persuades us to take a conservative view and assign this form tentatively to *Chamaeleo caroliquarti*.

The second author thanks Dr. O. Fejfar for bringing the first set of material and the Dolnice site to his attention, and we thank Dr. Wellnhofer for loaning us the Bavarian specimens. We appreciate the help of Dr. Wolfgang Böhme, Museum Alexander Koenig, Bonn, F.R.G., who provided us with comparative material of recent chamaeleons.

Special credit is extended to Dr. Richard Estes, San Diego State University, California, who supplied us with many helpful and constructive comments on an earlier draft. The first author is indebted to the Department of Palaeontology, Faculty of Natural Science, Charles University, for providing him with funds making it possible to visit Prague and study this material.

Conclusions

1. *Chamaeleo caroliquarti* sp. nov., an acrodont toothed fossil lizard, is described from dentary and maxillary fragments.
2. The type material comes from a Lower Miocene horizon near Cheb, Western Bohemia, and represents the oldest fossil referable to the family *Chamaeleonidae*.
3. Additional material assigned to *Chamaeleo* cf. *C. caroliquarti* comes from a slightly older Lower Miocene horizon from Wintershof - West, Bavaria.
4. *Chamaeleo caroliquarti* is distinct from members of the lizard family *Agamidae* by the presence of a strong dorsal nasal process of the maxilla, extensive anterior medial process of the coronoid, teeth with strongly laterally non-contacting bases, and absence of pleurodont teeth.
5. *Chamaeleo caroliquarti* is distinct from extant species of chamaeleons by the character combination of surface sculpturing of dorsal nasal process of maxilla, less blunt and squared anterior end of dentary, and nature of the Meckelian canal rotating onto the anterior ventral edge of the dentary.

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Explanation of plates

Drawings by I. Kolebaba

Plate I

1 - *Chamaeleo caroliquarti* holotype, DP-FNSP No. 101. Left dentary, labial view. × 12.3; 2 - *Chamaeleo caroliquarti* holotype, DP-FNSP No. 101. Left dentary, lingual view. × 12.3; 3 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 102. Right dentary, labial view. × 12.3; 4 *Chamaeleo caroliquarti* paratype, DP-FNSP No. 102. Right dentary, lingual view. × 12.3. The line illustrated with figures is 1.0 mm.

Plate II

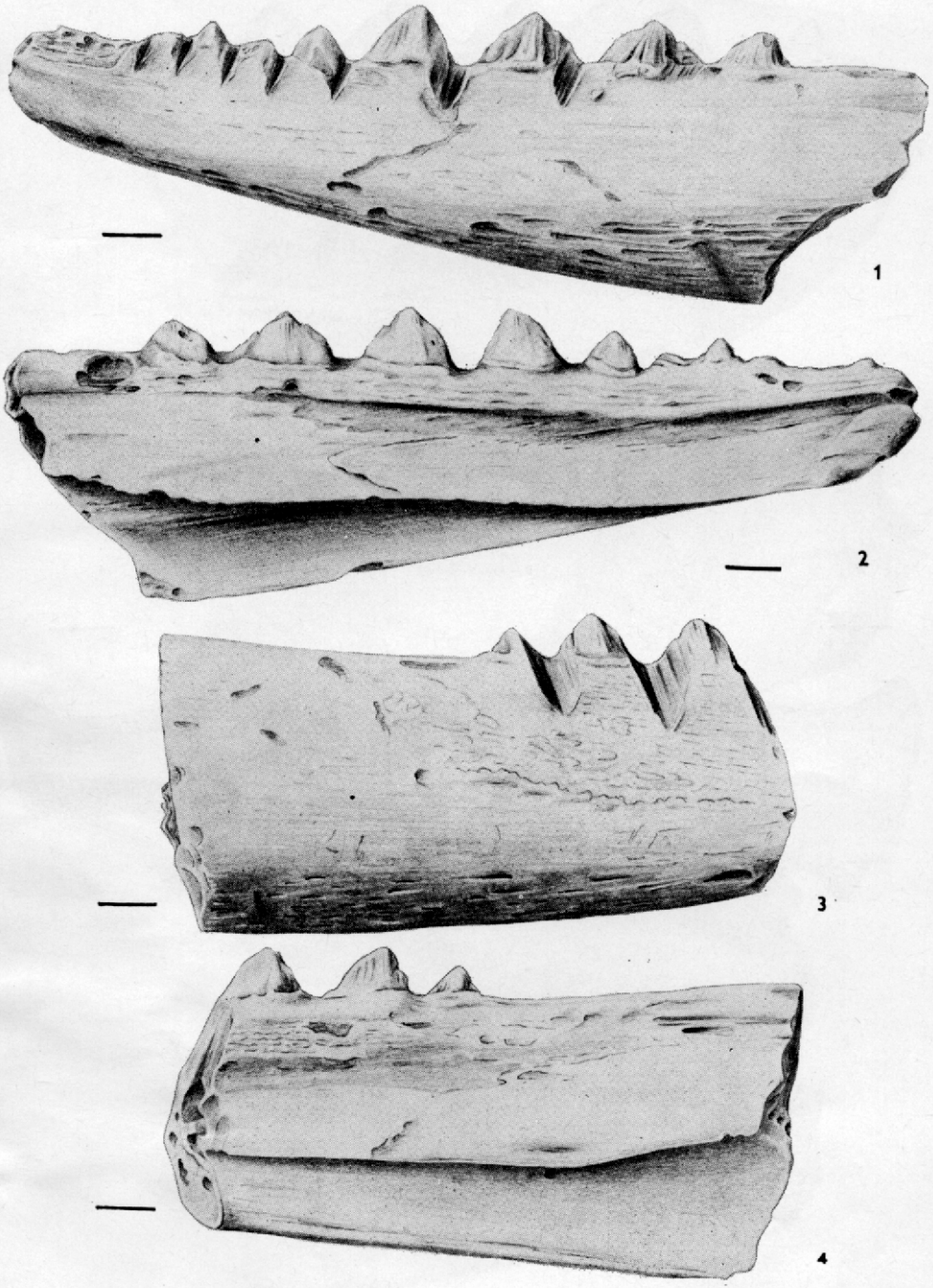
1 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 103. Left maxillary, labial view. × 20; 2 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 103. Left maxillary, lingual view. × 20; 3 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 104. Right maxillary including dorsal nasal process, labial view. × 20; 4 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 104. Right maxillary including dorsal nasal process, lingual view. × 20. The line illustrated with figures is 1.0 mm.

Plate III

1 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 106. Left maxillary, labial view. × 20; 2 - *Chamaeleo caroliquarti* paratype, DP-FNSP No. 106. Left maxillary, lingual view. × 20; 3 - *Chamaeleo* cf. *C. caroliquarti*, BSP 1937 II 19601. Left dentary, labial view. × 20; 4 - *Chamaeleo* cf. *C. caroliquarti*, BSP 1937 II 19601. Left dentary, lingual view. × 20. The line illustrated with figures is 1.0 mm.

Plate IV

1 - *Chamaeleo* cf. *C. caroliquarti*, BSP 1937 II 19602. Left dentary, labial view. × 20; 2 - *Chamaeleo* cf. *C. caroliquarti*, BSP 1937 II 19602. Left dentary, lingual view. × 20; 3 - *Chamaeleo* cf. *C. caroliquarti*, BSP 1937 II 19603. Left dentary, labial view. × 20; 4 - *Chamaeleo* cf. *C. caroliquarti*, BSP 1937 II 19603. Left dentary, lingual view. × 20. The line illustrated with figures is 1.0 mm.



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Pl. IV

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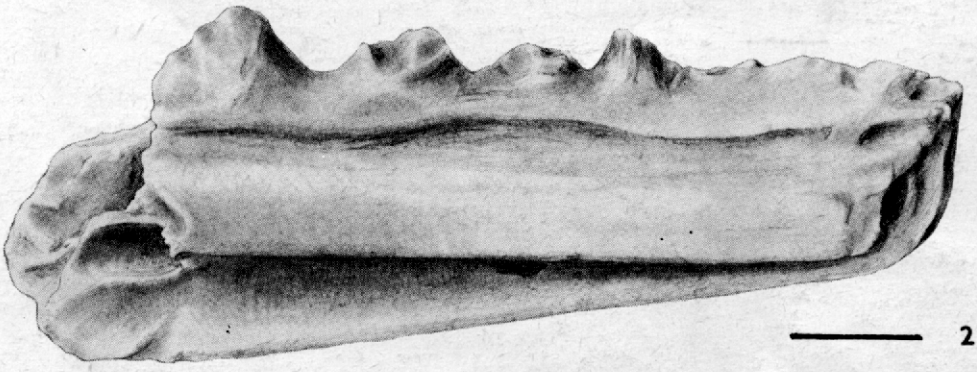

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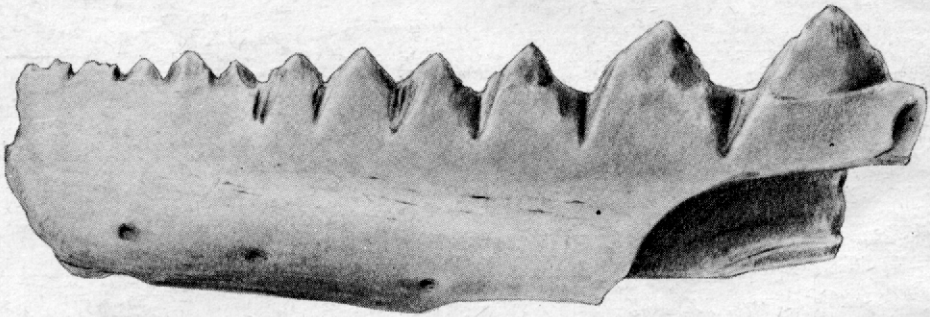

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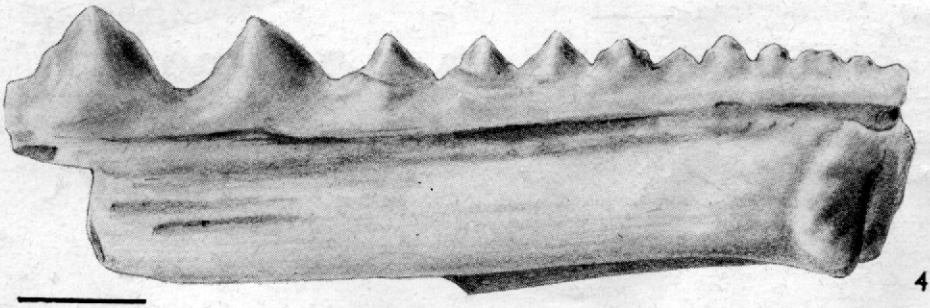

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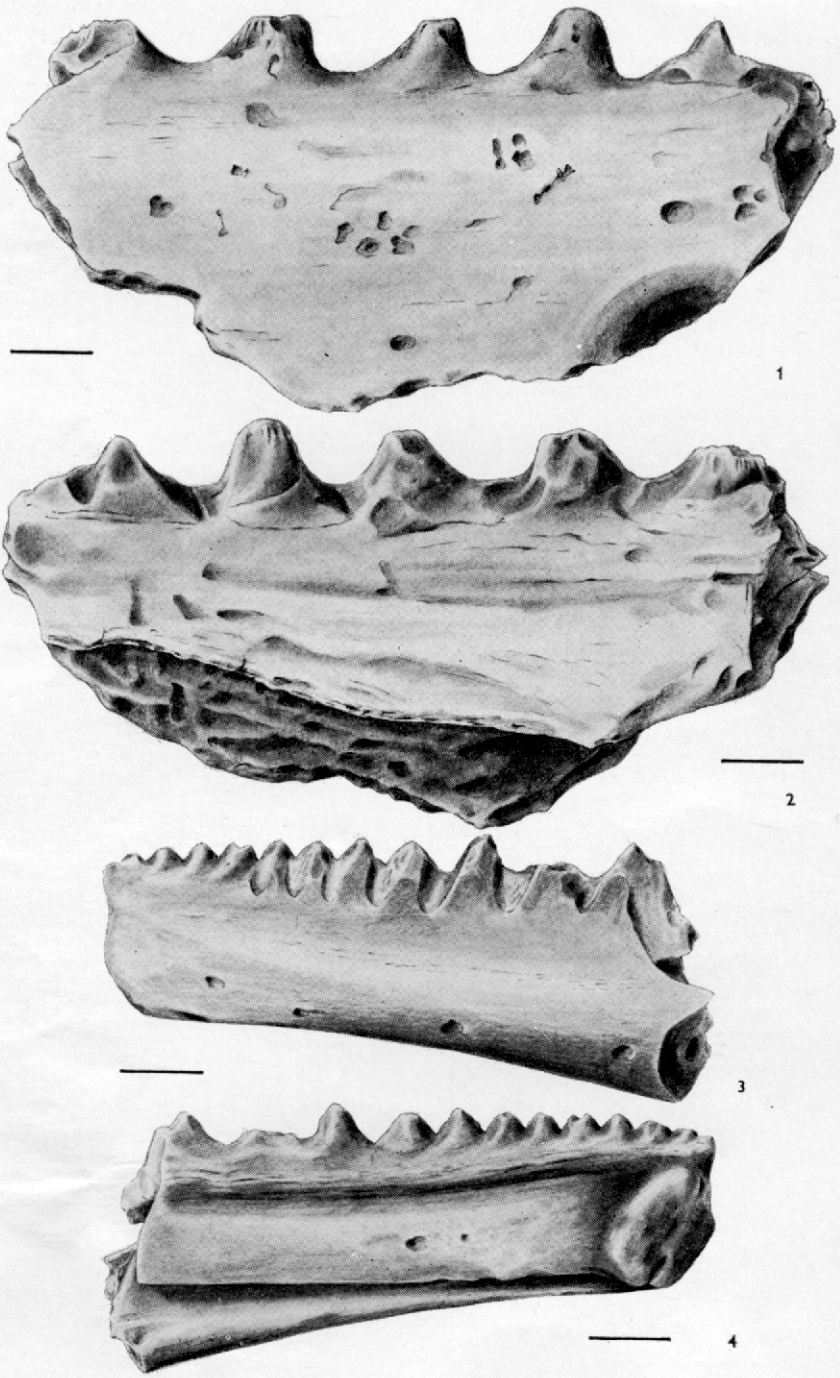
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Pl. II