COMPSOGNATHUS CORALLESTRIS, A NEW SPECIES OF THEROPOD DINOSAUR FROM THE PORTLANDIAN OF CANJUERS (SOUTHEASTERN FRANCE)[*]

ALAIN BIDAR, LOUIS BIDAY and GÉRARD THOMEL
Centre d'Etudes Méditerranéennes
Muséum d'Histoire Naturelle
60 bis, Boulevard Risso, 06300 Nice (France)

SUMMARY

The Portlandian lithographic limestones of the "Lesser Plain" at Canjuers (Var, France) have recently yielded a skeleton, practically complete and in a perfect state of preservation, of a small dinosaur belonging to the genus *Compsognathus*. This taxon was until now represented only by a single individual coming from the Late Jurassic limestones of Kelheim (Bavaria), for which A. WAGNER created the species *C. longipes.*

The bringing to light of a second specimen, which we distinguish specifically from the genotype under the name *C. corallestris*, provides a better appreciation of the family and supplies ecological details about this particularly interesting genus. Indeed, we sketch the outline of a group of theropods of very modest size, offering undoubtedly avian characters in their skull, certain traits of their hind limbs, and the lightening of their skeleton (vertebrae, limbs).

The genus *Compsognathus*, whose two representatives came from lagoonal deposits, seems to correspond to an entirely unusual adaptation among dinosaurs. It seems instead that it is a walking type, living on the beaches of atolls or even on the motus surrounding the lagoon. This carnivorous dinosaur fed itself on small prey (fish?, reptiles) that it probably captured directly with the aid of its jaws, furnished with small, sharp, posteriorly recurved teeth, and without the aid of its forelimbs. Thus, whereas the extremely flexible and elongate neck evokes that of a heron-like bird, the forelimbs are considerably reduced. It even seems in *C. corallestris* that an ankylosis of the articulation of the wrist is shown by the apparent existence of a dermal bone.

It seems then that this is a very particular specialization of the forelimb that, although always more or less reduced in bipedal dinosaurs, nevertheless generally preserves an essential role in the grasping of prey. In contrast, in *C. corallestris* the presumed ankylosis of the wrist and the reinforcement observed in the anterior part of the manus suggests an adaptation of this limb to a semi-aquatic mode of life.

GEOGRAPHIC AND

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GEOLOGIC CONTEXT

The fossil that is the subject of this Memoir comes from the open GHIRARDI quarries, not far from the hamlet of Bessons, on the Lesser Canjuers Plain (Var). This large, thoroughly very flat synclinal basin is bordered to the west by the Greater Canjuers Plain, to the east by the Artuby, a modest tributary of the Verdon, and to the north by the Verdon itself, whose gorges notch the imposing mass of supra-Jurassic limestones.

Geologically the Jurassic of Haut-Var is placed within a vaster complex, on the scale of the whole southeast of France. Indeed, with the Nummultic and to a lesser degree the Turonian, it constitutes the essential framework of the subalpine chains of Dauphiné, Haute-Provence and the Nice region.

The historical works of E. HAUG (1891), W. KILIAN (1917) and A. LANQUINE (1935) have permitted recognizing two regions of very distinct facies there:

— North of a line passing by Castellane and the southern border of the mass of Valensole conglomerates, the Upper Jurassic is presented under one pelagic facies comparable to that of Diois and the Baronnies. On the Callovo-Oxfordian, whose thickness can be considerable (= "Black Lands"), the Kimmeridgian is formed from gray limestone banks with past marbles. The Portlandian, which is presented under the "Tithonian" facies, forms a bar very marked in morphology. The fauna is characterized by Ammonoidea (essentially Perisphinctidae), brachiopods (pygopes), and calpionelles. The passage to the Lower Cretaceous is very gradual, the total thickness of the whole Kimmeridgian-Portlandian being on the order of 150 to 200 m.

This facies zone is thus characterized by its pelagic mark, as well as by the thickness of the series, testifying to a strong subsidence.

— South of this line, the Jurassic is exclusively limestone; its thickness declines considerably.

If the Kimmeridgian is always formed from sublithographic limestones, the Portlandian, whose thickness can attain 500 m (J. J. BLANC and Cl. TEMPER, 1963), presents facies of "white limestones". The reef limestones appear in this domain, constructed of corals and nerines. This ensemble, frequently dolomitic, can show phenomena of karst evolution (Canjuers Plains region).

It is important to mention that indications of the "Purbeckian" facies are observed at the top of the white limestones in the Nice region.

In this context, the observations carried out for close to a century (W. KILIAN, 1888, 1917; A. LANQUINE, 1935; J. GOGUEL, 1936; G. MENESSIER, 1959; J. J. BLANC and Cl. TEMPER, 1963; L. GINSBURG and G. MENESSIER, 1970) allow us to conceive, during the Portlandian, of the Lesser Canjuers Plain as a lagoon separated from the high sea by a reef barrier.

The presence of limestones built in the Verdon gorges indeed permits thinking that, during this period, the Canjuers Plains region formed a subsiding platform beneath an area of very shallow water. This high ground was eminently favorable for the construction of coralline formations.

The very regularly layered lithographic limestones that delivered *C. corallestris* were deposited in an environment of very weak hydrodynamics, just as the remarkable state of preservation of most of the fossils therein also testifies. Comparison with the

Bavarian localities of the same or nearly the same age (1), corresponding to lagoonal deposits, is irresistibly imposed. In this we share the paleogeographic interpretation of L. GINSBURG and G. MENESSIER (1970) whereby: “We will thus be tempted to see in the fossiliferous basin of the Lesser Canjuers Plain an atoll lagoon, at the heart of a reef zone that skirted the coasts of the emergent Maures massif *sensu lato* for a length of around forty kilometers to the north, and was connected to the other coralline formations that bordered the ancient crystalline emergent massifs on the outside of the alpine arc.”

SYSTEMATICS

ORDER SAURISCHIA
SUBORDER THEROPODA
FAMILY *COMPSOGNATHIDAE*

This family was more or less largely included by the authors. According to the works of O. MARSH (1890, 1896), it was restricted to the sole genus *Compsognathus*, itself represented by a single individual, the type species *C. longipes* WAGNER. Accordingly the genus *Hallopus*, of similar age but from North America (Colorado), was considered as characteristic of a distinct order. In contrast, G. BAUR (1882) placed this last taxon in synonymy with *Compsognathus*.

The current, more nuanced, position recognizes *Hallopus* as valid but arranged within the family Compsognathidae.

In fact, it forces us to recognize that our understanding of this group of dinosaurs is still very fragmentary because, taking into account the recent discovery of a Varois *Compsognathus*, the family is represented by only three individuals, of which only two are nearly complete.

The principal characteristics common to Compsognathidae can be summarized thus:

Very modest size (2). Vertebrae and limb bones hollow. Forelimbs very reduced relative to the extremely developed hind limbs. Femora shorter than tibiae. Metatarsals long and slender. Three functional digits on the pes. Pubis elongated anteriorly, ischia thin and very widened distally.

Genus Compsognathus WAGNER, 1861.

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(1) The rest of the signal is interesting that, just as in Solnhofen for example, if the vertebrates (fish, reptiles) and certain echinoderms (ophiuroids) are admirably fossilized, the calcareous tests (brachiopods, ammonites, echinoids) were not resistant. Of this fact the rhynchonelles are crushed, the ammonites reduced to the state of INDEGAGEABLES internal molds, forming a unit with the rock, and the *Cidaris* compressed and even sometimes broken. This selective fossilization, the inverse of normal, could have been tied to the chemistry of the water.

(2) *Compsognathus longipes* WAGNER is the smallest known dinosaur; while being sensibly larger, *C. corallestris* BIDAR, DEMAY and THOMEL remains a dwarf among this group of reptiles. *Hallopus victor* MARSH appeared, according to the known parts of its skeleton, to have attained comparable dimensions.

The two specimens of *Compsognathus* recovered to date being remarkably preserved, it is possible to make the description given above more specific, since it also holds for the genus *Hallopus*, known from very fragmentary information.

Dinosaur of very modest size, with small head, reduced forelimbs, very developed hind limbs and tail.

Elongated skull shows some remarkable avian characters and offers indisputable analogies with that of *Archaeopteryx*. The premaxillae and maxillae are furnished with small, sharp teeth.

Neck very long and flexible, formed from ten or eleven hollow vertebrae; the more anterior of these cervical vertebrae bear ribs elongated into rods. The number of dorsal vertebrae seems to vary between 10 (probable) in *C. corallestris*, and 11 or 12 in *C. longipes*. These vertebrae are remarkable for their wide, flat dorsal processes.

Ribs fine and gastralia very slender.

Small forelimbs — Mani apparently tridactyl. Sacral vertebrae, probably numbering 5, partially hidden by the ilium which is very elongated anteriorly and posteriorly.

Pubis very long, projected anteriorly and sinuous, recurved distally towards the rear.

Ischia thin and flat, very widened distally.

Hind limbs very elongated. In each limb the femur, slightly curved towards the front, is shorter than the tibia-fibula complex. The astragalus, narrowly connected to the calcaneum, is extended forward by a long process.

Three long, slender, narrowly linked metatarsals, corresponding to three functional digits terminated by claws. Digits I and V are vestigial.

Like the vertebrae, the limb bones are hollow. Tail extremely elongated, clearly exceeding the length of the rest of the body.

The two known specimens come from lagoonal deposits, suggesting an insular lifestyle.

Portlandian.

Compsognathus corallestris nov. sp.

Derivation of name. — The specific name of the Varois species was chosen to reflect its presumed mode of life, on coralline atolls.

Material. — The type was recovered from the Portlandian lithographic limestones, also called “Bessons”, Lesser Canjuers Plain (Var, France), by Mr. and Mrs. GHIRARDI. It is currently deposited in the Muséum d’Histoire Naturelle de Nice.

SKULL.

At least 100 mm long, 115 mm maximum, the skull was detached “post-mortem” from the rest of the body, and is shown in lateral position; packing brought the bones back together in the sagittal plane, the left side of the skull can be observed in this manner.

A series of breaks gravely affect the posterior part of the skull, rendering observation of the cerebral region difficult. However, some bony vestiges of plates allow supposing that the frontals and parietals were rather developed, as is the case in Archaeornithes.

The orbit (around 25 mm in diameter) is exceptionally large for a theropod.

The maxilla is excavated by a significant antorbital fossa (length: 15 mm, height: 10 mm).

The lacrimal ["adlacrimal"] bone is well preserved, separating this fossa from the orbit; 5 mm wide at its base, it is reduced to 3.5 mm in its middle part; the superior part is recurved in a long, anteriorly directed process (12 mm) that delimits the antorbital fossa towards the top. A maxillary ascending ramus, and without doubt part of the nasal, 5 mm wide and 3.5 mm tall, separate the antorbital fossa anteriorly from the external naris.

The lateral temporal fossa seems less important; the upper fossa, if it exists, corresponds to the region crushed by the breaks. The postorbital is represented by a 7 mm long fragment separating the temporal fossa from the orbit; similarly only the inferior part of the squamosal is visible, beside the opisthotic which is sutured to it.

The region of the mandibular articulation (quadrate, quadratojugal…) is somewhat disrupted by the fact that the mandible is not fossilized in anatomical connection.

The jugal, articulated with the maxilla anteriorly and the quadratojugal posteriorly, forms a complete suborbital bar, remarkable however for its slenderness.

The premaxilla, slightly displaced by fossilization, is furnished with teeth like the maxilla. These teeth, strongly recurved posteriorly, are very elongate and sharp; the largest of the visible teeth reaches 5 mm in length and is 2 mm wide at its base.

The mandible, only visible along a length of 94 mm, forms an angle of about 60 degrees with the maxilla. The right ramus is shown vertically and points its teeth upwards, whereas the left ramus was folded back in the plane of sedimentation.

On this ramus can be observed:

— The dentary, 55 mm long, furnished along a 28 mm length with small, posteriorly recurved teeth whose size does not exceed 3 mm.

— The clearly visible surangular (about 38 mm) and angular (about 20 mm), connected by a very thin floor of bone.

— The articular, 11 mm long, which is joined to the articulated ends of the angular and surangular.

Two very slender bony arches (1 mm) converge and seem to become joined; they originate beneath the mandible. They could be derived from a visceral arch and have formed a lingual support comparable to the hyoid apparatus of birds.

NECK.

The remarkably long neck is strongly projected backward. This disposition presents a troubling analogy with that observed in *C. longipes* WAGNER.

Indeed, just as in the Bavarian specimen, the neck, separated from the skull, is recurved on itself, the first cervical vertebrae coming nearly to contact the dorsals.

It is allowed supposing that the animal had a great amplitude of movement, depending on an significant mobilization of the cervical vertebrae. These number 10 or 11, and were hollowed and thereby crushed.

Cervicals 1 and 2 are a nearly indiscernible, affected by a limestone break.

The next four bear double-headed ribs, 25 to 30 mm long, whose ends taper to a point. The slightly visible spinous processes seem very discrete: subrectangular, they hardly extend 8 mm in length for 4 mm in height. The length of the vertebrae, which is difficult to appreciate, oscillates around 15 mm, nos. 6, 7 and 8 being smaller than the others. The last cervicals show neither ribs nor marked processes. However, some vestiges dubiously similar to small free ribs are observed on the last two.

DORSAL VERTEBRAE.

The vertebral column of *C. corallestris* corresponds, in its dorsal part, to a rather poorly preserved region of the skeleton, crushed and in part destroyed.

In fact only 9 dorsal vertebrae (1) are visible, but it is certain that at least a tenth existed. The break that affected the skeleton to the limit of the pectoral girdle and the (not observable) third dorsal vertebra is the cause of the defect.

D1: Length approximately 15 mm; width of vertebral centrum around 12 mm.

D2: The dimensions cannot be appreciated.

D3: Hypothetical; not visible (break in the skeleton).

D4: Length approximately 16 mm.

D5: Length 16.5 mm.

D6: Estimated length 15 mm (this vertebra is affected by a limestone break).

D7 and D8: The two vertebral centra are reduced to the state of imprints; traces of the spinous processes are also distinguished, not visible on the anterior vertebrae. These processes have lengths of 11 and 13 mm respectively, and heights 7 and 5.5 mm relative to the vertebral centrum.

D9: Relatively well preserved, this vertebra is 19 mm long. The perfectly distinct spinous process shows a length of 13 mm and a height of 8 mm.

D10: The last dorsal vertebra is also the longest; its length is 19.5 mm; the corresponding process is partly masked by the preacetabular elongation of the ilium.

THORACIC REGION.

The ribcage, whose preservation is relatively satisfactory, is short relative to the total length of the animal. Indeed, its anterior height can be estimated at 90 mm; it widens slightly posteriorly, the posterior height being 100 mm. Its length is around 165 to 170 mm.

The slender ribs are fairly clearly visible, although their ends are not entirely preserved. 9 pairs are counted thus presented for observation:

1) A double-headed rib inserted onto vertebra D1 is visible only for a length of 28 mm.

2) A rib visible for only 20 mm; its insertion on vertebra D2 is by a smaller articular head than the first.

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(1) It is thanks to an error, ascribable to the conditions of chance in which was effected the preliminary examination of *C. corallestris*, that we believed to recognize twelve cervical vertebrae for only eight dorsals. A more pushed preparation of this part of the fossil, moreover strongly crushed, permitted us to make appear the proximal ends of the ribs up to then masked by the matrix. We thus arrive at a scheme very comparable to that of *C. longipes* with ten or eleven cervical vertebrae and ten dorsals.

3) A pair of imprints not attached proximally to dorsal vertebra D3, which is not visible (1).

4) A pair, partly as imprints, showing the point of contact with the corresponding dorsal vertebra. These very slender ribs are around 55 to 60 mm long.

5) A pair showing one complete and one fragmentary imprint, as well as their insertion on vertebra 5.

6) A fragment of rib, in indisputable relationship with dorsal vertebra D6, and a very posterior imprint corresponding reasonably to the right rib of the same vertebra. The break that affects the whole body of the animal at this point unfortunately does not permit affirming this.

7) A rib very well preserved at its proximal end, the distal part, reduced to the state of an imprint, being in addition incomplete. At the level of its insertion with the corresponding dorsal (D7), the rib is flattened and shows a very marked widening.

8) A similar observation can be made at the level of dorsal vertebra D8.

9) A fragment of imprint of rib, in part hidden under dorsal vertebra D10, corresponds to the single vestige of the ninth pair of ribs still perceptible. It remained obviously shorter than the preceding ones.

10) No rib appears to be attached to the tenth dorsal vertebra D10.

The perfectly preserved ventral part of the thoracic region reveals the existence of twenty fine gastralia which become reduced laterally. Comparable to those known in other dinosaurs such as *Procompsognathus, Struthiomimus*, etc…, this dermal formation had an obvious role in contributing to the support of the visceral unit.

A very interesting observation can be made on the interior of the ribcage of *C. corallestris*. It regards vestiges clearly belonging to another animal. This debris appears immediately anterior to the third pair of ribs and goes up to the fifth. Within this bony cluster, subcircular in form and with a diameter of around 40 mm, it is possible to recognize various elements of a dissociated skeleton, notably some phalanges, of which certain are in articulation with the claws, some probable limb bones, besides three subrectangular vertebrae, still associated (length: 2.2 to 2.5 mm; width: 2.4 to 2.8 mm).

This observation brings new elements to the controversy surrounding the supposed viviparity of the genus *Compsognathus*, engaged since the fundamental work of O. MARSH on *C. longipes*. This important question will be approached in detail in the conclusions of this work.

PECTORAL GIRDLE AND FORELIMBS.

The pectoral girdle and forelimbs correspond to the region of the skeleton whose state is the most defective, the visible parts being nearly completely reduced to imprints.

The proximal regions of the scapula are destroyed, with only the articular heads being visible, posed on top of one another and incomplete. In spite of this very mediocre preservation, the very sensible widening of the heads of the scapular plates are nevertheless notable. Moreover, a semilunar imprint similar to a coracoid is distinguished at the articulation with the right scapula, in a subjacent position.

The two humeri, whose length can be estimated at 50 mm, are intersected; the left, in a superior position, is sigmoid; widened proximally, it is reduced in its median part; its distal end is indistinct. The right humerus is reduced to the state of an imprint. It

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(1) This part of the skeleton, enclosing the pectoral girdle, is only very partially preserved.

is the same for the radius-ulna, whose superposition renders their study still worse. Clearly twice as slender as the humerus, they are also a little shorter. Their dimensions can be appreciated fairly exactly for the limb

	RADIUS	ULNA
Approximate length….	45 mm	41 mm
Proximal diameter…….	6.5 to 7 mm	4 mm
Distal diameter……….	?	6 mm

Only part of the imprint of the left radius is perceptible in the extension of the left humerus.

Following the right radius-ulna, some small bony vestiges are noted, probably comparable to the carpals, whose length does not exceed 8 mm.

Beyond, the metacarpals are represented only by three poor, incomplete imprints. The eventual presence of claws cannot be detected.

A very enigmatic vestige is formed by an imprint weakly convex anteriorly and visible starting from the humerus-radius-ulna for a length of around 135 mm; less marked than the imprints left by the limb bones, it could correspond to the trace of a dermal bone, or at least to a reinforcement of the distal and anterior part of the limb.

This observation is very important because it provides a markedly different morpho-functional image from that admitted for the forelimb of *Compsognathus*.

Indeed, in *C. longipes* this appears not to terminate in three digits furnished with well-marked claws. There exist perhaps one or two other digits (functional or vestigial?) that do not appear for observation. This type of organization of the manus conforms to that known in other bipedal dinosaurs such as *Struthiomimus*; it is presumed for forms close to compsognathids: *Segisaurus*, *Ornitholestes*, etc… In *C. corallestris* it seems that this arrangement was different.

The presence of a dermal bone at the level of the forearm and manus would imply an ankylosis of the wrist articulation. In these conditions the anterior part of the limb, far from being adapted to seize prey, had undergone a transformation into the form of a rigid aileron. This adaptation, hitherto unsuspected in the theropods, would not contradict the ecological framework of this dinosaur.

However, it would not involve envisioning the realization of a swimming paddle, which would imply a shortening of the limb bones and a hyperphalangy not observed here. At most one a role as oars could be admitted for the forelimbs of *C. corallestris*.

PELVIC GIRDLE AND HIND LIMBS.

The pelvic girdle and hind limbs are, in their whole, admirably preserved.

The sacral vertebrae, mostly covered by the ilium, seem to number 5. Only their length can be estimated, the remainder rather roughly, with the exception of the fourth sacral vertebra, whose diameter is measurable.

S1	19 mm
S2	14.5 mm (supposed length)
S3	14 mm (*idem*)

S4 14.5 mm. Diameter: 9.5 mm.
S5 14.5 mm.

A slight hiatus (2.5 mm) separates sacral vertebrae 4 and 5.

The ilium is very elongated. Just as in *C. longipes*, the pre- and postacetabular extensions are very developed. Its total approximate length is from 73 to 75 mm over a maximum supposed width of 18 mm.

The pubes are remarkable for their length, which can be estimated at 140 mm taking into account their sinuous trajectory. The proximal region, by far the most important (95 mm), offers a sinuous shape; it is clearly projected anteriorly. The distal part presents an abrupt bend and leaves posteriorly in an ascending position; it is only 45 mm long.

At the level of the bend, the pubis widens in a very marked fashion.

The ischia, visible along a length of around 70 mm, are absolutely comparable in their form to those of *C. longipes*. Very spread out in their proximal part (around 50 mm) where they seem to be particularly thin, they are terminated distally by a rounded head 10 mm wide.

The hind limbs constitute the most satisfactorily preserved part of the skeleton. Nearly all the bones can be recognized, remaining in articulation. However, these bones being hollow, the superimposed elements (for example the femora or, for each limb, the tibia-fibula complex) are in general impressed on one another, which obscures them to a certain degree from observation. Nevertheless, the dimensions can be given for most of the skeletal elements of each limb (cf. table I).

The femora are slightly arched toward the front; the right cannot be measured; the left, whose length is 110 mm, is clearly larger than that of *C. longipes* (70 mm).

The tibia-fibula complex is straight, longer than the corresponding femur. Given the hollow character of these bones, which are crushed, the fibulae are less apparent. In contrast the subcircular astragalus can be distinguished very well in each limb,. The modest but well marked calcaneum appears clearly at the distal articulation of the leg.

An extremely important point was raised on this subject by Th. HUXLEY (1869) who, believing he could discern a complete suture between the astragalus and tibia in *C. longipes*, which would have constituted an avian character, he considered that the genus *Compsognathus* was very isolated relative to other dinosaurs based on this fact.

The critical analysis which O. MARSH (1896) delivered showed that this was nothing. It is interesting to remark that the discovery of a second specimen of the genus *Compsognathus* confirms the observations of the American paleontologist, the separation between the distal end of the tibia and astragalus being very apparent in *C. corallestris*. Nevertheless these two bony elements have remained narrowly in articulation in our specimen, and the measurements given in the table for each limb include the astragalus and tibia-fibula complex.

An excellent study of the hind legs of *C. longipes* was given by G. BAUR (1882). In *C. corallestris* this part of the skeleton is also better preserved.

The tarsals are clearly distinct, although very short; two certain elements are recognized on the right side, three probable on the left; they are much longer than tall, contrary to what is known in *C. longipes*.

The metatarsals are remarkable for their length and slenderness. Only three are visible on the left leg, the median (metatarsal 3) being clearly longer than the laterals (metatarsals 2 and 4). The right leg shows several supplementary details, notably a certain vestige of metatarsal 5, whose length attains a little less than one-quarter that of metatarsal 3.

In contrast, the attribution of another dissociated bony vestige to metatarsal 1 is much more doubtful.

The phalanges are articulated with the corresponding metatarsal or slightly displaced. The best-preserved digit is 4: indeed it still shows the 4 phalanges terminated by a claw. The claws are visible at the ends of the other digits, sometimes dissociated from the phalanges.

This observation agrees with that known in *C. longipes*.

TAIL.

The tail is disproportionate relative to the body; taking into account the hiatus due to the break in the limestone slab, its length is on the order of 700 mm.

The most anterior caudal vertebrae, numbering 4, are elongated by strong spinous processes; these vertebrae have remained in perfect articulation with the sacral region. With their continuation, the trace of the fifth caudal and its process can be distinguished, reduced to the state of an imprint; the sixth is missing due to a break in the limestone; the seventh is only partially visible; the eighth is defective.

Then a significant hiatus intervenes, of which mention is made above, that seems to correspond (taking into account the average length of the vertebrae) to caudals 9, 10 and 11, of which only the imprint of the spinous process is visible.

Beyond, caudal vertebrae 12 to 31 are perfectly preserved, a vestige of caudal 32 being perceptible at the end of the specimen.

As appears with the reading of table 2, the length of the caudal vertebrae rapidly increase from the first (15 mm) to the fourth (26 mm), being stabilized at around 19 to 20 mm. A new increase in size is observed at the level of caudals 20 to 23 (22 mm), the length of the last eight measurable caudals being appreciably 23 mm.

In contrast, the diameter decreases rather regularly, passing from 11 mm for caudal 1 to 5 mm for the thirty-second.

In this way, the tail appears more and more slender and tapered approaching its distal end. The rest of the spinous processes, very strong at the level of the attachment of the tail, are meanwhile tapering and being shortened; they are reduced to simple stubs at the end of the tail.

C. corallestris is thus remarkable for the extraordinary length of its tail, the remainder incomplete on our specimen. In *C. longipes* only fifteen caudal vertebrae are preserved, for a length of around 200 mm; here the length of the first fifteen caudals can be estimated at around 300 mm.

DIAGNOSIS

It is without hesitation that we refer the dinosaur from Canjuers to the genus *Compsognathus*, until now monotypic. Indeed, its very particular characters place it immediately among the theropod saurischians and, within this suborder, its position was limited from the start to a small number of possible taxa: *Compsognathus, Hallopus,* *Segisaurus, Coelurus, Ornitholestes*,… In fact, except for the size, appreciably double for our specimen, the affinities with the Bavarian theropod for which A. WAGNER had created the genus *Compsognathus* are immediately evident. Moreover, the identity of position between the Kelheim and Canjuers specimens is absolutely remarkable, the body showing the same very peculiar attitude, with the neck completely recurved over the back, the skull folded back behind, the hind limbs slightly bent, etc… The rest of the proportions are comparable, and the very great development of the hind limbs relative to the forelimbs, the considerable elongation of the tail, etc…are noted in both cases.

However, a deeper examination lets differences appear that justify a specific distinction.

The very comparable skulls are remarkably avian as a whole. Elongate and refined at their anterior ends, they are characterized by the thinness of their bones. The slenderness of the lower maxilla, a character used by A. WAGNER in the generic patronym, is particularly apparent in *C. corallestris*, where the preservation of this part of the skeleton is perfect. The pointed teeth, disposed in a single row and recurved backward, are also remarkable in the two cases. The orbits are very large, clearly more so than the lateral temporal fossae. In addition, the absence of the superior temporal fossae, certain in *C. longipes* and probable in *C. corallestris*, contributes further to removing *Compsognathus* from classic theropods. The nares can also be compared by their prominence and position. In contrast, the dimensions of the skulls are different, the length being 100 to 115 mm in *C. corallestris* against 75 in *C. longipes*.

The cervical vertebrae are entirely comparable in their number (10 or 11 in *C. longipes*, the same as in *C. corallestris*), their form, and the presence of long spinous processes on the most anterior. In the two cases, the neck is extremely long and flexible and must have offered great mobility during the life of the animal.

The subsequent dorsal vertebrae are a little less numerous in *C. corallestris* (10) than in *C. longipes* (11 or 12). In the two species the vertebral centrum is elongated dorsally by a large spinous process.

In total there are 22 presacral vertebrae for a length of 200 mm in the Bavarian species, versus 20 or 21 totaling 300 mm in the specimen from southeastern France. All these vertebrae are hollow and by this fact generally crushed.

The thoracic region does not appear to offer any notable difference between one species and the other, if it is not the number of ribs, clearly in articulation with the dorsal vertebrae.

In both cases the forelimbs are remarkably short relative to the hind limbs. Unfortunately, in *C. corallestris* the preservation of this part of the skeleton leaves much to be desired, and the comparison with *C. longipes* cannot be pushed forward. However, the very comparable form of the articular heads of the scapular plates are noted, besides the coracoids, the elongation of the humerus relative to the radius-ulna, etc… An important difference would seem to result from the arrangement of the manus: indeed the three digits (3 visible) are terminated by claws in *C. longipes*; in *C. corallestris* only the imprints of 3 probable metacarpals are visible; in contrast the Varois specimen shows a trace (dermal bone or probable thickening of the skin into a swimming paddle) in front of the forearm and manus that does not seem to have existed in *C. longipes*.

The comparison between the pelvic girdle of *C. longipes* and that of *C. corallestris* also reveals notable differences. The general form of the bones and their relationships are entirely similar. However the pubis is much more elongate in *C. corallestris* than in the genotype (1), just as the ischia are (2).

The similarities are also remarkable regarding the hind limbs. In both cases the femur of each limb is markedly shorter than the corresponding tibia-fibula-astragalus complex, and with very comparable proportions (3).

The relative comparison of the bony elements between the two specimens is also very instructive: in *C. corallestris* the length of the femur is 110 mm versus only 70 in *C. longipes*, for a ratio of 1.56. For the tibia-fibula-astragalus complex this ratio is a little smaller. Finally, the three functional metatarsals are narrowly linked, elongate and slender in both cases; it is also noted that metatarsal III is the most elongate, the length of the metatarsals varying from 71 to 82 mm in *C. corallestris* versus 60 in *C. longipes*, for a ratio of 1.18 to 1.31. The hind limb digits were terminated by claws.

Finally, the greatest similarity is raised between the tails, disproportionate relative to the body of the animal. In *C. longipes* the tail was broken relatively near its attachment so that only 15 vertebrae were preserved; in *C. corallestris* the tail, although incomplete, includes twice the number of vertebral elements (32). The comparison between the length corresponding to the first fifteen caudal vertebrae of *C. corallestris* (300 mm) and *C. longipes* (200 mm) provides a ratio of 1.50.

On the whole, as a result, the affinities between the two specimens from Bavaria and Var are indisputable and close. The size variation could be tied simply to age, the two specimens corresponding to adults. However, as we have just noted, some differences are raised that justify a specific distinction. Notably, it is very significant that the ratios between equivalent bony elements are far from being identical. The following results, presented in the form of a table, are reached by adopting as a reference base the ratio 1.50, the most frequently realized ratio between *C. corallestris* and *C. longipes*.

Examination of this table (tab. 3) calls for certain comments.

We have seen that the most frequently realized ratio corresponds to an elongation of one and a half between homologous parts of *C. corallestris* and *C. longipes*. Evidently, in this case the percentages obtained by ratio with the adopted reference base are on the order of 100%: such is the case with the femora, tibiae, presacral vertebrae, and the first fifteen caudals.

However, certain elements are exceptions in one sense or another. At first, the skull seems relatively shorter in proportion in *C. corallestris* than in *C. longipes*. However this result is perhaps slightly false, because the defective state of the posterior part of this skeletal element in the Varois specimen (1). Above all on a clear shortening in proportions of the metatarsals are noted. Inversely, the elements of the pelvis — pubis and ischium — are clearly more elongate in *C. corallestris* than in *C. longipes*.

Thus while being very close together, the two currently known specimens of *Compsognathus* differ by sufficient traits to justify a specific distinction.

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(1) 140 mm taking account of the part recurved posteriorly; 95 mm only rectilinear versus 55 in *C. longipes*, for a ratio of 1.72.

(2) 70 mm (visible) versus 40, for a ratio of at least 1.75 between *C. corallestris* and *C. longipes*.

(3) In *C. corallestris* the femur/tibia-fibula-astragalus ratio is 0.81, hardly higher than in *C. longipes*: 0.77.

(1) In the case where the length of the skull would have been 115 mm in *C. corallestris* the ratio with *C. longipes* (1.54) would have entirely conformed to the normal.

ECOLOGY

Problems of an ecological nature with regard to the study of *C. corallestris*, and more generally the genus *Compsognathus*, are very exciting, taking into account the environment that seems to have been inhabited by this theropod, as well as some morphological and anatomical observations that we have been able to make.

1. **The biotope of *Compsognathus*.**

After the discovery of the first *Compsognathus* in the lithographic limestone of Kelheim, it was not envisioned for a single instant, by the different authors who described it and tried to give it a precise image, that this small dinosaur could have lived in an environment other than the clear continental. Its bipedal, carnivorous, theropod-type appearance not being doubted, it seemed evident that this was one of numerous forms adapted to running according to a traditional design. In this work it was admitted that the cadaver of *C. longipes* had floated for a rather long time after its death before coming into the Kelheim lagoon.

However, it seems that there was an incompatibility, if not between the possible transport of a cadaver over a fairly considerable distance, then at least between the corrosion of the bones noted by certain authors and the magnificent preservation of the whole skeleton of *C. longipes*, whose bony elements had remained in articulation.

It is very evident that no definitive conclusion could be drawn from the examination of a single specimen.

Precisely the discovery of *C. corallestris* in an equivalent environment would come to fill this gap.

At first the absolute similarity of attitude between the two skeletons, *practically all of whose elements remained in articulation*, is absolutely astonishing and cannot be considered as the product of chance. Besides, *in both cases* the presence of an undigested prey item, whose bony elements are perfectly distinct, in the interior of the ribcage is noted. It is not doubted that prolonged flotation of the cadavers of *Compsognathus*(2) would have been accompanied by active putrefaction of the viscera, which was not the case. It is certain, concerning *C. corallestris* at least, that deposition on the bottom must have very closely followed the death of the animal, as the fine ribs of the abdominal wall show only a trace of the displacement that would be obligatorily produced in the event of inflation of the viscera.

It seems as a result that, at least for *C. corallestris*, we can envision a markedly different mode of life from that usually realized in dinosaurs.

The paleogeographic context of southeastern France, which we evoked at the beginning of this work, does not go against this hypothesis. Indeed, we know that at the end of the Jurassic the current emplacement of eastern Provence corresponded to a warm sea in which coralline formations would have formed more or less dense settlements. The possibility of emersion of certain of these reefs was not envisioned by J. J. BLANC and Cl. TEMPIER (1963), but in fact nothing opposes this, so that the Portlandian sea was furrowed with sublevel reefs. Nevertheless the undeniable existence of lagoonal deposits

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(2) Around forty kilometers for *C. corallestris* from the shores presumed from the Maures.

confers a high probability on these supposed "barrier reefs". It is now logical to admit the existence of more or less important islets, elevated at least several meters above the water and comparable to the recent "motus" of Polynesia, that were safe from these reefs, which could have formed an atoll or discontinuous barrier.

One can imagine a vegetative covering containing Benettitales on the surface of these islets; we specifically have just been informed of an inflorescence similar to this group discovered by Mr. and Mrs. GHIRARDI. Besides, the absence of insects, and more generally the extreme rarity of continental organisms, compared to the Bavarian localities is surprising. The fauna (rhynchonelles, ammonites, echinoids, ophiuroids, fishes, sea turtles, teleosaurians, etc…) is clearly marine. In the current state of understanding, the only indisputably terrestrial organism would be the pterodactyl noted by L. GINSBURG and G. MENNESSIER (1970). As a result, these observations constitute a stack of presumptions sufficiently solid to envision an insular mode of life for *Compsognathus* on the coralline atolls.

2. **Mode of displacement.**

The question of the mode of displacement of *Compsognathus* is also very important and must be carefully envisioned.

The great development of the hind limbs relative to the forelimbs, and notably the elongation of the metatarsals and phalanges of these limbs, at first suggest a form adapted for walking and running, the femur/tibia-fibula ratio, on the one hand, and the discreteness of the calcaneum immediately excluding all adaptation for jumping.

Besides, attentive examination of the forelimb reveals, just as we have seen, the trace of a dermal bone or more probably a thickening of the limb in front of the forearm and manus. Such an arrangement can seem surprising in a dinosaur. It is known above all in the group of iguanodontoids, in *Anatosaurus* where a swimming paddle is developed at the level of the manus. In *Compsognathus* a true paddle could be developed that was comparable, to a certain degree, to those of penguins. The presence of claws at the end of the forelimbs observed in *C. longipes* would not have been incompatible with such a transformation of the manus in the German specimen.

On the other hand, the excessive elongation of the tail is not obligatorily correlated with a balancing role during running. This organ was perhaps also susceptible to serve as a counterweight when the animal plunged into the lagoon.

R. T. BIRD (1944) showed besides that the tail of certain sauropods, which were capable of walking and eventually swimming in areas of water, could have floated passively on this occasion. In the case of *Compsognathus* the lightening of certain hollowed bony elements (vertebrae, limbs), considered an avian character, could have been linked to this mode of life and constituted an eminently favorable factor for flotation. It seems therefore that *Compsognathus* was adapted not only to walk and run on the emergent parts, but also to swim and pursue its prey in the calm waters of the lagoon.

3. **Mode of nutrition.**

These remarks, tending to accredit the thesis of an aquatic or semi-aquatic mode of life for *Compsognathus*, are corroborated by the length and suppleness of the neck, whose role must have been essential in the capture of prey.

The slenderness of the skull elements, and notably the weak size of the sharp teeth, arranged on a single row and not crenulated as in carnosaurs, exclude for them any role in mastication. They must have simply assured the prehension of prey, which is confirmed by the examination of the reptilian vestiges visible in the esophageal or stomach position in *C. corallestris*.

4. **Conclusion.**

After all this it seems less probable that *C. corallestris* could have been a clearly continental dinosaur whose cadaver would have come to the interior of the Bessons lagoon after a long transport. It is much more reasonably a type of adaptation until now unsuspected in theropods: that of an insular mode of life on the atolls and eventually in the lagoonal waters.

THE PROBLEM OF VIVIPARITY IN *COMPSOGNATHUS*

This eventuality was admitted by O. MARSH (1889) who, resuming the study of *C. longipes* following A. WAGNER (1961), distinguished the unfortunately incomplete remains of a small skeleton that he attributed to an embryo in the interior of the holotype. This hypothesis was not always supported by authors who, in the absence (it is true) of the entire anterior part of the body of the supposed fetus, instead concluded that it was a prey item (small reptile).

Specifically, attentive examination of the skeleton of *C. corallestris* permits confirming this point of view. Indeed, in the Canjuers specimen, a small bony cluster (40 mm diameter) is distinguished localized at the level of the third, fourth and fifth pairs of ribs. The attribution of these vestiges to some specific bony elements is rather delicate to formulate. Nevertheless some vertebrae, miniscule relative to those of *Compsognathus*, are recognized that remained in articulation, like the phalanges still associated with claws. These bones are not dispersed but in contrast are grouped and tangled up. They delimit a subcircular mass that suggests a flattened ball. A remarkable fact of the remainder, the phalanges and claws localized to the inferior part of this bony cluster, clearly draw the outline of a very regular curved surface.

It is thus logical to suppose that this is a small prey item ingested shortly before the death of *Compsognathus*, whose disposition suggests esophageal or stomach contents.

The abdominal region shows traces of a much more important cluster, reduced to the state of imprints and indistinct (digested prey in the course of evacuation?).

In any event nothing allows confirming a hypothetical viviparity in *C. corallestris*.

CONCLUSIONS

The discovery of a second specimen belonging to the genus *Compsognathus* brings new light to this taxon, until now known from the single Bavarian specimen.

Our preliminary examination leads to the design of a very small theropod dinosaur offering very pronounced avian characters. The affinities with Archaeornithes are undoubtedly clear. However, it is appropriate to remark that, in the present case, the traits common with birds observed in *Compsognathus* do not reflect an adaptation to flight, nor even obligatory family ties with Archaeornithes.

At the end of Jurassic times, dinosaurs went through an intense phase of adaptive radiation. Some very diverse biotopes were conquered: terrestrial and clearly continental but also semi-aquatic, probably amphibious and perhaps even arboreal.

On the evolutionary plane the acquisition of avian characters is a marked tendency in some groups, notably at the level of the skull, vertebrae and hind limbs. These traits, realized in *Compsognathus*, were actually announced since the Triassic in certain of their presumed ancestors (*Procompsognathus*) or in related forms. The acquisition of these characters appeared within diverse lineages, by no means implying becoming avian in every case. It was manifestly a widespread tendency at that time within dinosaurs, whereby the extent of the phenomena of convergence is observed.

In fact, just as we have seen, the genus *Compsognathus* seems to have marked an adaptation to an apparently exceptional biotope among dinosaurs: that of life on coralline atolls.

The uncommon environment that seems to have housed *Compsognathus*, and the very advanced specialization resulting from its behavior, assign to it an elevated position in the adaptational grid. It is certain that the modification of climatic conditions at the end of the Jurassic, and the marked tendency toward drainage during this time, must have brought a fatal blow to this modest group of theropods.

On the other hand, in the current state of understanding, the family Compsognathidae is known only from three individuals coming from Bavaria (*Compsognathus longipes* WAGNER), France (*C. corallestris* nov. sp.) and Colorado (*Hallopus victor* MARSH). This vast and fragmented area of dispersal agrees with what is known of the biogeography of the ends of lineages.

Engaged since the Triassic in an avian direction paralleling that of the ancestral forms of Archaeornithes, this group indeed seems not to have had any descendants because of its intense specialization.

At this proposal, it is evidently tempting to recall the very seductive hypothesis formulated by M. MENZBIER (1887) who envisioned a direct link with penguins starting from reptilian forms and via transformation of the forelimbs into a swimming paddle, considering them therefore as separate from true birds very early on, even right from the start. It is very evident that *Compsognathus* would have constituted the ideal stock reptilian form for this group. However, it is still only a remarkable convergence, G. G. SIMPSON (1946) having demonstrated, by the study of Tertiary penguins, their affiliation with true flying ancestral birds.

TABLE 1

Comparison between the bony elements of the right and left hind limbs

Dimensions in mm Bony elements	LEFT LEG					
	Proximal width	Median width	Distal width	Diameter	Height	Length
Femur						110
Tibia-Fibula-Astragalus Complex						135.5
Astragalus				8.4	10.5	
Tibia-Fibula Complex	19.5	12.4	13.2			125
Tarsals				6.5	1	
Metatarsal I (not observed)						
Metatarsal II	6.8		8.7			70.5
Metatarsal III	6.5		9.4			81
Metatarsal IV	5		4			72
Metatarsal V (not observed)						
Mt II Phalanges (2 phalanges)						33?
Mt II Claw						10.6
Mt III Phalanges: Ph. 1	9.2		6			23.5
Mt III Phalanges: Ph. 2	7.8		6.5			18.7
Mt III Phalanges: (or claw?)	5					8?
Mt IV Phalanges: Ph. 1	5		4 visible			72
Mt IV Phalanges: Ph. 2	?		?			?
Mt IV Claw	7(?)					15

Dimensions in mm Bony elements	RIGHT LEG					
	Proximal width	Median width	Distal width	Diameter	Height	Length
Femur (crushed under the left)	?	?	?			?
Tibia-Fibula-Astragalus Complex						134
Astragalus				?	?	?
Tibia-Fibula Complex	?	12	15.7			?
Tarsals				?	2.4	
Metatarsal I (not observed)						
Metatarsal II	~ 7		7 inc.			71.8
Metatarsal III	~ 4		8			82
Metatarsal IV	7		?			72
Metatarsal V	4.5		ends in point			24.5 visible
Mt II Phalanges (not visible)						
Mt II Claw (not visible)						
Mt III Phalanges: Ph. 1	9.4		6			23
Mt III Phalanges: Ph. 2	5		?			19
Mt III Phalanges: (or claw?)	?		?			?
Mt IV Phalanges: Ph. 1	~ 6.5		4			15
Mt IV Phalanges: Ph. 2	?		4			~ 11.5
Mt IV Phalanges: Ph. 3	5		4			10
Mt IV Phalanges: Ph. 4	5		4			6
Mt IV Claw (imprint)	5					5

TABLE 2

Measurements of the caudal vertebrae.

CAUDAL VERTEBRA NO.	LENGTH	DIAMETER (to center of vertebral centrum)	DORSAL PROCESS		VENTRAL PROCESS	
			Length	Height	Length	Proximal width
1	15	~ 11	9	?	23.5	7
2	18	15	?	?	33.5	6
3 (partial)	~ 18.5	?	?	?	30	?
4	26	18	?	?	~ 25	6.5
5 (imprint)	19	~ 14	?	?	26	5
6 (lacking)						
7 (partial)	?	11	?	9	?	?
8 (lacking)						
9 (lacking)						
10 (lacking)						
11 (partial)	?	?	?	?	~ 18	?
12	19	11			14 vis.	6
13	20	10.4			16	6.4
14	20.7	9.8			14	5
15	20.5	9.5			11	4
16	21	10			~ 10	?
17	20.8	10			6 vis.	~ 4
18 (deformed)	~ 18	9			stub	
19	20.4	9.3			stub 4	
20	22	9			13	
21	22	9			8.5 vis.	
22	21.7	8.5			6	
23	22.2	8			9	
24	22.6	8			(?) 9.5	
25	23	7.5			7.3	
26	22.5	7			not visible	
27	23.2	6.5			7.5 vis.	
28	22.3	6			stub 3	
29	23	6			no spine visible	
30	23.2	6			stub	
31	23	5.5			no spine	
32	(?) 23	5.3				

TABLE 3

Comparison of the relative dimensions and proportions between C. longipes WAGNER *and* C. corallestris *nov. sp.*

PART OF SKELETON	*C. longipes* Length in mm	*C. corallestris* Length in mm	*corallestris/longipes* ratio	% relative to the base reference 1.50
SKULL	75	~ 100 to 115 mm	1.33 to 1.54	88.6% to 102.6%
LENGTH OF PRESACRAL VERTEBRAE	200 (22 vertebrae)	300 (21 vertebrae)	1.50	100%
FEMUR	~ 70	110	1.56	104%
TIBIA	~ 90	135	1.50	100%
METATARSALS	~ 60 (III longest)	71 to 82 (III longest)	1.18 to 1.31	78.6% to 87.3%
PUBIS	55	95	1.72	114.6%
ISCHIUM	40	~ 70	1.75	116.6%
FIRST 15 CAUDALS	~ 200	~ 300	1.60	100%

FIGURE CAPTIONS

FIG. 1. — Geographic situation of the Portlandian locality of the Lesser Canjuers Plain (Var, France).

FIG. 2. — *Compsognathus corallestris* nov. sp. View of the whole specimen.

FIG. 3. — *Compsognathus corallestris* nov. sp. Drawing of the whole skeleton after the photograph.

FIG. 4. — *Compsognathus corallestris* nov. sp. Skull.

FIG. 5. — *Compsognathus corallestris* nov. sp. Drawing of the skull after the photograph. Legend: *al*, lacrimal; *an*, angular; *ar*, articular; *dt*, dentary; *fr*, frontal; *ju*, jugal; *mx*, maxilla; *na*, nasal; *opt*, opisthotic; *orb*, orbit; *pmx*, premaxilla; *po*, postorbital; *qj*, quadratojugal; *san*, surangular; *sq*, squamosal; *x*, bony arch similar to the hyoid apparatus of birds.

FIG. 6. — *Compsognathus corallestris* nov. sp. *N. B.* Note distinctly the semilunar imprint of the coracoid in front of the articular heads of the scapular plates. Also note the position of the intra-thoracic bony mass (prey) relative to the vertebral column, forelimbs and anterior ribs.

FIG. 7. — *Compsognathus corallestris* nov. sp. View of the whole vertebral column and ribcage. Note the perfect preservation of the abdominal ribs (gastralia).

FIG. 8. — *Compsognathus corallestris* nov. sp. View of the forelimbs. Note the imprint of the coracoid in front of the articular heads of the scapular plates. The two humeri are intercrossed; the radius-ulna nearly completely reduced to the state of imprints. In the entirely inferior part, the traces of metacarpals (imprints) are less distinct. Note the imprint of the swimming paddle (dermal bone? or thickening of the hand) in front of the left forearm and manus.

FIG. 9. — *Compsognathus corallestris* nov. sp. Forelimbs. Legend: *c*, carpus; *co*, coracoid; *cu*, ulna; *hu*, humerus; *mc*, metacarpals; *pn*, swimming paddle (?); *ra*, radius; *sc*, scapula.

FIG. 10. — *Compsognathus corallestris* nov. sp. Detailed view of the pelvic girdle and sacral vertebrae. Note the considerable elongation of the pubis, directed anteriorly then recurved posteriorly.

FIG. 11. — *Compsognathus corallestris* nov. sp. Drawing of the pelvic girdle after the photograph. Legend: *il*, ilium; *is*, ischium; *fé*, femur; *pu*, pubis.

FIG. 12. — *Compsognathus corallestris* nov. sp. Pelvic girdle, femur, and tibia-fibula complex.

FIG. 13. — *Compsognathus corallestris* nov. sp. Hind limbs: femora, tibia-fibula complex, tarsals and metatarsals.

FIG. 14. — *Compsognathus corallestris* nov. sp. Hind limbs: distal ends of the tibia-fibula showing astragali and calcanea; very short tarsals; elongated metatarsals; phalanges and claws.

FIG. 15. — *Compsognathus corallestris* nov. sp. Detailed view of the first caudal vertebrae. Note the length and strength of the spinous processes.

FIG. 16. — *Compsognathus corallestris* nov. sp. Tail (vertebrae 11 to 32).

FIG. 17. — *Compsognathus corallestris* nov. sp. Position of the intra-thoracic bony debris. Note very clearly the anterior mass (D = 40 mm), in which the bones are very recognizable, and the less distinct and more voluminous posterior masses (remains of prey in the course of evacuation?).

FIG. 18. — *Compsognathus corallestris* nov. sp. Detailed image of the anterior intra-thoracic bony cluster (prey).

FIG. 19. — *Compsognathus corallestris* nov. sp. Drawing of the anterior intra-thoracic bony mass (prey) after the photograph. Interpretation: *hu. g*., left humerus; *hu. dr*., right humerus; *c3*, third pair of ribs; *c4*, fourth pair of ribs; *c5*, fifth pair of ribs (only one visible); *D4*, fourth dorsal vertebra; *D5*, fifth dorsal vertebra.

FIG. 20. — *Compsognathus corallestris* nov. sp. General reconstructed scheme of the skeleton in a standing position (walking). (The bony elements not observed in our specimen are dotted.)

FIG. 21. — Attempted reconstruction of attitudes of *Compsognathus corallestris* nov. sp.