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FUNCTIONAL MORPHOLOGY AND MODE OF LIFE OF THE LATE TRIASSIC PLACODONT *PSEPHODERMA ALPINUM* MEYER FROM THE CALCARE DI ZORZINO (LOMBARDY, N ITALY)

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Key-words: *Psephoderma alpinum* (Reptilia, Placodontia), Description, Functional morphology, Palaeoecology.

Riassunto. Il ritrovamento di un nuovo esemplare completo del Rettile Placodonte *Psephoderma alpinum* Meyer, 1858 nel Calcare di Zorzino, consente di migliorare la conoscenza dell'osteologia della specie, pur non modificandone gli aspetti generali. Pur sulla base dei due soli esemplari completi conosciuti, è testimoniata la crescita allometrica degli arti. Si ritiene che il carapace, dalla forma idrodinamica e dotato di tre carene longitudinali, svolgesse un ruolo prevalentemente legato alla locomozione piuttosto che difensivo. La lunga coda e la piastra caudale servivano per l'equilibrio. Lo spazio privo di corazza sopra la regione sacrale permetteva a *Psephoderma* di nuotare almeno come le Tartarughe Trionichidi, benchè in assenza di adattamenti particolari del cinto pelvico e del femore. *Psephoderma* si nutriva di molluschi epibentonici che vivevano in banchi sui fondali poco profondi, che circondavano le parti anossiche dei bacini di deposizione del Calcare di Zorzino. Una ricca fauna di Pesci e invertebrati che si ritrova associata ai resti dei Placodonti consente di ricostruire un ambiente marino normale, perlomeno nella zona ossigenata dei bacini. Infatti le acque di superficie erano influenzate dalle maree, che generavano forti correnti nei pressi dello sbocco dei canali che attraversavano la piattaforma, e dal moto ondoso, benchè limitato dalle dimensioni e dalla posizione interna alla piattaforma carbonatica dei bacini stessi. Sui fondali ossigenati e in tutta la lama superficiale d'acqua, la vita era rigogliosa, anche se probabilmente poco diversificata per quanto riguarda gli invertebrati a causa della barriera ecologica rappresentata dalla piattaforma circostante. Le condizioni ambientali sulla piattaforma carbonatica erano decisamente più avverse, generando faune molto povere in specie. A causa della permanenza di stratificazione delle acque, in profondità si instaurava un ambiente anossico che permetteva la conservazione degli organismi (Konservat-Lagerstätten).

Abstract. The recent find of a new complete specimen of *Psephoderma alpinum* Meyer, 1858 in the Norian Calcare di Zorzino (Zorzino Limestone), in northern Italy, adds to our knowledge of the osteology of this species. The new specimen is the largest so far collected, reaching 180 cm in length. Allometric growth of the limbs during ontogeny is demonstrated. A new interpretation of its palaeoecology and mode of life is given on the bases of both functional morphology and palaeoenvironmental observation. The streamlined keeled carapace is interpreted as having a hydrodynamic rather than a defensive function. The long, stiff tail and, probably, the dorsal caudal plate served for balance. The gap in the carapace, above the sacral region, enabled *Psephoderma* to swim at least as well as trionychid turtles, though no particular swimming adaptations of the pelvic girdle and of the femur are observed. Invertebrates and a rich fish fauna were found together with these placodonts, allowing the restoration of the oxic part of the basins environment as a normal marine one. The surface waters were influenced by tides that possibly generated rather strong local currents close to the mouth of tidal channels crossing the platform. This provided for a rich nectonic and benthic life in the more superficial waters: *Psephoderma* fed on bissate molluscs, such as *Modiolus* and *Isognomon*, dwelling on shallow oxic bottoms at the basins edge. Due to water stratification, a long-lasting anoxic environment developed in the deepest part of the basins themselves, allowing fine preservation (Konservat-Lagerstätten) of allochthonous organisms.

Introduction.

The main fossiliferous unit for Norian vertebrates in northern Italy is the Calcare di Zorzino (Zorzino Limestone) which was deposited in basins surrounded by the huge Dolomia Principale carbonate platform (Tintori et al., 1985). Those basins were tens to hundreds of meters deep and several square kilometers in area (Jadoul, 1986; Jadoul et al., 1992, 1994). Their centre was anoxic but the superficial waters and the margins provided an oxic environment (Tintori & Zambelli, 1980; Jadoul, 1986; Tintori, 1992), which was inhabited by nectonic vertebrates and benthic invertebrates (corals, echinoderms, brachiopods, molluscs, crustaceans) that thrived on the sandy-muddy bottom. Durophagous fishes (Tintori, in press a, b) and the placodonts fed on these invertebrates. Further toward the platform there was a crown of patch reefs and organic mounds, sometimes giving rise to small islands covered by arboreal vegetation (Jadoul et al., 1992; Renesto, 1994a). Life on the platform was rather scarce, owing to the very shallow waters, which probably were warmer and more saline than normal marine ones (Tintori, 1992).

This Norian fauna is far from being completely studied; field work, started in 1978 under the guidance of one of us (A.T.), is still in progress (Tintori, 1995). An attempted restoration of this vertebrate assemblage

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lists more than 40 genera of fishes and 10 of reptiles, the latter assuming a great significance in the palaeoenvironmental interpretation of the area surrounding the basins. Though in the middle of a marine environment, terrestrial reptiles (Wild, 1978, 1991; Calzavara et al., 1980; Pinna, 1984, 1987; Renesto, 1993, 1994a, b, c) are more frequently found than aquatic ones, suggesting the close presence of land. So far marine reptiles are only represented by the very rare *Endennasaurus* (Renesto, 1992) and the more common placodont *Psephoderma*, subject of this paper because of the recent preparation of a superb, complete specimen.

Psephoderma alpinum Meyer, 1858 is an armoured placodont known from the Late Triassic deposits of Europe since the last century (Meyer, 1858; Curioni, 1863). However, the genus was poorly known until the discovery of more complete specimens in the Norian and Rhaetian beds of Northern Italy. On the basis of these specimens, Pinna (1976a, 1978, 1980) established that other Norian-Rhaetian placodont species erected on fragments of the skeleton (*Placochelyanus stoppanii*, *Placochelys malanchinii* and *Placochelys stoppanii* along with *Placodus zitteli* and probably *Macroplacus raeticus* and *Placochelys alpis-sordidae*) are junior synonyms of *Psephoderma alpinum*. More recently, Pinna & Nosotti (1989) extensively described the first two nearly complete specimens from the Zorzino Limestone, found in a locality (Endenna) close to the one yielding the newly prepared one. This specimen supplies additional information about the anatomy of *Psephoderma*. It is exposed on the dorsal side and its size (180 cm from the tip of the snout to the end of the tail) renders it the largest complete *Psephoderma* so far known.

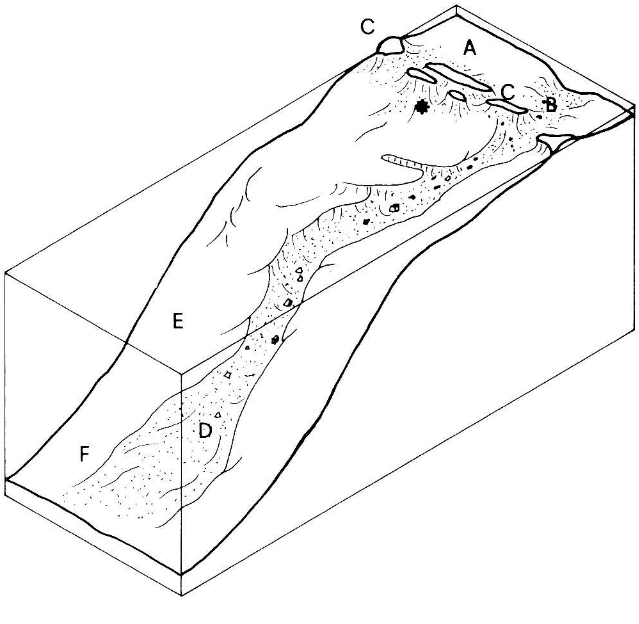

Fig. 1 - Skematic restoration of a basin margin (redrawn after Jadoul, 1986). The asterisk points to the supposed mollusk bank position, where *Psephoderma* and durophagous fishes fed. A) Shallow water carbonate platform; B) tidal channel; C) ephemeral islands with arboreal covering; D) turbidite flows; E) lower slope; F) undisturbed laminated sediments=fossiliferous levels. Vertical scale is exaggerated and the depth of oxic-anoxic waters boundary is not marked.

It allows the description of humerus, radius, and ulna; a new phalangeal formula for the pes and the allometric limb growth is also recorded. The gap of the dorsal armour in the sacral region, is confirmed: it may have played an important role in the swimming ability of *Psephoderma*, as shown in detail in the section on functional morphology.

The age of the Zorzino Limestone fossiliferous levels can now be confidently stated as around the Alaunian-Sevatian boundary (Middle-Late Norian) (Jadoul et al., 1994). Thus, as already assumed for several years (see for instance Tintori, 1980; Jadoul, 1986), the Norian comprises also the Argillite di Riva di Solto (Riva di Solto Shale) and the lower part of the Calcare di Zu (Zu Limestone; Jadoul et al., 1994). Only the middle, which also yields *Psephoderma* (Boni, 1948; Pinna, 1976b), and upper part of the Calcare di Zu, is now considered Rhaetian, together with most of the overlying Dolomia a *Conchodon* (*Conchodon* Dolomite). Thus, Lombardian specimens of *Psephoderma* must be considered ranging from Middle-Late Norian to early Rhaetian, not only Rhaetian as stated by Pinna (1990, fig. 1) and Pinna & Mazin (1993, fig. 1).

Systematic Palaeontology

The osteology of *Psephoderma alpinum* has been thoroughly described by Pinna (1976b, 1980) and Pinna & Nosotti (1989), while the pattern of the armour was discussed by Westphal (1976) and Pinna & Nosotti (1989). Thus, in the present paper, only new elements as well as those that contrast with former descriptions are discussed, and a new diagnosis, emending and translating that of Pinna (1976b) is proposed.

Class **Reptilia**
Subclass **incertae sedis**
Order **Placodontia** Owen, 1859
Family *Cyamodontidae* Nopcsa, 1923
Genus *Psephoderma* Meyer, 1858
Type species: *Psephoderma alpinum* Meyer, 1858

Diagnosis (emended). Large, armoured placodont reptile reaching at least 180 cm in total length. Skull triangular, dorsoventrally flattened; premaxillae edentulous, very narrow and elongate, forming a sharp rostrum; their posterior portions insert between the anterior parts of the frontals; well developed maxillae, forming part of the anterior margin of the nasal openings; frontals narrow, outlining most of the dorsal margin of the orbits; parietal unpaired with a well developed foramen near its anterior margin; squamosals flat, large and with a well developed posterior process tapering distally. Quadratojugal stout, forming most of the lateral margin of the temporal fenestra. Palatine bones larger than pterygoids. Mandible stout, with a large dentary, anteriorly repeating the shape of the premaxillary rostrum, becoming wide posteriorly where two large and flat teeth are present on each ramus of the mandible. Two flat, crushing teeth are present on the maxilla and on the palatine; the posterior palatine tooth is enormously developed.

Vertebral column consisting of 5 cervical, 15 dorsal, 3 sacral and up to 60 caudal vertebrae. Cervical vertebrae short, with low neural spines, short zygapophyses and well developed, laterally projecting parapophyses. Caudal centra bearing low neural spines and short chevrons. Shoulder girdle little developed, apart from the scapula that shows a stout, vertical scapular blade. Pelvic girdle with a rather high and stout ilium and rounded pubis and ischium. Humerus stout, with a thick proximal head, and an enlarged, flattened distal one. Femur of about the same length of the humerus; tibia and fibula longer than radius and ulna, forming a well developed spatium interosseum; tarsus consisting of rounded astragalus, calcaneum and fourth distal tarsal; first metatarsal short and broadened, the remaining four straight. Phalanges of the foot short, the more distal ones rounded and wider than long; phalangeal formula for the pes 2 (1), 3 (2), 3, 3, 2 (1).

Carapace rounded, stout, wide and very flat; sacral region not covered by armour, followed by expanded caudal plate just at the base of the tail, both carapace and caudal plate consisting of small hexagonal osteoderms probably covered in life by horny scutes. Three longitudinal ridges, made up by keeled osteoderms, are present on the carapace and on the caudal plate. No plastron on the ventral surface of the body, but the belly is protected by about 25 stout gastralia.

Psephoderma alpinum Meyer, 1858

Text-fig. 1-7

1858 *Psephoderma alpinum* Meyer, pp. 646-650.
1978 *Psephoderma alpinum* - Pinna, p. 343, pl. 71-74 (*cum syn.*).

Material. Specimen ST82003 (Fig. 2) from Zogno 2, Zorzino Limestone, Middle-Late Norian (Late Triassic), stored in the Museo della Vicaria di S. Lorenzo, Zogno (Bergamo, Italy).

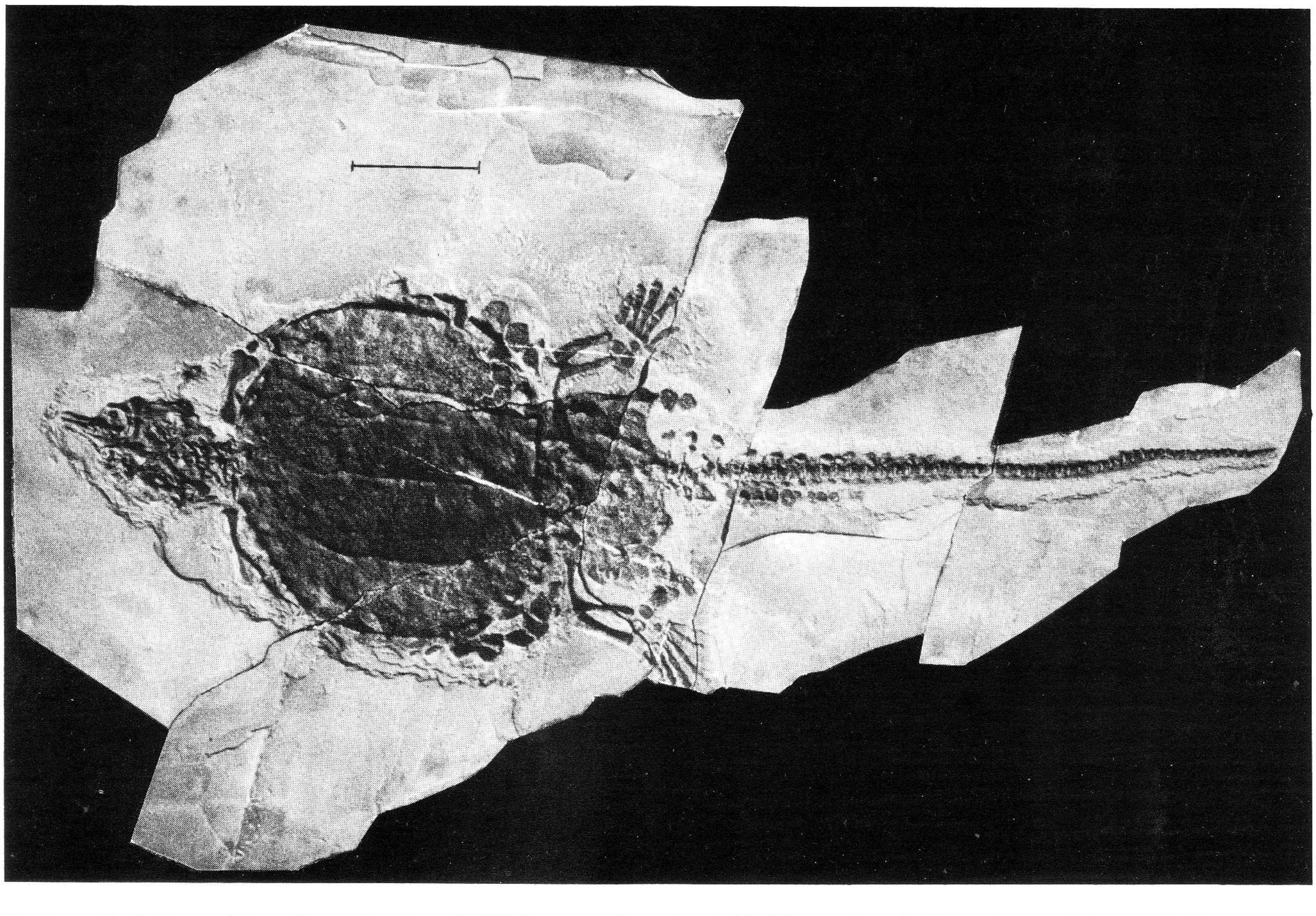

Fig. 2 - *Psephoderma alpinum* Meyer. Specimen ST82003, exposed from dorsal side. The specimen is 180 cm long; scale bar equals 20 cm.

Measurements.

In the following tables (Tab. 1-3) the measurements and ratios taken on specimen ST82003 are compared with those of specimen V527 described by Pinna & Nosotti (1989). Measurements are in mm if not otherwise specified.

Specimen	ST82003		V527
overall length	180 cm		125 cm
skull length from the tip of the snout to the occipital condyle	155 mm		
skull width at orbit level	95		
open area between carapace and caudal plate	40		19
length of presacral vert. column	500		296
length of the carapace	420		250
length of the temporal fenestra	52 L	41R	
width of the temp. fenestra	27 L	29R	
length of the humerus	107 L	110R	41.6
humerus proximal width	27 L	25 R	
humerus distal width	42 L	40 R	15.5
humerus cross section	11 L	10 R	
radius length		68 R	
ulna length	71 L		21
femur length	107 L	107R	40.4
femur proximal width		39 R	15
femur distal width		36 R	19.9
femur cross section	11 L	9 R	
tibia length	90 L	87 R	35.1
fibula length	82 L	80 R	30
metatarsal III length	42 L	40 R	14.4
tibia distal width	17 L	15 R	6.7
tibia proximal width		21 R	10.5
diameter of the calcaneum	20 L	20 R	5.2
diameter of the astragalum		19 R	5.4

Tab. 1

Specimen	ST82003	
humerus/femur	1	
humerus/radius	1.37	
femur/tibia	1.18 L	1.22 R
radius/tibia	0.82	

Tab. 2 - Ratios occurring among some limb sections.

Specimen	ST82003	V527
humerus/ps	21	14
femur/ps	21	13
ulna/ps	14	7
tibia/ps	18	11
metatarsal III/ps	8.4	5

Tab. 3 - Percentual ratios occurring between the length of some limb sections and that one of the presacral vertebral column (ps).

Description.

Cervical vertebrae. In the examined specimen the cervical vertebrae 3-5 are visible, exposed on their dorsal side; neural spines are low, the prezygapophyses are rather short (but this may be due, at least in part, to compression) and stout, while the parapophyses are elongate. Centra can not be seen, owing to the ovelapping of vertebral series.

Humerus. The shape of the humerus (Fig. 3A) does not agree with the hypothetic restoration given by Pinna & Nosotti (1989, p. 30, fig. 10). In its proximal portion the bone is stout but less expanded than at its distal end; the deltopectoral crest is rather well developed and there are traces of the insertion of the muscle latissimus dorsi. The shaft of the bone is quite narrow, especially in its middle part; the posterior border of the shaft is quite embayed, while the anterior one is only gently concave. In its distal portion, the bone becomes enlarged and dorsoventrally flattened; a well developed ectepicondylar groove is present near the anterior margin. The ectepicondyle is small and no distinct areas for the insertion of extensor muscles can be detected. The articular areas for the radius and for the ulna are gently convex and divided by an embayment of the distal margin of the bone.

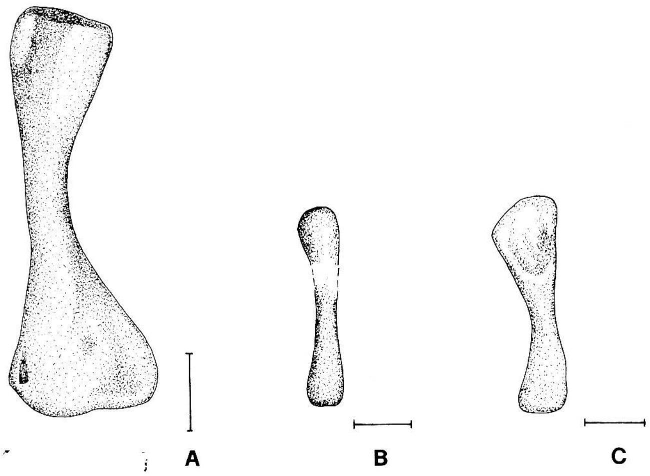

Fig. 3 - *Psephoderma alpinum* Meyer. The left humerus from ventral side (A), the right radius (B) and the left ulna (C) from dorsal view, as preserved in specimen ST82003. Scale bar equals 2 cm.

Radius and ulna (Fig. 3 B, C). These two bones are quite similar to each other and are about half the length of the humerus; their shaft is straight and their ends show no expansions. The proximal articular area is convex while the distal one seems to be rather straight.

Femur. The femur (Fig. 4) is a stout bone, as long as the humerus and well expanded both at its proximal and at its distal end. The ends are expanded in different planes, so that the proximal and the distal articular areas lie in nearly perpendicular planes. The proximal articular area is broad and occupies the entire head of the bone. The shaft is quite narrow in its middle, then the bone becomes dorsoventrally flattened and wide. The articular areas for tibia and fibula are, as in the case of the humerus, gently convex and divided by a small embayment. Apart for the expanded distal articular area, the shape of the femur does not reveal particular adaptations to swimming.

Tibia and fibula (Fig. 4). These two bones are both robust and elongate. The tibia is somewhat longer and stouter than the fibula, its proximal head is expanded and gently bent medially, enclosing a well developed spatium interosseum; the articular area for the femur is probably convex. The fibula shows an expanded proximal head, followed by a narrow shaft; the distal end of the bone is not expanded and its articular area is slightly convex; the proximal articular area of the fibula cannot be detected.

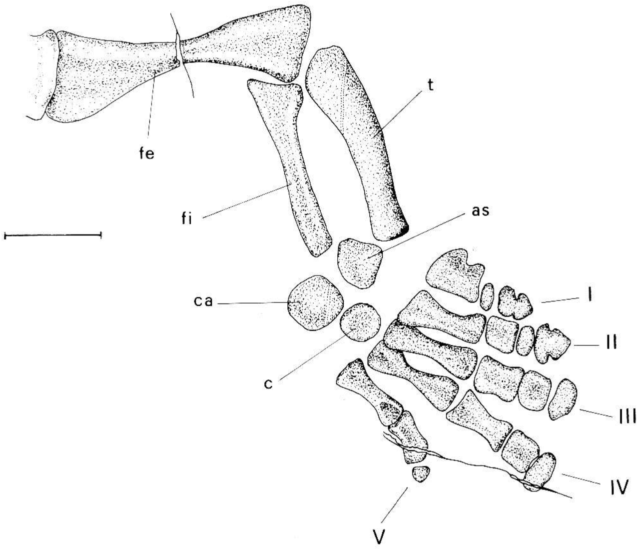

Fig. 4 - *Psephoderma alpinum* Meyer. The right posterior limb of specimen ST82003: fe) femur; t) tibia; fi) fibula; as) astragalus; ca) calcaneum; c) centrale; I-V) digits. Scale bar equals 4 cm.

Pes (Fig. 4). The tarsus shows the same pattern as the one described by Pinna & Nosotti (1989), but the degree of ossification of each element is much higher. Therefore these bones are proportionally wider in large specimens. The metatarsals are stout and expanded at both ends, with convex articular areas; the first metatarsal is very short and wide, and bears a deep embayment on its lateral margin. As already noted by Pinna & Nosotti (1989), the same feature can be observed in some aquatic turtles; these latter show also a modified last metatarsal, while in *Psephoderma* all the other metatarsals are similar to each other. The phalangeal formula for the pes is different from that given by Pinna & Nosotti (1989): 2, 3, 3, 3, 2, instead of 1, 2, 3, 3, 1. This latter is based on specimen V527 in which apparently some terminal phalanges are fused with the preceding ones, giving the appearance of claw-bearing structures (Pinna & Nosotti, 1989). In our specimen, the second phalange of all digits and the last one of digits III, IV and V are instead discoidal in shape and wider than long. Thus the last three digits did not bear claws.

Caudal armour. Posterior to the dorsal caudal plate some osteoderms are present on both the dorsal and ventral edge of the tail. The dorsal osteoderms are keeled and are present up to the 22nd caudal vertebra; the ventral osteoderms are flat and more numerous, reaching the 29th to 30th vertebra. They are circular and flat, and decrease in diameter gradually toward the tip of the tail.

Sizes and proportions. As already pointed out, the new specimen is the longest one known so far (180 cm), far exceeding the supposed maximum length of the species (about 125 cm following Pinna & Nosotti,

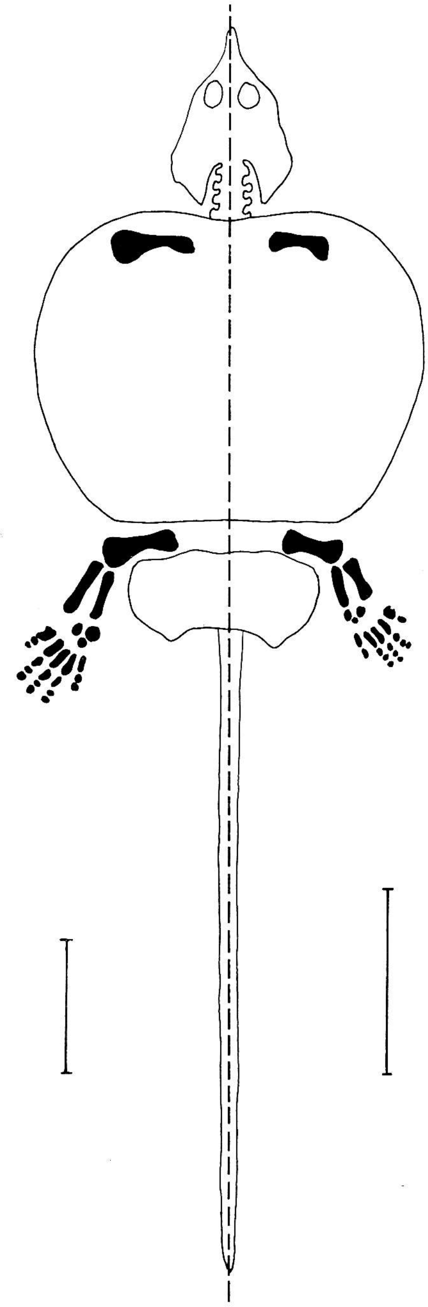

Fig. 5 - Composite sketch of the outline of *Psephoderma* based on specimen ST82003 (left) and V527 (right), with the body size reduced to the same length to show the positive allometry in the growth of the limbs. Scale bars equal 20 cm.

1989). Still longer specimens, perhaps more than 300 cm, could have existed, judging from the sizes of some isolated teeth observed by one of us (A.T.). Using the measurements given by Pinna & Nosotti (1989), a positive allometry of the limbs is evident (see Fig. 5 and Tab. 3). Even if only two specimens are considered, the variation is probably due to the different growth stages rather than to other factors like sexual dimorphism, as for example in pachypleurosaurids (Sander, 1989). In fact, the proportional difference remains the same for both anterior and posterior limbs as well as for different limb sections. In addition, no other morphological differences between the two specimens can be traced.

Functional morphology and mode of life

Morphological features.

Psephoderma alpinum was a very peculiar reptile: the skull was flat, with a narrow rostrum and a wide and stout posterior region. The enormous rounded teeth served to crush the hard shells of the molluscs. The dorsal carapace had an independent caudal plate, which is unique among vertebrates (a similar structure may have been present also in another placodont genus: *Cyamodus* Pinna, 1992), fused to the proximal part of the long, stiff tail.

The postcranial skeleton reveals adaptations to an aquatic life both in the limbs and in the flat carapace, the tail being not specialized as a propulsive organ owing to its shape and stiffness. Pinna & Nosotti (1989) hypothesized that swimming in *Psephoderma* was a paraxial discontinuous rowing (sensu Braun & Reif, 1985) in which the posterior limbs played a major role. According to Pinna & Nosotti (1989), swimming was slow and the carapace had no hydrodynamic function, serving only as a defensive device. Westphal (1976) suggested instead that the flat and keeled carapace of *Psephoderma* played a major active hydrodynamic role.

Available evidence suggests that swimming in *Psephoderma* may have been discontinuous (the distal portion of the anterior limb remains poorly known however, making a reliable decision difficult). According to Carroll (1985), secondarily aquatic reptiles inherited from their terrestrial ancestors an alternate (discontinuous) rather than a symmetrical movement of the limbs. This kind of locomotion is not very efficient for propulsion in water because it causes undulation of the body, which decreases efficiency of paddling. Most reptiles use lateral undulation of the tail (in some cases of the whole body) for aquatic propulsion, and limbs are consequently reduced in order to minimize drag. Propulsion by asymmetrical limb movements has been retained mainly by those modern reptiles in which the rigidity of the vertebral column prevents lateral undulation of the body axis, like freshwater turtles.

Plesiosaurs and marine turtles, however, adopted a more efficient swimming mechanism based on symmetrical movements. This switch to a symmetrical pattern of limb movements (subaqueous flying and/or continuous rowing; Braun & Reif, 1985) required a fundamental change of behavioural and morphological features that, as far as it is known, cannot be detected in *Psephoderma*. The limb girdles, in fact, seem to lack those adaptations that are characteristic of subaqueous flyers (Godfrey, 1984), for instance the presence of a ventrally elongated acromial process in the scapula to form, with other bones of the pectoral girdle, a truss as in marine turtles, or the exceptionally expanded ventral elements present in plesiosaurs. Also, the proportions of the different limb sections, together with their general shape, are those of an oar and not of a flipper. The most expanded area is the distal portion of the pes, and this represents the best adaptation for paddling (Webb & Blake, 1985). The tarsus and the pes are heavily modified for aquatic life. Reduced ossification of tarsal elements is frequently found in aquatic reptiles (Rieppel, 1989), and in *Psephoderma* only three rounded tarsal elements are ossified. The toes are mainly formed by rounded phalanges wider than deep, and feathering and flexion of the toes was limited, rendering the pes a wide, stiff paddle. Because feathering of the toes is the way in which modern rowers minimize drag during the recovery stroke, *Psephoderma* had to act in different way, perhaps keeping the paddle horizontally oriented (this was made possible by the large degree of rotation of the proximal head of the femur). One aspect of the pes is rather puzzling: a tendency to hyperphalangy is present both in subaqueous flyers and in some rowers (Romer, 1956; Hildebrand, 1978; Braun & Reif, 1985; Carroll, 1985) and can be recognized even in some freshwater turtles (Walker, 1973). *Psephoderma* shows a reduced phalangeal formula instead. The functional significance of this adaptation is unclear. However, the morphology of the phalanges and the poor ossification of the tarsus testify that the pes gave very little support to the body during walking on land. Thus, *Psephoderma* had to spend most of its time in water or just resting on a beach.

Swimming efficiency.

Psephoderma swimming may have been more efficient than was hypothesized by Pinna & Nosotti (1989): both the humerus and the femur are stout bones with enlarged and flattened distal heads and bear traces for the insertion of powerful muscles. The ilium is rather tall and shows traces of the insertion of well developed iliotibialis and iliofemoralis muscles. The presence of stout transverse processes on the more proximal caudal vertebrae suggests that also the caudifemoralis muscle must have been strong. Thus, the posterior limb of *Psephoderma* was capable of powerful adduction and retraction. In addition, the sacral gap in the dorsal armour increased freedom of movement, so that the posterior limb of *Psephoderma* could have described an arc, pivoting around the head. Freshwater turtles must limit their hind limb movements to the horizontal plane, because of the massive plastron and carapace (Walker, 1973).

It may be hypothesized that such adaptations in *Psephoderma* allowed it to swim at least as well as the best swimmers among freshwater turtles, the Trionychidae, even in absence of their peculiar specializations like the shape of the femur (Walker, 1973). If this was the case, *Psephoderma* could have reached enough speed to exploit the hydrodynamic properties of its carapace. According also to Westphal (1976) and Pinna & Nosotti (1989), the flat carapace is streamlined and bears three longitudinal keels, whose height may have been increased by horny scutes. Such keels are present in some well swimming turtles like *Carettochelys* and *Dermochelys* and are considered useful for controlling water flow around and past the body of the animal to increase stability (Westphal, 1976; Hildebrand, 1978). In the presence of water currents, the streamlined, very flattened carapace allowed *Psephoderma* to stay at the bottom with little effort also in presence of currents and, if properly oriented, the carapace may have exploited other hydrodynamic effects, acting as an hydrofoil producing lift, and thus saving energy. It is likely that the limited swimming ability assumed by Pinna & Nosotti (1989) for *Psephoderma*, was restricted mostly to the early growth stages, when the limbs were relatively shorter than in the adults. Poorer swimming adaptation suggests a shallower and closer to land habitat for the juveniles.

The expanded caudal plate could hardly have played a mere defensive role because the posterior limbs were too long to be housed under it, as suggested by Pinna & Nosotti (1989). As for the carapace, the caudal plate had to have some hydrodynamic function, possibly together with the long tail. It may have limited lateral undulation of the sacral and caudal regions in order to minimize drag. The tail had no propulsive role: it is long and heavy, but not laterally compressed, as is usual for undulatory swimmers. The morphology of the zygapophyses (Pinna & Nosotti, 1989) reveals that lateral undulation was limited, while greater vertical mobility was possible.

If *Psephoderma* was a rather efficient swimmer (at least in comparison with other discontinuous rowers), the long, heavy tail was undoubtedly useful for balance. It probably rendered the posterior portion of the body fairly massive, possibly shifting the centre of gravity of *Psephoderma* somewhat posterior to the centre of lift (where the propulsive forces apply; Fig. 6). If this hypothesis is correct, *Psephoderma* might have tended to lift during swimming, making this reptile capable to reach rather quickly the surface for breathing. Actually bottom feeding tetrapods have a specific gravity that is somewhat higher than that of water (Hildebrand, 1978), e. g., freshwater turtles have a specific gravity ranging from 1.07 to 1.39 (Walker, 1973). *Psephoderma*, with its very flattened body and heavy skeleton, had probably a high specific gravity, requiring no particular efforts to dive. Reaching the surface to breath was more difficult, so that the combined action of the streamlined carapace, the caudal plate, and long tail was an important aid in these vertical movements, especially if water energy raised the relative speed. The vertical run to the water surface was not great because the molluscs on which *Psephoderma* fed thrived at 10-20 m of depth.

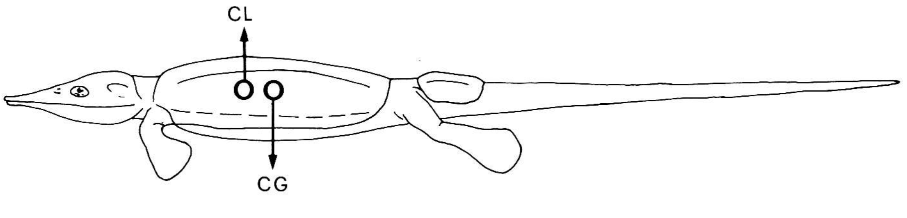

Fig. 6 - Hypothetical positions of the centre of lift (CL) and of the centre of gravity (CG) in *Psephoderma*.

Function of the armour.

Pinna & Nosotti (1989) suggested that *Psephoderma* had the possibility of burrowing in the soft sediments by the use of the stiff tail. They compared the mode of life of *Psephoderma* with that of the Myliobatidae, durophagous rays with flat bodies that live in shallow water and dig themselves in using undulatory movements of the large, modified pectoral fins. This comparison with the Myliobatidae should be avoided for many reasons, first of all the presence of a carapace in *Psephoderma* in contrast to the highly flexible body and fins of rays. If this reptile ever dug itself into the sediments, it could have managed much

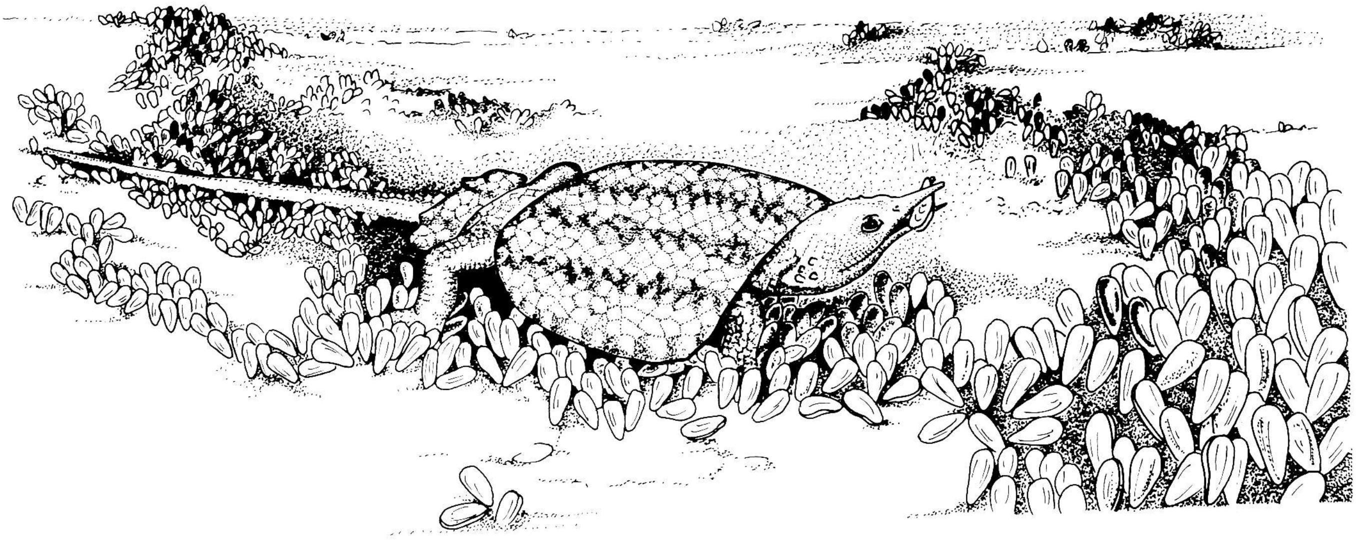

Fig. 7 - Life restoration of *Psephoderma alpinum* in its environment, feeding on a *Modiolus* bank.

better with its anterior and posterior limbs, as turtles do, rather than with a long, tapering, stiff tail. In addition, burrowing for defense seems rather unlikely for a large, armoured, lung breathing animal, in order to escape predators much smaller and gill breathing. Most freshwater turtles dig themselves in to prey in ambush, rather than to avoid predators (Arambourg & Bertin, 1958; Guibé, 1970). Furthermore no potential predators on adult *Psephoderma* are known in the Norian fauna from the Alps. These faunas lack the huge Late Triassic ichthyosaurs, perhaps the only animals capable of grasping and injuring them. The Zorzino Limestone basins were far from the open sea, and the only connection were long tidal channels. We assume that the channels represented ecological barriers to the entry of huge nectonic organisms. The largest fishes in the fauna, such as *Saurichthys*, *Birgeria* and *Holophagus* are mainly piscivorous (Bürgin, 1990; Tintori in Boucot, 1990, tab. 23) and in any case, their sharp conical teeth were not able to crush the placodont carapace, even in young individuals. Durophagous fishes are very common in the fauna (Tintori, in press a, b), but were usually rather small, and all of them had small gape. Pterosaurs are known (Wild, 1978), but their eventual predation on placodonts (hypothesized by Pinna & Nosotti, 1989; Mazin & Pinna, 1993) had to be restricted to hatchlings, as in modern marine turtles that are preyed by sea birds. Another predator to be considered is the large gavial-like phytosaur *Mystriosuchus* (Pinna, 1987). This animal is known from the Zorzino Limestone, but only as an isolated skull, without lower jaw nor postcranial elements. *Mystriosuchus* is large and probably did not prey exclusively on fish, but it is unlikely that its long and slender jaws could have crushed the massive carapace of *Psephoderma*. Furthermore, on taphonomic and palaeoenvironmental ground, we think that *Mystriosuchus* was not living nearby. Thus, at least adult *Psephoderma* had no predators from which it had to escape by burrowing in the sea bottom. For this reason, the hypothesis of Westphal (1976) suggesting the shift from an originally defensive toward an hydrodynamic function for the *Psephoderma* carapace seems reasonable, even if a limited protective role was retained.

Westphal (1976) noted that any attempt at a phylogenetic interpretation of the placodont armour is not reliable, since the hexagonal pattern is known from the Lower Muschelkalk to the Triassic-Jurassic boundary, that is for the entire placodont record. The various arrangements of the osteoderms in placodonts are probably the answer to functional requirements related to different environments and modes of life. According to Westphal (1976) an exclusively defensive role can be supported for *Henodus* Huene, 1936, and *Psephosaurus* Fraas, 1896, while in other genera the need of mobility or hydrodynamic adaptations also influenced the structure of the carapace. In the case of *Psephoderma*, the original defensive function was probably of much smaller importance than the hydrodynamic function.

Mode of life.

When at the bottom, *Psephoderma* wandered in search of food by walking slowly like many freshwater turtles (in bottom walking very little support is required; Walker, 1973). It likely fed on molluscs that thrived on the muddy bottom (Fig. 7), mainly *Isognomon* and *Modiolus*, both epifaunal forms attached by byssus. These molluscs are commonly found in the Zorzino Limestone vertebrate beds, even as allochthonous fossils, while shelly endofauna is absent. This suggests that *Psephoderma* used its "beak" not for searching in the sand or mud like a platypus or some shore birds (Pinna & Nosotti, 1989; Mazin & Pinna, 1993), but rather to twist the molluscs off before crushing the shells. The edentulous rostrum is considered here to be analogous to the anterior teeth of *Placodus*, *Paraplacodus*, and *Cyamodus* (Kuhn, 1969), also used to feed on epifaunal molluscs. Lumps of shell fragments are very common together with the vertebrate remains, but they can be attributed also to durophagous fishes, such as *Paralepidotus ornatus* (Agassiz 1833-1844), which had a similar diet (Tintori, in press a, b) and was much more common than *Psephoderma*. Owing to the different size (*Paralepidotus* not exceeding 50 cm in standard length), these durophagous animals could well live together in the same environment, perhaps preying on specimens of the same mollusc species, but in different growth stages.

The functional analysis of the complete specimens and of the whole faunal assemblage, suggests that the comparison between *Psephoderma* and Myliobatidae should be rejected, and allows the hypothesis that the mode of life of this reptile was much more similar to that of trionychid turtles, even if in a marine environment. Like trionychids, and most other placodonts, *Psephoderma* usually lived rather close to land and probably came up on the muddy-sandy islands only to lay eggs or rest close by the water. In addition, some trionychids are represented by very large animals (their rounded, flattened carapace may reach 95 cm in length, thus being comparable with that of *Psephoderma*), and the family also comprises genera that feed on molluscs, whose shells are crushed by the powerful jaws provided with flat grinding surfaces (Guibé, 1970).

Conclusions.

In conclusion, it can be stressed that the armoured placodont *Psephoderma alpinum* was a large reptile well adapted to an aquatic life, showing specialized feeding and swimming mechanisms. This placodont was probably able to reach quickly the surface for breathing, propelled by the powerful posterior limbs and exploiting the hydrodynamic properties of its streamlined carapace. These adaptations may explain the wide distribution of the genus: three complete specimens, skulls, armour fragments and isolated teeth from several localities in England, Italy, Germany and Austria (Meyer, 1867; Curioni, 1863; Pinna, 1978) render *Psephoderma* the most abundant placodont in the Late Triassic of Europe.

Regarding the specimens from the Zorzino Limestone, we think that, even if *Psephoderma* was not as skilled a swimmer as subaqueous flyers are, some individuals may have occasionally reached the central area of the basins, perhaps sinking into the anoxic, deepest part just before or after death. This can at least in part explain why almost all the *Psephoderma* collected in the Zorzino Limestone have been found complete and fully articulated, while terrestrial reptiles are sometime incomplete as a consequence of a more or less long post-mortem transport into superficial oxic waters (Renesto, 1993; Wild, 1978).

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