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# The sweet spot of a biological hammer: the centre of percussion of glyptodont (Mammalia: Xenarthra) tail clubs

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The importance of the centre of percussion (CP) of some hand-held sporting equipment (such as tennis rackets and baseball bats) for athletic performance is well known. In order to avoid injuries it is important that powerful blows are located close to the CP. Several species of glyptodont (giant armoured mammals) had tail clubs that can be modelled as rigid beams (like baseball bats) and it is generally assumed that these were useful for agonistic behaviour. However, the variation in tail club morphology among known genera suggests that a biomechanical and functional analysis of these structures could be useful. Here, we outline a novel method to determine the CP of the glyptodont tail clubs. We find that the largest species had the CP very close to the possible location of horny spikes. This is consistent with the inference that they were adapted to delivering powerful blows at that point. Our new analysis reinforces the case for agonistic use of tail clubs in several glyptodont species.

**Keywords:** palaeobiology; biomechanics; centre of percussion; glyptodonts

## 1. INTRODUCTION

Few species use an appendage as a biological hammer to generate high peak forces over short time periods (i.e. large impulses) while crushing or fighting; mantis shrimp (Patek & Caldwell 2005), snapping shrimp (Beal 1983), several bird species (Snyder & Snyder 1969; Butler & Kirbyson 1979) and humans (Walker 1975; Wilk *et al.* 1983) are the most studied examples. Similar crushing mechanisms have been suggested for some fossil vertebrates, such as some carnivorous flightless birds of the Phorusrhacidae family (Blanco & Jones 2005) and early hominids (Blumenschine 1995; Selvaggio 1994 and references therein), perhaps useful for breaking long bones in order to access bone marrow. In some sports such as tennis, baseball and golf, the mechanical properties of the corresponding tools have been studied (Brody 1979, 1981, 1986, 1987; Hatze 1994; Cross 1998*a*,*b*, 2004; Carello *et al.* 1999). A peculiar kind of biological hammer, commonly named a tail club, has evolved in at least two groups of terrestrial vertebrates: dinosaurs and mammals. Ankylosaurid dinosaur tails present several features suggesting adaptations for defence and intraspecific fighting (Coombs Jr. 1979). The other group is the one studied here: the armoured glyptodonts. These are xenarthran mammals of the Glyptodontidae family, from the late Eocene to the early Holocene of America. Their geographical distribution was originally restricted to South America but in the Pliocene–Pleistocene they arrived in North America. The largest of these mammals reached body masses close to two tonnes (Alexander *et al.* 1999 and references therein). The most characteristic feature of this group is their bony external armour, including a cephalic shield and caudal bony external rings, that covers most of their bodies. In some species there is also ventral armour and several osteoderms in the facial region and on the limbs (Burmeister 1874; Rinderknecht 2000; Tauber & Di Ronco 2000). All species had stout tails protected by rings of dermal bony scutes, which would nonetheless have allowed a broad range of tail movements. In several species such as *Glyptodon clavipes*, the tail was formed exclusively by free bony rings. These structures probably allowed tail bending, increasing the extent of the swing and enabling the animals to use their muscles along the tail to enhance the power of the blow (Burmeister 1874; Paula Couto 1979; Alexander *et al.* 1999). In glyptodonts such as *G. clavipes*, owing to high flexibility throughout the length of the tail, the effective mass involved in the collision would be small, producing lower impact forces and impulses. In these cases the tail cannot be considered as a rigid beam for our analysis and other approaches would be needed. However, in several other species, such as *Doedicurus clavicaudatus*, several rings of dermal bony scutes of the distal end are completely fused, forming a caudal sheath or tail club made of a single piece of solid bone (Burmeister 1874; Lydekker 1894; Paula Couto 1979). These rigid caudal sheaths are very large, reaching more than 1 m of length in some species (figures 1 and 2). A rigid caudal sheath implies a larger effective mass in tail-club collisions and thus greater forces and perhaps impulses in impacts. The corresponding caudal vertebrae are bound to these caudal sheaths and thus have negligible mobility. Therefore, the caudal tail club of several species was almost like a rigid piece of bone. In species with this anatomical condition, several of the most proximal rings are not fused, allowing the bending of the tail for proper swinging and blow

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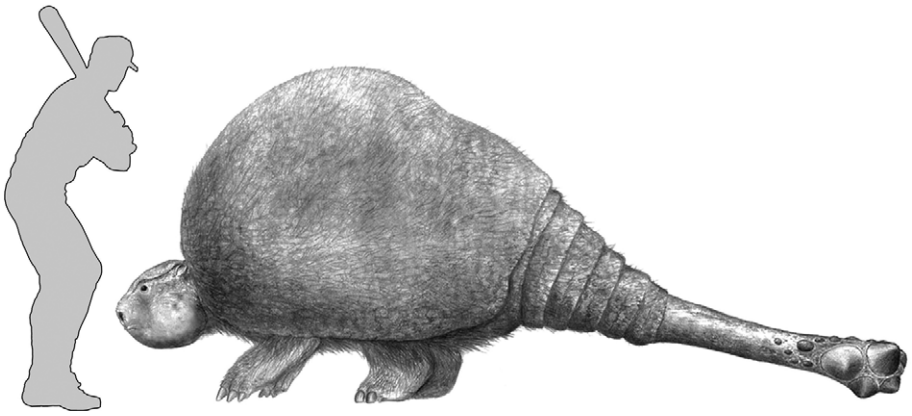


Figure 1. Artistic reconstruction of *Doedicurus clavicaudatus*, with a human for scale. The distal rigid caudal sheath and the mobile free rings are shown. Adapted from Ubilla *et al.* (2008) (fig. 13.3, with permission of Perea, D. ed. 2008).

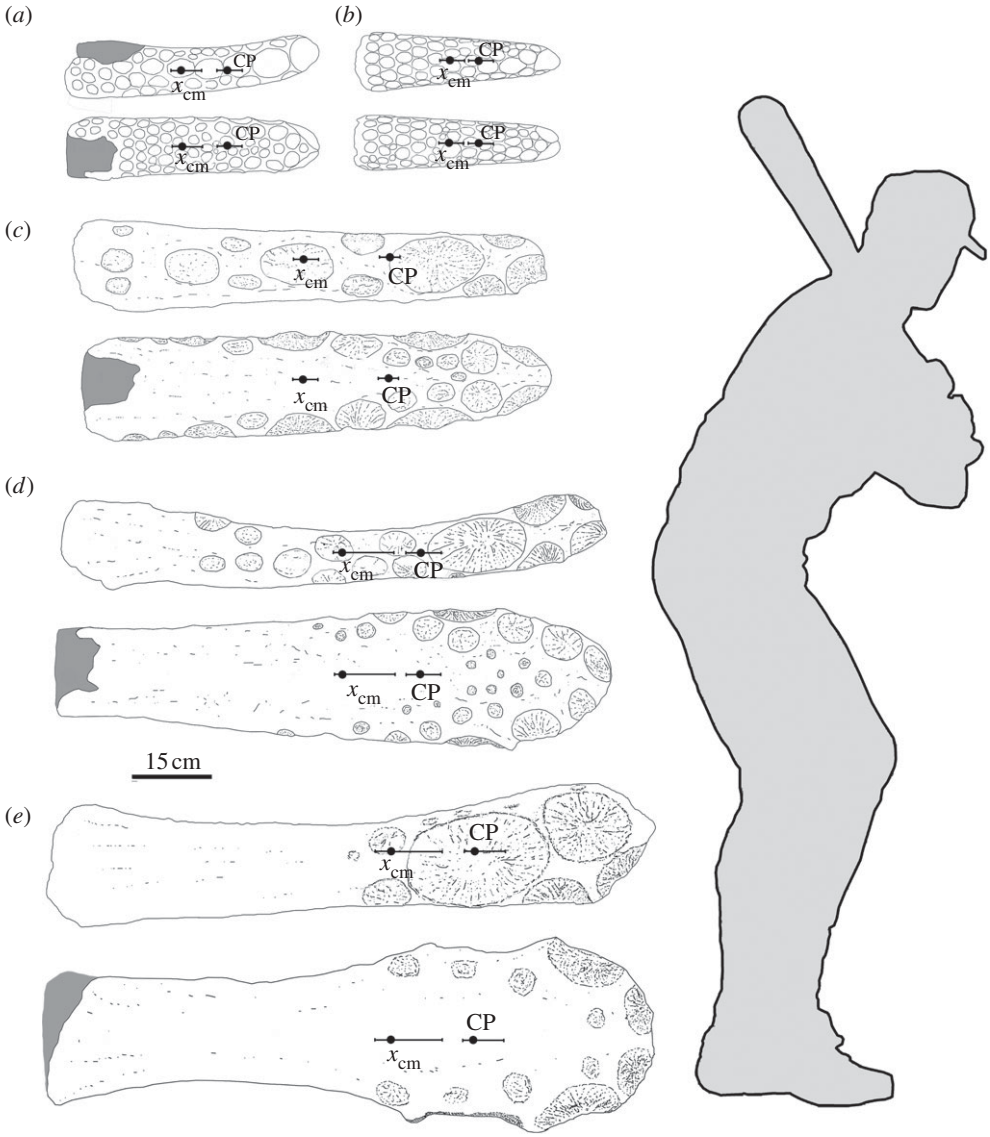



Figure 2. Lateral (above) and dorsal (below) views of caudal bony sheaths: *Neosclerocalyptus* spp. (*a*), *Pseudoplohophorus absolutus* (*b*), *Panochthus tuberculatus* (*c*), *Castellanosia* spp. (*d*), *Doedicurus clavicaudatus* (*e*). The solid circles indicate the positions of the centre of mass ($x_{cm}$) and CP using 1400 kg m$^{-3}$ for internal density. The error range for $x_{cm}$ and CP based on variations of internal density are shown. Scale bar, 15 cm.

delivering (figure 1). Therefore, we restricted our biomechanical study only to the species with a rigid caudal sheath (figure 2), ignoring the glyptodont species presenting tails formed only by free mobile rings. The rigid tail clubs are festooned with depressions of elliptical shape with a very rough inner surface, generally named depressed discs. Some authors have suggested that horny spikes, probably composed of keratin, were situated

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on the depressed discs (Lydekker 1894; Paula Couto 1979). Other authors suggested that the depressed discs supported horny pads (Paula Couto 1979 and references therein). In nearly every palaeoartistic reconstruction of glyptodonts, the depressed discs are depicted with horny spikes (see Paula Couto 1979, fig. 252; Ubilla *et al.* 2008, figs 13.2 and 13.3; and figure 1 in this paper).

Many studies have assumed that tail clubs were weapons used in intraspecific competition for resources or in sexual contests (Fariña 1995, and references therein). Some biomechanical analysis of the tail blows and carapace resistance (Alexander *et al.* 1999) and references to healed carapace fractures (Lydekker 1894; Ferigolo 1992) provide good evidence of the widely assumed glyptodont fighting behaviour. However, the caudal sheaths of different genera show wide morphological variation. The advantages and disadvantages of each morphology in delivering powerful blows deserve closer consideration. Here, we study the caudal sheaths of several genera, applying the physical methods developed to study some tools used by humans (tennis rackets and baseball bats among others) and try to understand if different morphologies imply differences in fighting behaviour. Here, we consider two subfamilies of the 4 or 5 included in the Glyptodontidae family according to previous systematic analyses (Simpson 1945; Hoffstetter 1958; Paula Couto 1979; McKenna & Bell 1997). The subfamilies not considered here are Glyptatelinae, without rigid caudal sheaths and of doubtful inclusion in the family (Downing & White 1995; Vizcaíno *et al.* 2003); Propalaehoplophorinae, generally without caudal sheaths and Glyptodontinae, without caudal sheaths at all.

The following species were selected because they cover a broad morphological diversity of caudal sheaths and the general osteological anatomy is very well known (with only the exception of the poorly known *Castellanosia*, with unique caudal morphology in the family). We studied a specimen of *Pseudoplohophorus absolutus* from the late Miocene of Uruguay, a representative of the subfamily Hoplophorinae (Plohophorini tribe), which has an almost cylindrical caudal sheath with lateral depressed discs that are more developed towards the distal end. These depressed discs are shallow and the surface is not rough, and probably did not support highly developed structures such as horny spikes. Another genus of the same subfamily studied here is *Neosclerocalyptus* spp. (tribe Neosclerocalyptini), which is characterized by medium-sized forms of the Pleistocene from Argentina and Uruguay. This genus has caudal sheaths of similar shape to *Pseudoplohophorus*, but slightly flattened in their dorsoventral axis and with large convex scutes at the distal end. We also studied a representative of the same subfamily (Hoplophorinae) from the Panochthini tribe of the species *Panochthus tuberculatus* from the late Pleistocene of South America. It had a very large caudal sheath, like all the representatives of this tribe, that was laterally expanded with very large laterally depressed discs along its length. These depressed discs have a very rough surface. The subfamily Doedicurinae includes the larger forms of this family. The caudal sheaths of this subfamily are generally very large with a dorsoventral flattening and have very large, deep and rough depressed discs at the distal end. In this group, the distal end is the broadest part of the caudal sheath. We studied two specimens of this subfamily: *Doedicurus clavicaudatus* from the late Pleistocene of South America and an undetermined species of the genus *Castellanosia* from the Pleistocene.

Here, we consider the tail clubs as rigid beams in order to estimate the position of the centre of percussion (CP) in all the specimens. We also discuss some palaeobiological implications of our results.

## 2. MATERIAL AND METHODS

We studied caudal sheaths included in the collections of the Museo Nacional de Historia Natural (MNHN); Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and the palaeontological collection of Facultad de Ciencias de la Universidad de la República (FCDPV). The specimens studied were a complete caudal sheath broken at a mid-sagittal plane of *Panochthus tuberculatus* MNHN 1410, and the complete caudal sheaths of *Doedicurus clavicaudatus* MNHN 2205, *Neosclerocalyptus* sp. MACN 18031, *Castellanosia* sp. MNHN 2206 and *Pseudoplohophorus absolutus* FCDPV-595 (holotype). Other fragmentary materials in those collections were also used to estimate the internal diameters of the tail clubs.

The CP of a hand-held implement (such as a baseball bat or a tennis racket) is the point where the application of an impact force (for example by a collision with another object) produces very small forces in the wrist (or other proximal joint), minimizing the risk of damage (Brody 1979, 1981, 1986, 1987; Hatze 1994; Cross 1998*a*,*b*, 2004; Carello *et al.* 1999).

Bone is a very rigid living tissue. The maximum strain that can be resisted by bones without breaking is of the same order of magnitude as the maximum strain resisted by dry wood (Wainwright *et al.* 1976; Alexander 1983). In both materials the maximum strain is roughly $10^{-2}$, a very low value indeed. Therefore, modelling a single piece of bone as a rigid beam is appropriate. It is roughly as good as modelling a wooden beam (for example a baseball bat) as a rigid beam. Tennis rackets, modelled by other authors as rigid beams in order to estimate the position of the CP, suffer even larger strains during normal use (see Brody 1987). Moreover, it is generally accepted in the biomechanical literature that the human body modelled as a system of interconnected rigid bodies is an appropriate approach for human dynamic analysis (see Zinkovsky *et al.* 1996). Therefore, considering a tail club composed of a single piece of bone as a rigid beam seems to be an appropriate biomechanical approach. During a blow delivered by a glyptodont, the forces acting in the tail club are a very large impact force $F$ (acting only during the impact) and the forces produced by muscles. But the effect of muscle forces has already been discussed for hand-held implements (Cross 2004), showing that they can be neglected if the relative speed between the racket (or other tool) and the ball (or other target) is high. The main reason is that if the relative speed increases, the time of impact decreases producing an increase in the mean impact force. Over short times and with large impact forces, the effect of muscles is almost negligible. A rough estimate of the speed of the club's centre of mass speed was obtained for the genus *Doedicurus* (Alexander *et al.* 1999) from

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prior studies of the tail blow energy. The speed at the tip of the tail was estimated as 15 m $s^{-1}$. This value is close to the usual speed of hand-held implements (Brody 1979, 1981, 1986, 1987; Hatze 1994; Cross 1998*a*,*b*, 2004). Therefore, the tail club is properly modelled as a free rigid beam during an impact.

An impact force $F$ applied at right angles to a free beam at a distance $b$ from the centre of mass (that will cause the centre of mass to translate at a speed $V_{cm}$) is given by,

$$F = M_b\left(\frac{dV_{cm}}{dt}\right), \tag{2.1}$$

where $M_b$ is the mass of the beam. The torque of the force $F$ is given by,

$$Fb = I_0\left(\frac{d\omega}{dt}\right), \tag{2.2}$$

where $I_0$ is the moment of inertia of the beam about the centre of mass and $\omega$ the angular velocity of the beam. If we consider a point $p$ located at a distance $A$ from the centre of mass ($p$ and the impact point are on opposite sides of the centre of mass), the speed $v$ of such a point is given by $v = V_{cm} - A\ \omega$, so

$$\frac{dv}{dt} = \left(\frac{1}{M_b} - \frac{Ab}{I_0}\right)F. \tag{2.3}$$

If the beam is initially at rest (that approximation can also be applied to moving beams by a proper change of the inertial reference frame), then $v$ is given by

$$v = \left(\frac{1}{M_b} - \frac{Ab}{I_0}\right)\int F\,dt. \tag{2.4}$$

The axis of rotation coincides with a point where $v = 0$ (a point where there are no changes of the speed then a point where the force produced during the impact is zero) and hence the corresponding CP is located at a distance $b$ given by

$$b = \frac{I_0}{AM_b}. \tag{2.5}$$

From this simple model, the distance between the centre of mass of the tail club and the CP is given by:

$$b = \frac{I_{cm}}{Mx_{cm}}, \tag{2.6}$$

where $M$ is the total mass of the club, $I_{cm}$ the moment of inertia of the club about the centre of mass for lateral swing and $x_{cm}$ the distance between the proximal end and the centre of mass (Cross 2004).

Here, we assume that it would be important to minimize the forces at the joint of the rigid part of the tail and the flexible part formed by several free mobile rings (figure 1). This joint is the analogue of the wrist joint of a human wielding a hand-held implement. Therefore, in our model the flexible part of the tail composed of free mobile rings is analogous to the tennis (or baseball) player's arm and the completely rigid tail club is analogous to the tennis racket (or baseball bat). For this reason, we assume that delivering blows close to the CP is important to reduce the risk of damage at the joint between the flexible and rigid parts of the tail. We consider only the rigid distal end of the tail as a free rigid beam and we follow the methods detailed in Cross (2004) as explained above.

For each specimen we made a geometrical model consisting of several hollow cylindrical slices with elliptical bases for modelling the mass distribution of the tail club. A similar method to modelling the geometry of a biological structure has already been used to estimate the body masses and positions of centres of mass of ground sloths (Bargo *et al.* 2000). The density of the bony caudal sheath of the tail was considered as 2000 kg $m^{-3}$ (Currey 1984) and the internal density was assumed as 1400 kg $m^{-3}$ (as was estimated for the forearm of a large mammal in Fariña & Blanco 1996). The position of the centre of mass and the moment of inertia were estimated from the usual expressions in elementary physics (see Alexander 1983). If the mass of each geometrical slice is $m_i$ and the distance of that slice to the proximal end is $x_i$, then the centre of mass distance to the proximal end $x_{cm}$ is given by,

$$x_{cm} = \frac{(\sum m_i x_i)}{\sum m_i}, \tag{2.7}$$

and the total mass of the club is

$$M = \sum m_i. \tag{2.8}$$

Then, the $I_{cm}$ is given by

$$I_{cm} = \sum m_i(x_i - x_{cm})^2, \tag{2.9}$$

providing all the required input for the application of equation (2.6).

To construct the geometrical models, we measured the external anteroposterior and transversal diameters directly in several points of each club (table 1 and figure 2). The mass contribution of unpreserved structures such as horny spikes or horny pads were neglected. The soft tissues considered were those lying inside the caudal sheath. Modelling the shape of the external unpreserved structures would be highly speculative because at present there is no direct evidence of them. In addition to this, the density of these horny structures was probably much lower than the bone density, for example the density of a cow horn is around 1283 kg $m^{-3}$ (Mason 1963 and references therein), giving a little uncertainty to our estimates. However, the possible influence of the horny structure's mass will be qualitatively considered in our discussion.

The internal diameters were estimated in different ways in each case. For *Panochthus tuberculatus* MNHN 1410, the club was broken at the mid-sagittal plane and the internal diameters were directly measured. In *Doedicurus clavicaudatus* MNHN 2205, the ratio between external and internal diameters was estimated from two broken clubs (one at 60 cm MNHN 2213, and the other at 75 cm MNHN w/n of the proximal end) of the same genus that allows direct measures and was linearly extrapolated to the intermediate sections. In *Neosclerocalyptus* sp. (MACN 18031), the internal diameters were estimated from a similar-sized broken club (MNHN 2214) at 25 cm from the proximal end and the other measurements were extrapolated by a

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Table 1. Caudal sheath measurements.

| species | *Pseudoplophorus absolutus* | *Neosclerocalytpus* sp. | *Panochthus tuberculatus* | *Castellanosia* sp. | *Doedicurus clavicaudatus* |
|---|---|---|---|---|---|
| total length/interval of diameters (cm) | 34/3 | 47.8/5 | 89/5 | 102/5 | 105/5 |
| external anteroposterior diameters (mm) | 95, 94, 85, 82, 75, 72, 68, 65, 59, 53, 45 | 103, 102, 93, 87, 81, 78, 76, 77, 69, 48 | 168, 167, 152, 144, 139, 134, 130, 128, 125, 123, 120, 119, 113, 108, 111, 106, 93 | 160, 156, 152, 141, 134, 127, 109, 107, 97, 93, 93, 95, 96, 104, 119, 121, 121, 123, 104 | 226, 213, 195, 189, 174, 170, 170, 150, 153, 147, 149, 146, 153, 156, 168, 177, 195, 210, 217, 216, 159 |
| external transverse diameters (mm) | 79, 77, 75, 72, 70, 68, 67, 64, 61, 59, 50 | 116, 115, 111, 109, 109, 106, 105, 92, 83 | 201, 198, 200, 201, 196, 197, 196, 192, 198, 190, 190, 191, 187, 172, 166, 142, 94 | 155, 148, 149, 158, 171, 179, 183, 190, 197, 206, 214, 219, 223, 223, 231, 210, 184, 137, 71 | 214, 208, 199, 188, 182, 181, 173, 187, 211, 228, 238, 287, 299, 284, 299, 311, 350, 339, 302, 273, 197 |
| internal anteroposterior diameters (mm) | 85, 75, 69, 63, 54, 48, 41, 33, 27, 21, 12 | 83, 76, 68, 62, 53, 48, 40, 36, 26 | 129, 116, 105, 89, 85, 75, 73, 68, 68, 62, 57, 52, 49, 46, 39, 30, 22 | 122, 120, 113, 105, 99, 90, 80, 70, 63, 53, 53, 50, 48, 53, 50, 47, 43, 43, 36 | 189, 163, 150, 140, 130, 125, 120, 111, 100, 95, 85, 83, 80, 78, 85, 75, 75, 75, 75, 75, 75 |
| Internal transverse diameters (mm) | 65, 60, 54, 48, 45, 39, 33, 30, 24, 18, 15 | 97, 88, 76, 64, 50, 44, 32, 24, 16 | 123, 108, 99, 99, 92, 86, 86, 80, 80, 71, 65, 58, 49, 46, 39, 30, 22 | 133, 129, 134, 139, 149, 156, 143, 125, 116, 113, 94, 88, 91, 83, 79, 59, 50, 40, 21 | 185, 178, 173, 170, 160, 158, 150, 145, 140, 135, 130, 125, 120, 115, 111, 105, 98, 93, 88, 83, 76 |

linear approximation. In *Castellanosia* sp. (MNHN 2206), owing to the difficulty of removing the internal sediments and the lack of broken clubs of the same genus, we estimated the ratio between external and internal diameters as the same as in the other representatives of the same tribe *Doedicurus clavicaudatus* (MNHN 2205). In *Pseudohoplophorus absolutus* (FCDPV-595; holotype) internal measurements were extrapolated from a similar-sized club of the same genus (*Pseudohoplophorus francisi* FCDPV 23-VIII-63-1) broken at 21 cm to the proximal end. All data are shown in table 1.

A sensitivity analysis was performed considering the variations of the results with variations of the density in the internal cavity. We studied the extreme cases of inner density equal to 2000 kg m$^{-2}$ and inner density equal to zero. We also considered the effect of adding or subtracting a slice at the proximal end of *Doedicurus* and *Castellanosia*, simulating the effect of possible error in reconstructing the proximal end owing to lacking portions of the tail club (figure 2). Here, we considered the mass of the rigid sheath and ignored the mass of the mobile rings attached to the sheath. Actually the mobile rings are articulated to the rigid sheath and thus may have some dynamic influence during the impact. For this reason the CP position could be affected to some degree by the mass of the rings. In previous studies of CP in hand-held implements, it was shown that the CP position of a free simple wood beam is altered when the mass of the hand is included. In that case the CP is shifted significantly towards the hand (Cross 2004). In our case to estimate the sensitivity of our model, we added an arbitrary extra 10 per cent mass at the ring end owing to motion of the most distal rings attached to the rigid sheath to check for significant shifts in the CP.

From our hollow cylindrical approximation, we calculated the second moment of area (e.g. Alexander 1983) at the the most proximal part of the sheath and at the CP. The second moment of area was calculated for both lateral bending ($I_x$) and dorsoventral bending ($I_y$) from the following equations:

$$I_x = \frac{\pi A^3 B}{64} - \frac{\pi a^3 b}{64}, \tag{2.10}$$

$$I_y = \frac{\pi A B^3}{64} - \frac{\pi a b^3}{64}, \tag{2.11}$$

where $A$ and $B$ are the external transverse and external anteroposterior diameters and $a$ and $b$ are, respectively, the internal transverse and internal anteroposterior diameters at the section considered in each case.

All the measurements were taken with dial calipers and a tape measure.

## 3. RESULTS

The results are shown in table 2 and depicted in figure 2. The sensitivity analysis shows that the difference in the centre of mass position among the two extreme assumptions for internal density is 10 cm in the case of *Castellanosia*, in a caudal sheath with a total length of 102 cm. For *Doedicurus*, the variation of the centre of mass is 11 cm in a total length of 105 cm. These values

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Table 2. Results. (Between parentheses the results obtained in the sensitivity analysis using a solid model of the tail club with an internal density assumed as 2000 kg $m^{-3}$) [Between brackets the results obtained in the sensitivity analysis using a completely hollow model with internal density zero].

| species | estimated total mass of the club (kg) | position of centre of mass from proximal end (cm) | moment of inertia (kg $m^2$) | position of centre of percusion from proximal end (cm) |
|---|---|---|---|---|
| *Pseudoplohophorus absolutus* | 2.24 (2.59) [1.42] | 16 (15) [18] | 0.019 (0.021) [0.012] | 21 (20) [23] |
| *Neosclerocalyptus* spp. | 5.64 (6.38) [3.93] | 23 (22) [26] | 0.091 (0.102) [0.062] | 30 (29) [32] |
| *Panochthus tuberculatus* | 29.55 (31.84) [24.18] | 40 (39) [42] | 1.622 (1.744) [1.330] | 54 (53) [55] |
| *Castellanosia* spp. | 27.95 (31.55) [19.54] | 50 (48) [58] | 1.884 (2.200) [1.216] | 64 (63) [69] |
| *Doedicurus clavicaudatus* | 65.12 (72.31) [48.34] | 62 (60) [71] | 6.005 (6.941) [3.730] | 77 (76) [82] |

constitute around 10 per cent of variation in both cases. Furthermore, in the other specimens the differences are less than 4 cm in absolute values and the relative variation is close to 10 per cent. The smallest variation occurs in *Panochthus*, only 3 per cent. The sensitivity analysis, however, shows that the variation in the position of the CP is smaller than the variation of the centre of mass in all the cases. It is only 6 per cent in *Castellanosia* and *Doedicurus* and around 2 per cent in *Panochthus*.

Adding an artificial extra cylindrical slice (5 cm of length) at the proximal end of *Doedicurus* and *Castellanosia* caudal sheaths had the effect of shifting the centre of mass by around 3 per cent of the total length, but the CP was shifted around 1 per cent towards the proximal end. If we add two cylindrical slices of 5 cm at the proximal end, the shift of the CP position over the caudal sheath is close to 2 per cent towards the proximal end. Similar variations, but in the opposite direction, are found if we ignore the first proximal cylindrical slices of the caudal sheaths. The results of the sensitivity analysis indicate that the error derived from possibly absent parts of the caudal sheath at the proximal end are smaller than the errors due to variations in density distribution estimations. The CP position is a much less variable estimation than the centre of mass position.

The error due to ignoring the mass of the mobile rings (estimated by adding 10% of the sheath mass to the most proximal slice) in the CP position is smaller than 1 cm in *Neosclerocalyptus* and around 1 cm in all the other cases. Curiously, the centre of mass distance $x_{cm}$ to the proximal end decreases a considerable amount (around 5% in *Doedicurus*), but this effect is balanced by an increase of $b$ (see equation (2.6)), the distance between the CP and the centre of mass (around 4% in *Doedicurus*). The variation in the centre of mass is very intuitive, but the fact that the CP position does not vary too much is less intuitive due to the non-simple dependence of the equation (2.6) on mass increases on each slice (the total mass $M$ increases but so does the moment of inertia $I_{cm}$). This implies an error influence lower than 1 per cent in the large forms *Castellanosia*, *Doedicurus* and *Panochthus*. The largest relative error is only 3 per cent in *Pseudoplohophorus*.

The most relevant error seems to be the one derived from the uncertainties in the value of the internal density (depicted in figure 2). But even these errors are smaller than 6 per cent in the CP position.

The second moment of area values are shown in table 3. The lateral and dorsoventral second moments of area are almost equal in *Pseudoplohophorus*. In the three larger species the lateral second moment of area at CP is several times larger than the dorsoventral second moment of area by a factor of almost 2–5. *Panochthus* have similar ratios between the lateral and dorsoventral second moments at the base and the CP. The other large species have a second moments ratio closer to unity at the base.

## 4. DISCUSSION

As was described previously elsewhere (Brody 1979, 1981, 1986, 1987; Hatze 1994; Cross 1998*a*,*b*, 2004), the CP is the point where the baseball bat, tennis racket or any rigid body taken by hand will produce little change of the wrist speed after the impact. That means lower peak forces in the wrist while delivering a powerful blow. An impact in the CP reduces the probability of damage at the wrist joint in humans (Brody 1979, 1981, 1986, 1987; Hatze 1994; Cross 1998*a*,*b*, 2004) and the CP position can be perceived by humans to some degree (Carello *et al.* 1999) showing the relevance of CP in hand-held implements. In some species of glyptodont the distal caudal sheath is a rigid body that could be moved laterally due to the flexibility of the proximal part of the caudal backbone axis and the tail rings adjacent to it. It is very reasonable to think that low peak forces at the junction between the rigid sheath and the flexible rings are very desirable in order to avoid structural damage on this mobile joint. In addition to this, glyptodonts show several depressed discs in the caudal sheath where horny spikes were suggested to be located (Lydekker 1894; Paula Couto 1979 and references therein) that probably concentrated the force of the impact in a small area to produce more damage due to higher peak stresses on target tissues. In all species with possible exception of *Pseudoplohophorus*, the biggest discs where probable spines were to be found are found mostly on the lateral margins of the tail clubs near the CP (figure 2). This evidence supports the hypothesis of agonistic behaviour by delivering lateral blows with the tail clubs. Our results

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Table 3. Second moment of area.

| species | lateral bending—proximal cross section ($m^4$) | lateral bending—CP cross section ($m^4$) | dorsoventral bending—proximal cross section ($m^4$) | dorsoventral bending—CP cross section ($m^4$) |
|---|---|---|---|---|
| *Pseudoplohophorus absolutus* | $1.2 \times 10^{-6}$ | $0.6 \times 10^{-6}$ | $1.4 \times 10^{-6}$ | $0.6 \times 10^{-6}$ |
| *Neosclerocalyptus* sp. | $4.2 \times 10^{-6}$ | $4.3 \times 10^{-6}$ | $3.5 \times 10^{-6}$ | $2.2 \times 10^{-6}$ |
| *Panochthus tuberculatus* | $5.5 \times 10^{-5}$ | $4.0 \times 10^{-5}$ | $3.4 \times 10^{-5}$ | $1.6 \times 10^{-5}$ |
| *Castellanosia* sp. | $1.5 \times 10^{-5}$ | $5.0 \times 10^{-5}$ | $1.9 \times 10^{-5}$ | $0.9 \times 10^{-5}$ |
| *Doedicurus clavicaudatus* | $5.0 \times 10^{-5}$ | $21.5 \times 10^{-5}$ | $6.0 \times 10^{-5}$ | $6.6 \times 10^{-5}$ |

show that in the species with distal distribution of depressed discs as in *Panochthus*, *Castellanosia* and mainly in the highly specialized club of *Doedicurus*, the CP seems to be very close to the centre of the largest depressed disc (figure 2). In *Panochthus* and *Castellanosia*, the CP was located slightly more proximal to the centre of the largest depressed disc. However, in the living animals the mass of the spikes or other unpreserved structures in the depressed disc (sited more distally than the estimated CP) would move the CP an unknown distance towards the distal end. Therefore, the situation in the living animals was probably similar to that in *Doedicurus*. The proximity between the estimated CP and the possible position of the largest spikes suggests that in the three largest genera the agonistic use of the tail is supported. It is not strictly likely to produce the impact exactly at the CP during a dynamic movement (even a top tennis player like Roger Federer fails with some balls), so the main goal is to hit as close as possible to the CP. The presence of several small spikes around the largest one seems to be consistent with our conclusion. The model presented here and the analysis already made by Alexander and co-workers (1999) seem to support a function of caudal sheaths related to agonistic use of the tail clubs in *Doedicurus* and other glyptodonts. However, more mechanical considerations are needed to reinforce our argument.

The structural strength of the sheath deserves careful consideration. The second moment of area of the sheath's cross sections can be easily calculated from our data (see §2; table 3). Interestingly, the ratio of second moments of area (lateral/dorsoventral) in *Pseudoplohophorus* is close to 1 suggesting that forces may act on the tail club from any direction and suggesting a use of the tail club in a relatively wide range of movements. In *Doedicurus* and *Castellanosia* it is very clear (table 3 and figure 2) that the second moment of area related to the strength against lateral forces (as impact forces would be) is larger than the strength for supporting vertical forces (as tail weight) at CP by a factor roughly between 2 and 6. This is consistent with lateral movements of the tail club and the position of the largest discs. *Panochthus* appears to have had highly lateralized movements owing to similar ratios at the base and the CP, whereas *Doedicurus* and *Castellanosia* have ratios closer to unity at the base suggesting that forces may be more unpredictable in this region compared with the mainly lateral movements of the tail club. This could be due to the important requirements for supporting the caudal sheath's weight while walking or standing.

Most differences seem to be mediated by size. Smaller clubs are lighter and their owners were probably more manoeuvrable, whereas larger species with heavier clubs would have been less manoeuvrable and their clubs too heavy to move in many directions. If the tail clubs were used primarily for intraspecific combat, the behaviour of the larger species would have appeared as much more ritualized than that of the smaller more mobile flexible-tailed species. The position of the CP in the largest forms as *Doedicurus* can be interpreted as an adaptation to deliver very energetic blows without receiving damage on the mobile caudal vertebrae. On the other hand, this morphological adaptation implies a behavioural correlation: the animal needed to exert the tail blows with enough accuracy to obtain an impact near the CP. This is not very efficient for fighting against fast-moving rivals as some predatory species as sabre-tooth cats. These weapons seem better suited to more static situations. This could have been produced ritualized patterns of movement as in the intraspecific fighting of several extant species (Kitchener 2000 and references therein). Therefore, it seems that *Doedicurus*, and to a lesser degree *Castellanosia* and *Panochthus*, probably used the caudal sheath mainly for powerful blows in ritualized intraspecific fighting or in some other static situations. Other species studied did not have such extreme specialization and probably used the caudal sheath in a more varied way with lower power and much less precision required for the impact point.

The present study reinforces the idea of the presence of spikes or other horny structures with similar function in the deeper depressed discs of caudal sheaths for several species of glyptodonts. The methods used here would be useful for studying ankylosaurid dinosaur tails and other biological hammers.

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