The deeper the rounder: body shape variation in lice parasitizing diving hosts

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Supplementary Material

A. Figure S.1

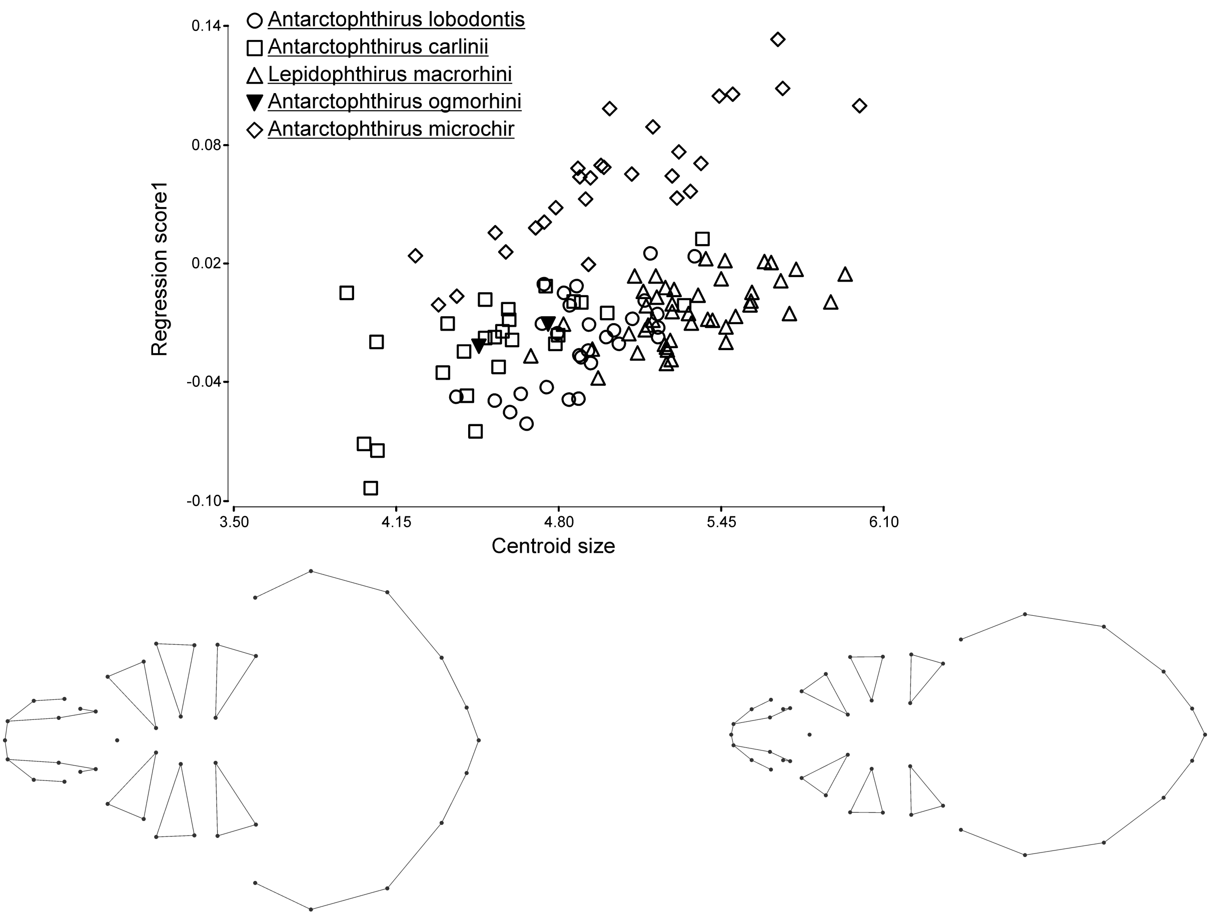

Figure S.1: Pooled within-species multivariate regression of ventral shape (regression score1) onto size (centroid size). Shapes at the opposite extremes of the range of allometric variation are shown by using wire-frame, indicates the predicted shape shift from small (left) to big size (± 1.5 scale factor of the centroid size).

B. Discussion on the mechanical aspects of prevalent lice shape development under deep ocean conditions

The main [macro] difference, from the morphological point of view of deep immersed and coastal divers (shallow-depths immersion) lice is their spatial shape distribution. As it was statistically described in this article (Figures 2 through 5 in main document), marine lice show an oblate-like predominant shape (see Note below) with a high degree of isotropy in its lateral and longitudinal sizes ($a = c = \beta b$, being β a real number and $\beta > 1$, see Fig. S.2, while coastal divers lice have predominant prolate-like distribution with low bi-axial anisotropy (ventral/dorsal and lateral axes, $a = \gamma b = \gamma c$, with $\gamma > 1$). Average values for their sagital sizes have been considered for the two predominant shapes. As we will discuss later, this difference have a direct impact on the lice hydrostatics/mechanics performance during its life immersed at high depths with its hosts while they spend time at deep sea depths.

[Note: The definition of the geometry of an ellipsoidal body is given to define the factors to be be considered in mechanical and numerical model proposed in this paper. Spheroids bodies aligned with the Cartesian coordinates are described geometrically by the general equation $x^2/a^2 + y^2/b^2 + z^2/c^2 = 1$, where a, b, and c are the principal axes. For ellipsoidal bodies, the sphere-degenerate cases are (a) bodies that have two equal axes, such as $a = b$, generally referred to as spheroid or ellipsoid of revolution, and (b) variations results in different shapes of bodies, which can be expressed as a function of their aspect ratios, defined as $\alpha_r = c/a = c/b$. $\alpha_r < 1$ for an oblate spheroid, $\alpha_r = 1$ for a sphere, and $\alpha_r > 1$ for a prolate spheroid. The shapes of oblate and prolate spheroids are schematically shown in Fig. S.2.]

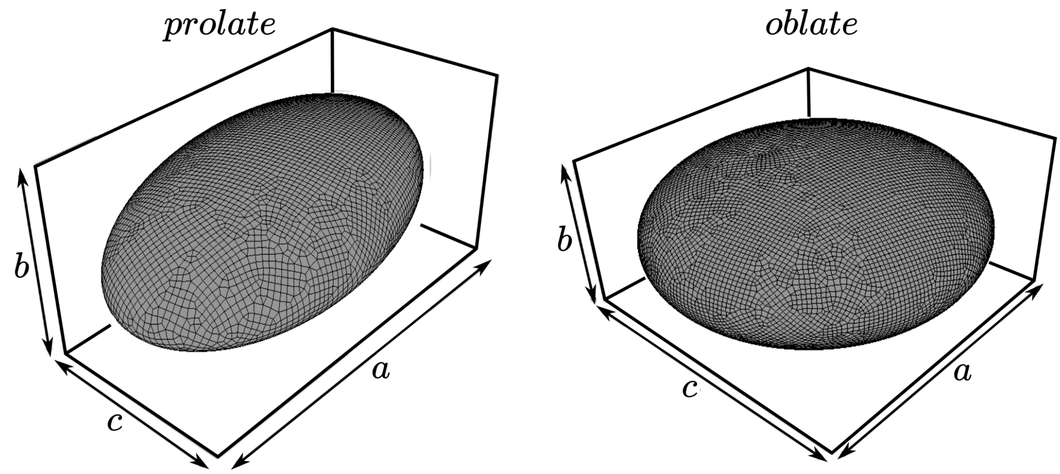

Figure S.2: Prolate and Oblate ellipsoids definitions.

Generally speaking, there are two possible paths or natural mechanisms for an organism like seal louse to develop its prevalent rounded shape in adult stages: one is *Developmental Growth* and the other is *Selection Pressure*.

Developmental Growth is an attractive tool, that uses an inter-disciplinary set of theories, such as Biology, Physics and Mathematics, to describe how the mass [and the volume] of a body evolve in time, while it interacts with the surrounding environment and life conditions. The grow, change and evolution of a living organism and/or its internal/external vital organs can be described in terms of physical fields arising in the context of the Continuum Mechanics theory[1]. The development of many organs of different species have been successfully studied using this framework. While it may be tempting to explain the displacement reported in this article using a well-established and proven theory, we believe that developmental growth (specifically its volumetric version or framework) cannot account for this feature, for two clear reasons: a) lice start diving into deep waters attached to their hosts when they have reached their adult stages, where its final shape, mass and volume have already converged; and b) the immersion and life with its host takes place after the louse has already molted its exoskeleton, a change that means a profound alteration of its structure.

Although other fish and animals living at high hydrostatic pressure environments in deep-sea and the Abyssopelagic Zone have not developed round shapes on their bodies (the departure morphology of deep-diving sea lice is developed while its terrestrial early life), it is clear (and based on the facts above) that deep-diving sea lice have been subject to Pressure Selection in such conditions when compared with the shape characteristics of coastal (or shallow) divers allometry.

From the physical point of view, a rounded shape of an insect can help it to better adapt to high hydrostatic pressure due to structural advantages. These advantages are (a detailed mechanical model supporting the observations is described in section 1.):

i) Increased surface area in the plane normal to its revolution axis: An increased area on its ventral/dorsal plane (Fig. S.2) makes the external pressure to be better re-distributed along the entire body volume reducing the internal energy spent to bear the undergoing body deformations, making a louse with bigger wet area more suitable to withstand the external pressure. As an increase in the external pressure is proportional to the surface area (and not the volume), an oblate shaped individual will experience lower levels of stresses triaxility in the embedded organs, while the energy consumption due to pressure compression for both shapes are comparable. This feature can be seen related to only hydrostatic pressure at high depths (see section D.).

ii) Oblate shape has also an important role from the hydrodynamics point of view; this is when the sea elephant is swimming at moderately high velocity and the lice remain attached to it. This aspect falls beyond the scope of this article and it will be studied further in a future article.

In the next sections we develope a mechanical explanation of a first order model, in terms of the body shape complexity, using the Continuum Mechanics theory and a numerical model for the simulation of the elephant immersion and the pressure acting on the lice bodies. We propose and derive three different metrics that are standard in Continuum Mechanics to evaluate the performance of the simplified model.

1. Conformation performance

Lice that dive into water attached to their hosts will be subjected to equal compressive stress in all directions, i.e. a hydrostatic state. Assuming that the body of the louse can undergo a certain level of deformation, but without changing its original shape, the generalized Hooke's law and first-order theory can be used as a first estimate.

2. Problem formulation

As the stress state is hydrostatic and the constitutive response is isotropic, the resulting deformations can only cause a change in volume (ΔV). Volumetric strain (e) measures the rate at which the volume changes as the external pressure increases and is defined as follows:

$$e = \frac{\Delta V}{V} = \lambda_1 \lambda_2 \lambda_3 \tag{1}$$

where $\lambda_i, i \in \{1, 2, 3\}$ is the i-principal stretch.

In this derivation we will assume that Ogden's hyperelastic hypothesis represents the material constitution accurately enough and the energy density function is defined by:

$$W(\lambda_1, \lambda_2, \lambda_3) = \frac{\mu}{\alpha} \left[\frac{\lambda_1^\alpha + \lambda_2^\alpha + \lambda_3^\alpha}{(\lambda_1 \lambda_2 \lambda_3)^{\alpha/3}} - 3 \right] + \frac{\alpha \mu (1+\nu)}{3(1-2\nu)} \left[\lambda_1 \lambda_2 \lambda_3 - 1 - \ln \lambda_1 \lambda_2 \lambda_3 \right]. \tag{2}$$

The three parameter that define the material response is the Poisson ratio ν, the shear modulus μ and the exponent α.

The Second Piola-Kirchhoff (P_i) is the energy conjugate of the Green strain tensor and can be obtained from the energy density function:

$$P_i = \frac{\partial W}{\partial E_i} = \frac{1}{\lambda_i} \frac{\partial W}{\partial \lambda_i} \tag{3}$$

It is then possible to obtain each of the components of the tensor, resulting in the following:

$$P_1(\lambda_1, \lambda_2, \lambda_3) = \frac{\mu}{3\lambda_1^2} \left((\lambda_1 \lambda_2 \lambda_3)^{-\frac{\alpha}{3}} (2\lambda_1^\alpha - \lambda_2^\alpha - \lambda_3^\alpha) - \frac{\alpha(\nu+1)(\lambda_1 \lambda_2 \lambda_3 - 1)}{2\nu - 1} \right) \tag{4}$$

$$P_2(\lambda_1, \lambda_2, \lambda_3) = -\frac{\mu}{3\lambda_2^2} \left((\lambda_1^\alpha - 2\lambda_2^\alpha + \lambda_3^\alpha) (\lambda_1 \lambda_2 \lambda_3)^{-\frac{\alpha}{3}} + \frac{\alpha(\nu+1)(\lambda_1 \lambda_2 \lambda_3 - 1)}{2\nu - 1} \right) \tag{5}$$

$$P_3(\lambda_1, \lambda_2, \lambda_3) = -\frac{\mu}{3\lambda_3^2} \left((\lambda_1^\alpha + \lambda_2^\alpha - 2\lambda_3^\alpha) (\lambda_1 \lambda_2 \lambda_3)^{-\frac{\alpha}{3}} + \frac{\alpha(\nu+1)(\lambda_1 \lambda_2 \lambda_3 - 1)}{2\nu - 1} \right) \tag{6}$$

The principal components of the Cauchy stress are given as:

$$J\sigma_i = P_i \tag{7}$$

where $J = \lambda_1\lambda_2\lambda_3$ is the determinant of the stretch tensor. Thus, the principal components of the Cauchy stress tensor can be written as:

$$\sigma_1(\lambda_1,\lambda_2,\lambda_3) = \frac{\mu}{3\lambda_1^3\lambda_2\lambda_3}\left((\lambda_1\lambda_2\lambda_3)^{-\frac{\alpha}{3}}\left(2\lambda_1^\alpha - \lambda_2^\alpha - \lambda_3^\alpha\right) - \frac{\alpha(\nu+1)(\lambda_1\lambda_2\lambda_3-1)}{2\nu-1}\right) \tag{8}$$

$$\sigma_2(\lambda_1,\lambda_2,\lambda_3) = -\frac{\mu}{3\lambda_1\lambda_2^3\lambda_3}\left(\left(\lambda_1^\alpha - 2\lambda_2^\alpha + \lambda_3^\alpha\right)(\lambda_1\lambda_2\lambda_3)^{-\frac{\alpha}{3}} + \frac{\alpha(\nu+1)(\lambda_1\lambda_2\lambda_3-1)}{2\nu-1}\right) \tag{9}$$

$$\sigma_3(\lambda_1,\lambda_2,\lambda_3) = -\frac{\mu}{3\lambda_1\lambda_2\lambda_3^3}\left(\left(\lambda_1^\alpha + \lambda_2^\alpha - 2\lambda_3^\alpha\right)(\lambda_1\lambda_2\lambda_3)^{-\frac{\alpha}{3}} + \frac{\alpha(\nu+1)(\lambda_1\lambda_2\lambda_3-1)}{2\nu-1}\right) \tag{10}$$

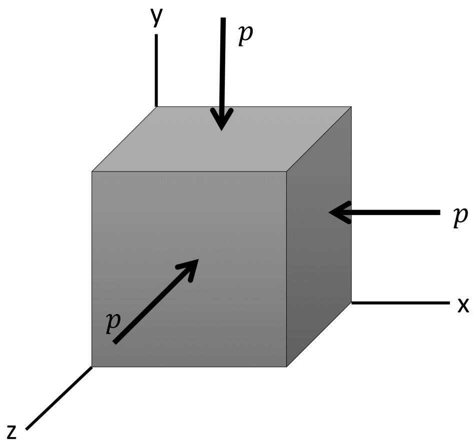

Figure S.3: Stress state cube

In the state of hydrostatic stress, the only action is the water pressure (Fig. S.3), and therefore:

$$\sigma_1 = \sigma_2 = \sigma_3 = -p \tag{11}$$

$$\lambda_1 = \lambda_2 = \lambda_3 = \lambda \tag{12}$$

Therefore, the equations above reduce to:

$$p = \frac{\alpha\left(\lambda^3-1\right)\mu(\nu+1)}{\lambda^5(2\nu-1)} \tag{13}$$

Isolating λ^3, which is the volumetric deformation itself, we have:

$$\lambda^3 = e = \frac{c_1}{c_1 - \lambda p} \tag{14}$$

where

$$c_1 = \frac{\alpha\mu(\nu+1)}{2\nu-1} \tag{15}$$

For the same level of pressure and stretch, both forms will have the same volumetric contraction and also the same strain energy ($u = \sigma_i\lambda_i$). Note that u is equivalent to W but written in terms of stresses and stretches.

C. Morphology implication

Prolate-predominat shape (costal or shallow divers). In this ellipsoidal shape we have $b = c = a/2$. The volume of this shape (V_p) is:

$$V_p = \frac{4}{3}\pi abc = \frac{4}{3}\pi a(a/2)(a/2) = \frac{\pi a^3}{3} \tag{16}$$

The energy stored is:

$$U_p = \int_V u dV = uV_p = \frac{3}{2E}(1-2\nu)p^2\frac{\pi a^3}{3} = \frac{\pi(1-2\nu)p^2 a^3}{2E} \tag{17}$$

Oblate-predominat shape (deep divers). For this other ellipsoidal shape we have $b = a/2, c = a$. The volume of this shape (V_o) is:

$$V_o = \frac{4}{3}\pi abc = \frac{4}{3}\pi a(a/2)(a) = \frac{2\pi a^3}{3} \tag{18}$$

Similarly, the accumulated energy is:

$$U_o = \int_V u dV = uV_o = \frac{3}{2E}(1-2\nu)p^2\frac{2\pi a^3}{3} = \frac{\pi(1-2\nu)p^2 a^3}{E} \tag{19}$$

These results show that:

$$U_p = \frac{1}{2}U_o \tag{20}$$

This equation means that assuming the two shapes have the same major axis size, the oblate will have more energy absorbed and will therefore be able to conform more to the surface it is attached to. Prolate would be much more stiff in this case, what is indicative of disadvantage, in particular for its ability to accommodate micro-cracks (abrupt failure). The same mechanical principle is found in shock protection devices.

D. Comparing stress distributions

In addition, the mechanical performance of the two forms can be inferred qualitatively and quantitatively by means of a stress distribution analysis using Finite Elements Analysis (FEA) techniques. For this purpose we have built a numerical model for two representative specimens of both lice families using the software LS-DYNA©[2,3]. LS-DYNA solves the equations of motion of a body made of a tissue material that mechanically obeys the law described by its consitutive equation (2), when it is hidrostatically compressed with an increasing pressure field as it happens when the elephant seals dive from the ocean surface toward deep waters. Basically, the numerical model consists of an ellipsoid with the statitiscal dimension reported in this work, made of an Ogden (quasi-incompressible tissue) hyperelastic material with homogenous mechanical properties and an external layer of a slightly harder (than the body) material representing the louse dermis (see Fig. S.4).

The three material parameters defining the model are $\nu = 0.495$ and $\alpha = 1$ and $(\mu_{\text{body}}, \mu_{\text{dermis}}) = (10, 15)$ MPa.

Fig. S.5 shows a comparison between the principal stress fields for the two forms. In both cases it is noticed a steep gradient variation in the region close to the skin which quickly dissipates and becomes homogeneous within the material domain. The same behaviour is observed for the internal pressure field (Fig. S.6). Note the smooth transition of the gradient in the region near the outer surface indicating a good-accuracy numerical solution, what often is challenging for nearly incompressible materials.

Additionally, the Lode parameter is a handful to distinguish between different three dimensional stress states (from axisymmetric tension to in-plane shear). It is a function of the third invariant of stress deviator and is shown in Fig. S.7 comparing both morphologies. The central regions show a high level of triaxiality (modulus close to unity) while the points near to the surface show low triaxiality (Lode parameter close to zero). High levels of triaxiality have been associated with shear-type mechanical rupture. Note that at the same level of dive depth, the prolate shape has a larger area subject to high values of the Lode parameter, which may indicate a physiological disadvantage depending on the positioning of the internal organs and their ability to resist triaxial states of stress.

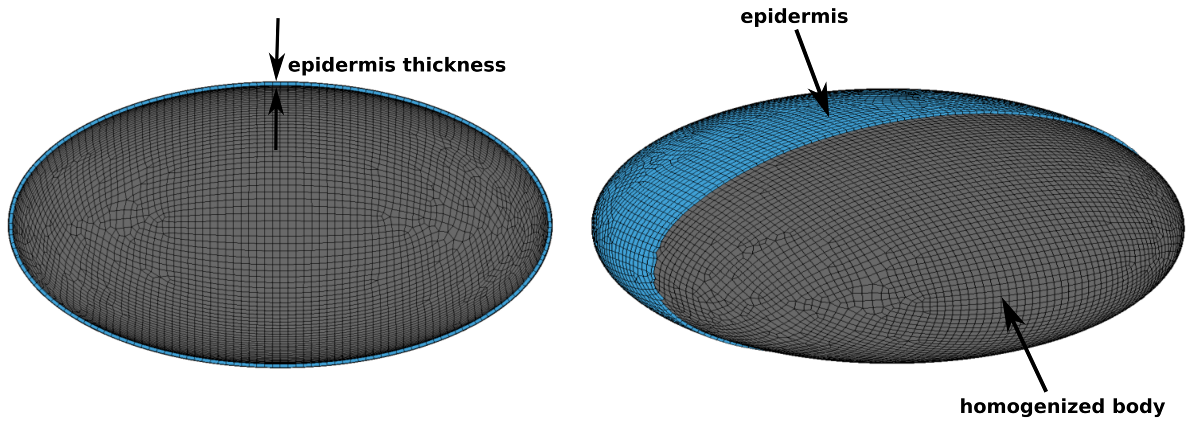

Figure S.4: Numerical model and FEA mesh of the simplified lice shapes.

These results suggest that at greater depths the oblate shape is more advantageous from a mechanical point of view.

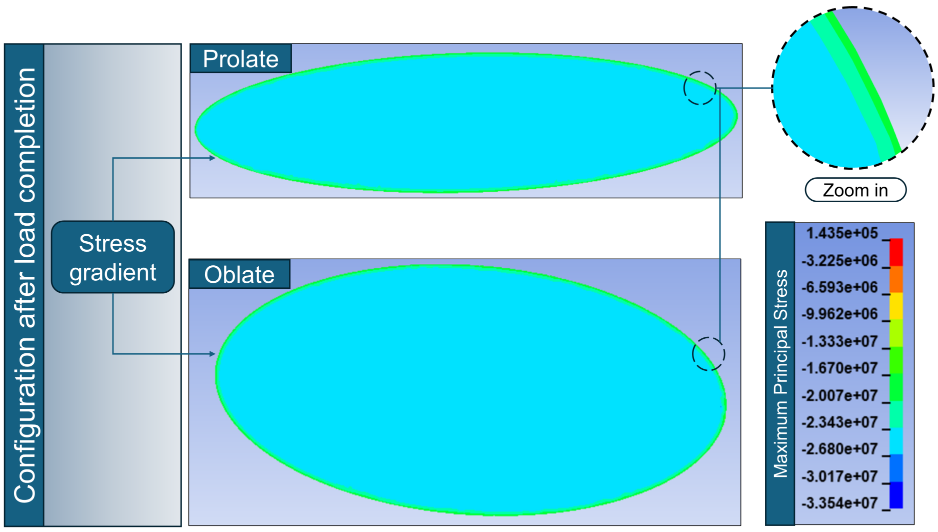

Figure S.5: Comparison of the First Principal Stress field (cross section plane with normal (0; 1; 0).

References

[1] Goriely, A. *The Mathematics and Mechanics of Biological Growth*. Interdisciplinary Applied Mathematics (Springer, New York, 2017).

[2] LS-DYNA. *LS-DYNA User's Manual* (2024).

[3] Hugo L. Oliveira, Gustavo C. Buscaglia, Rodrigo R. Paz, Facundo Del Pin, José A. Cuminato, Monica Kerr, Sean McKee, Iain W. Stewart, and David J. Wheatley. Three-dimensional fluid-structure interaction simulation of the wheatley aortic valve. *International Journal for Numerical Methods in Biomedical Engineering* DOI: https://doi.org/10.1002/cnm.3792 (2023). In Press.

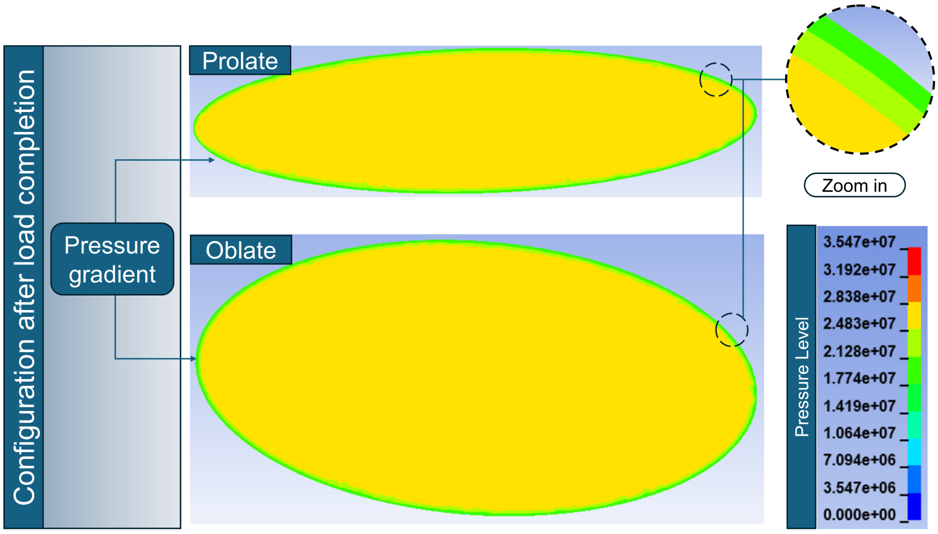

Figure S.6: Comparison of the pressure fields for the two forms (cross section plane with normal (0; 1; 0).

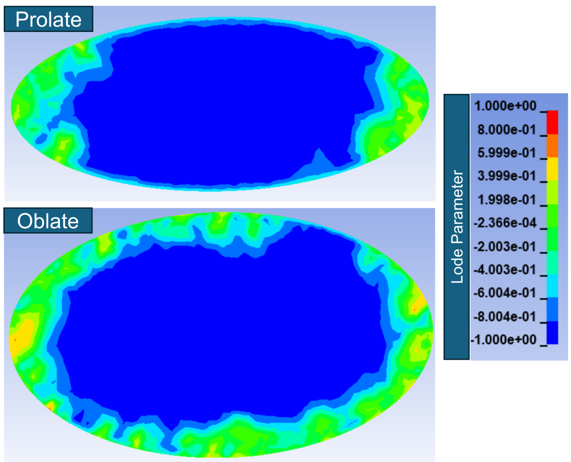

Figure S.7: Comparison between Lode Parameter for the two forms (end loading level).